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Conserving and Enhancing Biological Control of Nematodes

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Abstract: Conservation biological control is the modification of the environment or existing practices to protect and enhance antagonistic organisms to reduce damage from pests. This approach to biological control has received insufficient attention compared with inundative applications of microbial antagonists to control nematodes. This review provides examples of how production practices can enhance or diminish biological control of plant-parasitic nematodes and other soilborne pests. Antagonists of nematodes can be enhanced by providing supplementary food sources such as occurs when organic amendments are applied to soil. However, some organic amendments (e.g., manures and plants containing allelopathic compounds) can also be detrimental to nematode antagonists. Plant species and genotype can strongly influence the outcome of biological control. For instance, the susceptibility of the plant to the nematode can determine the effectiveness of control; good hosts will require greater levels of suppression than poor hosts. Plant genotype can also influence the degree of rhizosphere colonization and antibiotic production by antagonists, as well the expression of induced resistance by plants. Production practices such as crop rotation, fallow periods, tillage, and pesticide applications can directly disrupt populations of antagonistic organisms. These practices can also indirectly affect antagonists by reducing their primary nematode host. One of the challenges of conservation biological control is that practices intended to protect or enhance suppression of nematodes may not be effective in all field sites because they are dependent on indigenous antagonists. Ultimately, indicators will need to be identified, such as the presence of particular antagonists, which can guide decisions on where it is practical to use conservation biological control. Antagonists can also be applied to field sites in conjunction with conservation practices to improve the consistency, efficacy, and duration of biological control. In future research, greater use should be made of bioassays that measure nematode suppression because changes in abundance of particular antagonists may not affect biological control of plant parasites.

Key words: antagonists, biological control, crop rotation, farming practices, organic amendments, pesticides, plant genotype, tillage.

In biological control of plant-parasitic nematodes, the goal of many public- and private-sector research efforts has been to identify organisms that can be applied to the seed, planting furrow, or transplant medium to suppress nematode populations. The expectation is that a specific organism will act rapidly to reduce nematode populations and/or protect the growing seedling from damage. Persistence and proliferation of the organism in the root zone has been considered a useful trait, but mainly to increase the level of nematode suppression in the crop to which the organism is applied (Stirling, 1991; Kerry, 2000). This strategy is referred to as inundation biological control (Eilenberg et al., 2001); although it can be effective, it is not the only strategy for achieving biological control. Conservation biological control is the modification of the environment or existing practices to protect and enhance specific natural enemies or other organisms to reduce the effect of pests (Eilenberg et al., 2001). This strategy has been widely utilized in integrated management of insect pests (Barbosa, 1998) and to a lesser extent of plant pathogens (Cook, 2007; Mazzola, 2007), but has been largely neglected in management of nematode pests (Sikora, 1992).

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For conservation biological control to be successful, antagonistic organisms must be present in the environment, whether indigenous or introduced. There are numerous organisms that are capable of reducing populations of plant-parasitic nematodes. The term "antagonist" is used to cover diverse organisms that include natural enemies such as parasites and predators, but also organisms that produce antibiotics, extracellular enzymes, or induce systemic resistance in plants (Stirling, 2011a). Many of the fungi that parasitize nematodes are common soil inhabitants such as *Purpureocillium lilacinum* (syn. *Paecilomyces lilacinus*), *Pochonia chlamydosporia* (syn. *Verticillium chlamydosporium*), and trapping fungi. Bacteria in the genus *Pasteuria* are also regularly found parasitizing nematodes in soil. Carnivorous nematodes and micro-arthropods such as collembolans and mites are abundant in soil and can consume large numbers of nematodes. Given the common occurrence of many nematode antagonists, it is likely that one or more types are present in most agricultural soils (Stirling, 1991). What is unclear is whether indigenous antagonists are routinely limiting populations of plant-parasitic nematodes.

Biological suppression of nematode populations can be determined by comparing nematode multiplication in untreated field soil with multiplication in soil treated with a broad-spectrum biocide or heat to kill antagonistic organisms (Westphal, 2005; Stirling, 2011b). Because multiplication is assessed after one or more nematode

generations, the bioassay can take 1 to 3 months to complete. An alternative bioassay is to determine survival of free-living stages of a nematode after several days in treated and untreated soil (McInnis and Jaffee, 1989; Sanchez-Moreno and Ferris, 2007; Timper et al., 2012). Although this alternative provides more rapid results, it primarily measures the activity of organisms that consume migratory nematode stages; organisms that are specialized for parasitizing nematode eggs and other sedentary stages are overlooked. In both bioassays, a nematode not present in the field soil is often used to assay the level of biological suppression to avoid the confounding influence of indigenous nematodes. Thus, a host-specific parasite can be overlooked. For example, using the reniform nematode (*Rotylenchulus reniformis*) to assay for biological suppression in soil infested with the southern root-knot nematode (*Meloidogyne incognita*) may not detect a host-specific parasite such as *Pasteuria penetrans*. A solution to this concern is to mix a small amount of field soil into sterilized soil (Westphal, 2005; Stirling, 2011b). Because only small numbers of the target nematode are transferred with the field soil, additional target nematodes can be inoculated into the soil with little confounding effects. However, the antagonistic organisms transferred with the soil must be given time to reproduce to suppressive levels.

In the soil environment, there are two recognized types of biological suppression: general and specific (Cook and Baker, 1983; Stirling, 2011a). General suppression is not specific to a particular pathogen and is caused by the combined activity of numerous soil organisms. General suppression is thought to occur in most soils, but the level of pathogen suppression is typically low to moderate. In contrast, specific suppression is the result of only a few organisms antagonistic to a specific pathogen. Specific suppression is relatively rare, but the level of suppression is typically very high. There are several well-documented cases of specific nematode suppression (Stirling, 1991; Westphal, 2005; Timper, 2011). These suppressive conditions were discovered primarily because the nematode populations were very low despite soil characteristics and cropping history that were conducive to the nematode. General suppression of nematodes is more difficult to identify and has not been well studied. Another difference between the two types of suppression is that specific suppression is predicted to involve density-dependent forces, whereas general suppression could involve both density-dependent and independent forces. In density-dependent mortality, the rate of host mortality increases with increasing host population density, thus maintaining the host population at low equilibrium densities. Organisms that produce toxic metabolites or induce plant resistance are predicted to act in a density-independent manner. Moreover, polyphagous antagonists that act in a density-dependent manner with respect to the total nematode community, may cause density-independent mortality of specific species within the community, particularly if they are a minority species.

Whether the suppression is general or specific, it is likely that the level of suppression can be increased or decreased by human intervention. The purpose of this review is to stimulate research on identifying strategies for protecting and enhancing antagonistic organisms for suppression of plant-parasitic nematodes. Three previous reviews have also made a case for directing a greater research effort on conservation biological control as a strategy for managing plant-parasitic nematodes. Stirling (1991) provided an extensive analysis of research conducted up to 1991. Sikora (1992) described conservation biological control as managing the "antagonistic potential" of soil ecosystems and provided examples of how to enhance the activity of specific groups of antagonists. Stirling (2011a) proposed developing farming systems to enhance general nematode suppression in soil, with an emphasis on increasing organic matter via minimum tillage and generating large amounts of plant residue. This review expands these reviews both in terms of updating the scientific knowledge since 1992 and the scope of conservation practices that could be employed to enhance indigenous or introduced antagonists. Enhancing biological control organisms through phenotypic selection, mutagenesis, or genetic engineering is not covered in this review. The organization is based on the types of conservation practices that are likely to influence antagonists of nematodes, with examples from plant nematology or other closely related disciplines.

Providing Supplementary Resources

Increasing the abundance of nematode antagonists by providing alternative food sources is a seemingly simple approach to enhancing biological control. Many predators and parasites of plant-parasitic nematodes have a broad host range and can prey on a wide variety of nematodes. Furthermore, some fungal and bacterial antagonists have saprophytic abilities and can proliferate on organic matter in the soil. Therefore, the application of organic matter has been frequently proposed as a means of enhancing biological control of plant-parasitic nematodes. In addition to providing a substrate for growth of antagonists, the organic matter increases populations of microbial-feeding nematodes that may serve as alternative hosts for antagonists (Linford et al., 1938; Oka, 2010; McSorley, 2011). Organic amendments come in many forms: animal manures, chitinous materials, composts, and plant residues (either applied as dry material or grown in situ). Recent reviews by Akhtar and Malik (2000), Oka (2010), McSorley (2011), and Thoden et al. (2011) discuss the different mechanisms by which organic amendments

can suppress plant-parasitic nematodes (e.g., toxins produced during decomposition, enhancing antagonistic organisms, and increasing plant tolerance) and also the difficulties in distinguishing which mechanisms are operating for a given amendment. Although numerous studies have demonstrated increased abundance of nematode antagonists following addition of organic matter, only a few studies have attempted to show that these organisms are responsible for suppression of plant parasites (Oka, 2010; McSorley, 2011).

Distinguishing between nematode mortality caused by antagonistic organisms and mortality from toxic metabolites produced during decomposition can be difficult. Both mechanisms require the presence of living organisms. However, the organisms involved in decomposition may not be specialized nematode antagonists; their toxins are byproducts of primary metabolism and not intended to specifically inhibit other organisms (e.g., antibiotics). For nematode parasites, measuring the percentage of individuals that are parasitized and correlating that to the level of population suppression provides good evidence for the role of parasites in suppression. As predicted, amending soil with a variety of organic materials increased parasitism of *M. incognita* eggs by unidentified fungi over a 10-wk period compared to nonamended soil (Chavarria-Carvajal and Rodriguez-Kabana, 1998). Similarly, the incorporation of dry neem (*Azadirachta indica*) leaves into field soil increased the percentage of females parasitized and egg masses colonized by three fungal antagonists, *P. chlamydosporia*, *P. lilacinum*, and *Trichoderma harzianum*, compared to the fungi alone (Khan et al., 2012). There was also greater reduction in galling when the fungi were combined with the neem amendment. Bioassays can be successfully used to evaluate the impact of organic amendments on biological control if they are done several months after incorporation to avoid the confounding effects of toxic metabolites. Using bioassays, Stirling et al. (2005, 2012) demonstrated biological suppression of *Pratylenchus zeae* 5 months after amending soil with sugarcane residue, and suppression of *M. javanica* 1 and 2 yr after amending soil with a combination of poultry manure and sawdust. Leaving crop residue on the soil surface as mulch also enhanced biological suppression of *M. javanica* and *P. zeae* (Stirling et al., 2011a). The mulch not only provided a source of carbon to sustain the soil community, but also improved habitat stability by reducing temperature and moisture fluctuations. Experiments where the antagonist and amendment are applied in a factorial design can also be used to assess whether biological control is enhanced or diminished by a particular amendment. When *P. lilacinum* was applied alone or in combination with a killed cover crop of rye (*Secale cereale*), percentage suppression of *M. incognita,* based on the no fungus control, was greater in the soil previously planted to rye than in fallow soil (Timper and Parajuli, 2012). However, removal of the rye residue from the soil surface negated the beneficial effects, indicating that the root residue alone was insufficient for enhancing biological control.

Despite the above examples, the response of antagonists to organic matter is not always positive. The ability of an amendment to stimulate antagonists depends on the type of organic matter, how much material is added, and the types of antagonists present. For example, amendments of sunn hemp (*Crotalaria juncea*) and pineapple (*Ananas comosus*) increased the percentage of parasitized *R. reniformis* vermiform stages compared to bare soil, but rapeseed (*Brassica napus*) and marigold (*Tagetes erecta*) did not, and only sunn hemp increased egg parasitism (Wang et al., 2001). Jaffee (2004) found that the abundance of two nematode-trapping fungi, *Arthrobotrys oligospora* and *Dactylellina candidum*, increased following addition of either grape (*Vitis vinifera*) or alfalfa (*Medicago sativa*) leaves to soil, but trapping activity was increased only with *D. candidum*. Network trappers such as *A. oligospora* are typically good saprophytes and not greatly dependent on nematodes for nutrition; whereas, adhesive-knob trappers such as *D. candidum* are more dependent on nematodes for nutrition (Cooke, 1963; Jansson and Nordbring-Hertz, 1980). The leaf amendments increased bacterial-feeding nematodes, which presumably served as alternative hosts for *D. candidum*. Interestingly, even though bacterial feeders were increased at both the low and high rate of alfalfa amendment, abundance, and trapping activity of *D. candidum* was only increased at the lower rate of amendment (Jaffee, 2004). The higher rate of amendment may have either produced fungicidal compounds or stimulated more fungal feeders that consumed *D. candidum,* offsetting the benefits of increasing alternative hosts for the fungus. Bao et al. (2013) applied liquid swine manure to field sites that were suppressive and conducive to *H. glycines*. The manure did not influence egg production by the nematode at either site compared to the inorganic fertilizer, but it did reduce numbers of second-stage juveniles (J2) 45 d after planting in the suppressive site only. It is unclear whether the reduction in J2 numbers was attributable to the interaction between the microbial community and the manure or to the lower pH of the suppressive soil (Mahran et al., 2008).

There is also evidence that some amendments can have antagonistic effects on biological control. Incorporating rape as a green manure had no effect on egg parasitism; whereas, incorporating mustard (*Sinapis alba*) and oil radish (*Raphanus sativus*) significantly reduced parasitism (Nicolay et al., 1990). Extracts of shoots, but not roots, of mustard and oil radish inhibited the growth of the egg-parasitic fungus *P. chlamydosporia* on agar. Owino et al. (1993) showed a similar suppression of egg parasitism by this fungus when mustard was incorporated into soil. In another study, when *P. chlamydosporia* was applied at the time of cover

crop planting, the fungus increased in soil planted to black oats (*Avena strigosa*) and oil radish, but declined in fallow soil and soil planted to tomato (*Solanum lycopersicum*); nevertheless, although the fungus reduced galling and egg production by *M. javanica* in the tomato crop that followed fallow or tomato, it failed to do so following either black oats or oil radish (Dallemole-Giaretta et al., 2011). In both field and greenhouse studies, amendments containing either composted animal manure or plant material suppressed parasitism of plant-parasitic nematodes by *Hirsutella rhossiliensis* (Jaffee et al., 1994).

It is clear from the literature that organic matter can have positive, neutral, or negative effects on biological control of nematodes. Although the interactions between organic matter and nematode antagonists are complex, a few general observations can be made. Caution should be employed when utilizing plant materials that produce allelopathic compounds because they may suppress predatory invertebrates or fungal antagonists of nematodes. Similarly, amendments with a low C/N ratio can be detrimental to some nematodes and fungi because they produce high concentrations of ammonia (NH_3) during decomposition (Rodriguez-Kabana et al., 1987); these include animal manures, chitin, oil cakes, cottonseed, and some legumes (Mian and Rodriguez-Kabana, 1982; Oka, 2010). With these amendments, smaller quantities of amendments may be better for enhancing biological control than larger quantities (Jaffee et al., 1994). While amendments with low C/N ratios (< 20) are often associated with chemical suppression of plant-parasitic nematodes (predominately NH_3), amendments with a high C/N ratio may be more commonly associated with biological suppression (Rodriguez-Kabana et al., 1987; Stirling, 2011b). Furthermore, the decomposition rate of organic matter is slower on the soil surface than when it is buried below the surface (Holland and Coleman, 1987). Organic matter applied as mulch, therefore, may produce less toxic metabolites that can diminish the activity of nematode antagonists than organic matter that is incorporated.

Identifying Conducive Attributes in the Host-Plant

Although it is common to identify attributes of the antagonists that contribute to their success as biological control agents, comparatively little effort has been directed toward identifying plant attributes that lead to successful biological control. Yet, the host plant can play a critical role in the success of a biological control organism. The susceptibility of the plant to the nematode is one of the more widely recognized traits that can influence biological control. For instance, to limit population increase of nematodes, hosts that support higher reproductive rates require greater levels of biological suppression than hosts with lower reproductive rates (Kerry and Bourne, 1996). Plant susceptibility can also influence the ability of a parasite to infect its host nematode. Stirling et al. (1979) found that a greater percentage of *M. incognita* eggs were parasitized by *Brachyphoris oviparasitica* (syn. *Dactylella oviparasitica*) on peach (*Prunus persica*) than on tomato (96% vs. 57%), perhaps because the fungus was more efficient at parasitizing nematode eggs contained in the smaller egg masses produced on peach than in the larger egg masses produced on tomato. Similarly, *P. chlamydosporia* parasitized more eggs of *M. incognita* on potato (*Solanum tuberosum*) than on tomato (Bourne et al., 1996). Potato had smaller galls and more exposed eggs, whereas tomato produced larger galls with more eggs embedded in the gall tissue where they were protected from parasitism. Parasitism of *Heterodera schachtii* by *B. oviparasitica* was greater in *A. thaliana* than in cabbage (*Brassica oleracea*) because the developing juveniles broke through the root surface sooner in *A. thaliana* where they were exposed to fungal infection (Becker et al., 2013).

Colonization of the rhizosphere/endosphere: For some fungal and bacterial antagonists of nematodes, the ability to colonize the rhizosphere of plants is essential to their success as biological control organisms (Becker et al., 1988; Kloepper et al., 1992; Bourne et al., 1994). This trait places the antagonist in the zone where plant-parasitic nematodes are feeding, developing, and producing eggs. The capacity to grow endophytically in the roots is also an advantage for antagonists because they are located within the root along with endoparasitic nematodes and may experience less competition from microorganisms that are abundant in the rhizosphere (Stirling, 2011a). Rhizosphere and endosphere competence is viewed as such an important trait that when screening for potential antagonists of nematodes, many studies select only microorganisms that are located in one or both of these zones (Becker et al., 1988; Athman et al., 2006; Aravind et al., 2010; Aballay et al., 2011).

Root exudates from plants contain a wide array of organic compounds, including sugars, amino acids, and other organic acids, which provide an important resource for microorganisms. Populations of microorganisms are often manyfold greater in the rhizosphere than in the bulk soil; this has been referred to as the "rhizosphere effect" (Richter et al., 2007). Plant species and genotypes within a species vary both quantitatively and qualitatively in their root exudates, which strongly influences the composition of the microbial community (Grayston et al., 1998; Hawkes et al., 2007; Andreote et al., 2010; Inceoglu et al., 2010). Even small genetic changes, such as mutation of a single gene or insertion of a transgene, can alter root exudation and the microbial communities (Yan et al., 2007; Li et al., 2009; Aira et al., 2010). Given the growing evidence that plant genotype can selectively influence microbial communities in the rhizosphere and endosphere, it seems reasonable that the plant also influences biological

control in these locations by affecting colonization and antibiotic production by antagonists. Convincing evidence for this was provided by Smith et al. (1999) using recombinant inbred lines of tomato showing variation in biological control of *Pythium torulosm* by *Bacillus cereus*. They identified three quantitative trait loci (QTL) contributing to biological control. One QTL accounting for 27% of phenotypic variance corresponded to both disease suppression and growth of *B. cereus* on the seed, indicating that the level of colonization is involved in disease suppression. The other two QTLs, however, were not associated with growth of the bacterium, only with disease suppression by *B. cereus*, each accounting for 13% to 15% of the variance.

A few studies have shown differential colonization of plant species by nematode antagonists, primarily *P. chlamydosporia*. In the absence of nematodes, Bourne et al. (1996) found that rhizosphere colonization by *P. chlamydosporia* varied among crop species and was greatest on kale (*B. oleracea*) and cabbage, and least on eggplant (*Solanum melongera*) and a breeding line of tomato. The presence of *M. incognita* greatly increased root colonization by the fungus; this increase corresponded to the time egg masses appeared on the root surface. Plants that were better hosts for the nematode tended to have greater fungal colonization in the presence of nematodes. In another study, *P. lilacinum* was more abundant in the rhizosphere of oilseed rape and sugar beet (*Beta vulgaris*) than in potato or wheat (*Triticum* spp.) in the absence of nematodes (Manzanilla-Lopez et al., 2011). Some nonplant-pathogenic strains of *Fusarium oxysporum* are effective biological control agents of plant-parasitic nematodes (Sikora et al., 2008). Endophytic colonization of tomato roots by one of these strains (Fo162) was influenced by cultivar (Dababat et al., 2008). All of the tomato cultivars were colonized 3 wk after inoculation, but after 6 wk, the fungus could not be detected in three of the 11 cultivars. The degree of colonization was not related to whether or not the cultivar was resistant to Fusarium wilt. Suppression of *M. incognita* penetration and galling by the fungus was partially related to the level of endosphere colonization; however, other host plant factors appeared to be involved in the level of suppression.

The degree of root colonization by *P. chlamydosporia* is also not always correlated with the level of nematode suppression (Kerry, 1995; Bourne et al., 1996). Though this may seem to contradict the claim that rhizosphere colonization is essential, the interaction between the fungus, host plant, and nematode is complex. In these studies, abundance of *P. chlamydosporia* was determined based on colony-forming units (cfu) from dilution plates that do not differentiate between conidia and hyphae. In an earlier study, Bourne et al. (1994) found only a weak correlation between cfu and hyphal growth on the roots of a variety of plant species indicating that both sporulation and hyphal growth of *P. chlamydosporia* differ among plant species. Additionally, the exudates of some host plants may be nutritionally sufficient to favor the saprophytic phase over the parasitic phase of the fungus. Finally, as I have noted, nematodes may be less exposed to fungal infection in some plant species.

The ability of some microbial control organisms to grow prolifically within roots or in the rhizosphere of some plant species could be utilized in an integrated management program. Crops that support growth of antagonists, but are poor or nonhosts for plant-parasitic nematodes could be used in rotation with a susceptible crop to both reduce nematode populations while maintaining or increasing populations of antagonists. For example, crops that promote arbuscular mycorrhizal (AM) fungi, such as clover or leek, could be planted to increase mycorrhizal inoculum in soil (Hallmann and Sikora, 2011). AM fungi are common symbionts of plants and are known to suppress populations of plant-parasitic nematodes (Hallmann and Sikora, 2011). Kerry and Hirsch (2011) suggest a similar approach for deploying *P. chlamydosporium* to control nematode populations throughout a crop rotation rather than only on the susceptible crop. Putting this concept into practice will be discussed in more detail under the section "Crop rotation."

Antibiotic production: Fluorescent *Pseudomonas* spp. have been extensively studied as biological control agents of soilborne plant pathogens, including nematodes (Jamali et al., 2009). This group of bacteria are adapted to the rhizosphere and are known to produce several antibiotics involved in pathogen suppression, including 2,4-diacetylphloroglucinol (DAPG) and HCN. The role of the host plant in antibiotic production was first demonstrated by Notz et al. (2001) using a reporter gene for biosynthesis of DAPG. Levels of gene expression in *P. fluorescens* strain CHA0 were similar in the rhizospheres of maize (*Zea mays*) and wheat but were significantly lower on bean (*Phaseolus vulgaris*) and cucumber (*Cucumis sativus*). Gene expression also varied among cultivars of maize; however, this variation did not correspond to observed differences in rhizosphere colonization by the bacterium. In another study with *P. fluorescens* CHA0, host cultivar was again shown to have a strong influence on the production of both DAPG and HCN but not on rhizosphere colonization (Jamali et al., 2009). Interestingly, bean cultivars that showed high expression of DAPG genes also showed high expression of HCN genes. Differential production of DAPG and HCN is likely triggered by qualitative and quantitative difference in root exudates.

Both DAPG and HCN contribute to suppression of plant-parasitic nematodes by *P. fluorescens* CHA0 (Siddiqui and Shaukat, 2003b; Siddiqui et al., 2006). Suppression of *M. incognita* by CHA0 was greater on soybean (*Glycine max*), mung bean (*Vigna radiata*), and tomato than on chili (*Capsicum annuum*), or eggplant (Siddiqui and Shaukat, 2003a). Although these crop plants differed in

colonization of the bacterium, colonization was not related to the level of suppression (e.g., eggplant had the highest and mung bean the lowest colonization) indicating that perhaps antibiotic production by strain CHA0 differed among plant species.

Induced resistance: Systemic induced resistance is an enhanced defensive capacity throughout the plant that is triggered by a specific stimulus such as a chemical inducer, a pathogen or insect, or a nonpathogenic microorganism (van Loon et al., 1998; Walters et al., 2013). There are two recognized types of induced resistance, systemic acquired resistance (SAR) and induced systemic resistance (ISR) that are differentiated by their signal transduction pathways (van Loon et al., 1998). Plant genotype influences the expression of both types of induced resistance, with some genotypes not expressing induced resistance (reviewed in Walters et al., 2013).

To demonstrate induced resistance from rhizosphere organisms, a split root technique is used where two parts of a root system are physically separated and the inducing organism is applied to one side while the pathogen is applied to the other side (van Loon et al., 1998). Using this technique, several nonpathogenic microorganisms have been shown to induce resistance to plant-parasitic nematodes. In tomato, *P. fluorescens* CHA0 induced resistance to *M. javanica* (Siddiqui and Shaukat, 2003b; Siddiqui et al., 2006). Interestingly, greater nematode suppression was observed when *M. javanica* and CHA0 were added to the same side than when added to opposite sides, suggesting that both induced resistance and the toxic effects of DAPG and HCN were involved in nematode control. In the case of *P. fluorescens*, the antibiotic DAPG is the primary trigger for induced resistance (Siddiqui and Shaukat, 2003b; Weller et al., 2012). A nonpathogenic, endophytic strain of *F. oxysporum* (Fo162) induced resistance to *Radopholus similis* in banana (*Musa* sp.) and to *M. incognita* in tomato (Vu et al., 2006; Dababat and Sikora, 2007). Arbuscular mycorrhizal fungi induced resistance in banana to *P. coffeae* and *R. similis*, and in grapevine to *Xiphinema index* (Elsen et al., 2008; Hao et al., 2012). Colonization of roots by both an endophytic strain and a rhizospheric strain of the trapping fungus *A. oligospora* reduced nematode numbers and increased defense-related enzymes, phenolics, and phenylalanine ammonia lyase (PAL) activity in tomato compared to plants inoculated only with *M. incognita* or without nematode and fungus (Singh et al., 2013), providing circumstantial evidence of induced resistance.

Reducing Disturbance

Compared to many natural ecosystems, agroecosystems receive numerous human inputs that result in severe disturbance of the fauna and flora. For example, the soil is tilled before planting; fungicides, insecticides, nematicides, and herbicides are applied; plants are harvested or killed; often different crop species are sequentially planted in the field site to improve soil nutrition and reduce pest numbers; and between crops, there can be long periods of fallow. These crop production practices can cause direct mortality of nematode antagonists or can indirectly harm them by reducing numbers of nematode hosts or creating an unfavorable environment for the antagonists.

Crop rotation: Rotating crops that are nonhosts with a crop that is a good host for a particular plant-parasitic nematode is an effective management strategy. In the years when a nonhost is planted, nematode populations progressively decline to very low population densities. This decline, however, can be detrimental to nematode- or plant-specific antagonists. Indeed, most documented cases of specific suppression of plant-parasitic nematodes have been in situations where a host plant for the nematode is present over an extended period of time such as in a monoculture of an annual crop or in perennial crops (Stirling, 1991; Timper, 2011).

Pasteuria penetrans is an obligate parasite of root-knot nematodes. Any production practice that reduces the abundance of its host nematode should reduce the number of new infections by *P. penetrans* and subsequent production of endospores. Rotations with poor or nonhost crops for *Meloidogyne* spp. resulted in lower endospore densities than planting continuous host crops (Madulu et al., 1994; Timper et al., 2001; Timper, 2009). Similarly, Ciancio and Quénéhervé (2000) observed fewer endospores in rotations that included long fallow periods and nonhosts than rotations with shorter fallow periods and good hosts. Planting winter cover crops that were susceptible to *Meloidogyne* spp. also increased endospore densities of *P. penetrans* compared with weed-free fallow or a nonhost cover crop (Oostendorp et al., 1991; Chen et al., 1994).

Hirsutella rhossiliensis is a fungus that exhibits density-dependent parasitism of mobile nematode stages (Jaffee et al., 1992). In soybean, populations of *H. glycines* increased and so did the percentage of nematodes parasitized by *H. rhossiliensis* (Chen and Reese, 1999). However, when maize was planted in rotation with soybean, populations of the nematode declined and so did the rates of parasitism. Likewise, rotations with nematode-resistant soybean also reduced the percentage of parasitized juveniles (Chen and Liu, 2007). Therefore, rotating susceptible soybean with maize or resistant soybean could diminish the contribution of *H. rhossiliensis* in suppressing *H. glycines*.

As I have already discussed, the host plant can directly influence the abundance of microbial control organisms via root exudates and perhaps other plant traits. Weller et al. (2012) suggests that plant species preferentially select and support populations of microorganisms to defend themselves against soilborne pathogens; strong evidence for this comes from research

with DAPG-producing *P. fluorescens* (Cook, 2007). Continuous cultivation of a crop species can lead to a selective increase in antagonistic organisms and the creation of disease suppressive soils. The classic example of this are soils suppressive to take-all of wheat caused by *Gaeumannomyces graminis*. Wheat monoculture results in the accumulation of DAPG-producing genotypes of *P. fluorescens* that are adapted to the wheat rhizosphere. Crop rotation can disrupt the microbial community leading to the return to disease-conducive soil (Cook, 1981). Likewise, Rotenberg et al. (2007) found that populations of DAPG-producing Pseudomonads were lower in maize rotated with soybean than in continuous maize. In watermelon, induction of suppressive soils by continuous cultivation was dependent on the cultivar. Soil from a monoculture of the watermelon cultivar Crimson Sweet, but not soil from monocultures of four other cultivars, was suppressive to Fusarium wilt when planted with a susceptible watermelon (Hopkins et al., 1987). Compared with the watermelon cultivar Florida Giant, monocultures of Crimson Sweet increased populations of microorganisms likely involved in suppression of Fusarium wilt (Larkin et al., 1993). Planting successive crops of Florida Giant in suppressive soil resulted in soil that was conducive to Fusarium wilt in watermelon.

Crop rotation does not always destroy a suppressive soil; in some cases, it can even alter the microbial community to create suppressive conditions. Apple replant disease in Washington State is caused by a complex of soil fungi (*Pythium, Phytophthora, and Rhizoctonia*) that become abundant in soils planted to apple for 2 or more yr (Mazzola, 1999). Growing wheat in the disease-conducive soil for 12 wk, however, improved apple growth and reduced infection from *Pythium* and *Rhizoctonia* (Mazzola and Gu, 2000). The wheat selectively enhanced fluorescent pseudomonads that were antagonistic to *R. solani*, with a greater proportion of antagonistic genotypes following the wheat cultivar Penewawa than the cultivars Eltan and Rely. 'Penewawa' also improved apple growth better than the other two wheat cultivars. Atkins et al. (2003) evaluated the effectiveness of combining crop rotation with *P. chlamydosporia* for managing *M. incognita*. In a field with high populations of *M. incognita*, the fungus was applied to the soil and then two poor hosts for the nematode (bean and cabbage) were planted consecutively before planting tomato. Nematode populations were low during the bean and cabbage crops in both plots treated with the fungus and control (no fungus) plots. However, after tomato was planted, populations of *M. incognita* increased to high levels in the control plots, but remain low in plots treated with the fungus several months earlier. Parasitism of eggs in the tomato roots was 70% in plots treated with the fungus indicating that *P. chlamydosporia* persisted in the rotation crops at sufficient levels to control *M. incognita* in tomato. Selection of the right rotation crop is important for maintaining pathogen suppression by antagonistic organisms. A soil suppressive to *H. schachtii* was compromised by planting wheat while maintained by planting an *H. schachtii*-resistant sugar beet, even though both crops equally reduced populations of the nematode (Westphal and Becker, 2001). Presumably, *B. oviparasitica,* the fungus primarily responsible for the suppression of *H. schachtii* in the soil, was able to proliferate in the rhizosphere of resistant sugar beet, but not wheat. Rumbos and Kiewnick (2006) observed differences in persistence of *P. lilacinum* strain 251 with different plant species; bean (*Phaseolus vulgaris*) resulted in more rapid decline in abundance of the fungus compared with other plant species.

Tillage: Tillage is used to loosen the top layer of soil, prepare the seed bed, and destroy weeds. Conventional tillage is considered the most disruptive to the soil community because it rips and inverts the soil, killing some organisms by mechanical damage and others by burying them deep in the soil or exposing them to desiccation and heat on the soil surface. In addition to the physical disturbance to the soil, tillage buries plant residues, thus increasing rates of decomposition. With no tillage, residue is left on the soil surface where it decomposes more slowly, improves water infiltration, and moderates soil temperatures (Bradford and Peterson, 2000). There are several types of minimum tillage that are intermediate between conventional and no tillage in that they limit the amount of soil subjected to tillage or the frequency of tillage. These tillage practices also leave 30% or more of plant residue on the soil surface (Kassam et al., 2012). Therefore, tillage practices not only differ in the level of mechanical disturbance, but also in their effect on biological processes through incorporation of organic matter and changes to soil moisture and temperature.

The effect of tillage on fungal parasites of nematodes has been inconsistent. Bernard et al. (1996) monitored parasitism rates of *H. glycines* eggs over a 2-yr period under different tillage regimes, most of which were in place 7 yr before the data collection. Although rates of egg parasitism were low ($< 10\%$), there were differences among tillage regimes with greater parasitism in treatments that were disc plowed than in moldboard plowed or the no-till treatments. *Hirsutella* spp. are sensitive to soil disturbance because their conidia are only infective when attached to the conidiophore; once detached the fungus must expend energy reserves to produce new conidia (McInnis and Jaffee, 1989). However, no differences were observed in the percentage of *H. glycines* juveniles that were parasitized by *H. rhossiliensis* and *H. minnesotensis* in three field sites with conventional tillage and no-tillage soybean (Chen and Liu, 2007). The probability of the juveniles encountering infectious conidia will vary according to soil moisture, temperature, and nematode density, which would likely differ between conventional and no tillage. Therefore, tillage may have reduced the number of

conidia without reducing rates of parasitism. In a related study, the percentage of *H. glycines* parasitized by *H. rhossiliensis* and other fungal parasites was lower in field soil subjected to simulated tillage (passing soil through a sieve) than in soil with minimal disturbance (Bao et al., 2011). However, the simulated tillage may have been more destructive to the fungus than actual tillage practices.

Predators of nematodes, such as mites and carnivorous nematodes, are sensitive to many types of environmental disturbances (Bongers, 1990; Koehler, 1999). Predatory and omnivorous nematodes tend to be lower in conventional tillage than in no tillage (Wardle et al., 1995; Lenz and Eisenbeis, 2000; Okada and Harada, 2007; Sanchez-Moreno et al., 2009). Similarly, abundance of predatory phytoseiid mites was reduced in conventional tillage compared with minimum or no tillage (reviewed in Koehler, 1999). Few studies, however, have determined whether this reduction in predator abundance has an impact on general suppression of nematodes. Using a bioassay based on survival of plant-parasitic nematodes, the relative abundance of carnivores (predators and omnivores) in the nematode community was positively correlated with suppression in two studies (Sanchez-Moreno and Ferris, 2007; Timper et al., 2012). However, in both of these studies, carnivores were correlated with suppression only during certain times the year; at other times, reduced survival of the bioassay nematodes was attributable to other organisms. In the study of Sanchez-Moreno and Ferris (2007), predation by tardigrades likely played a part in nematode suppression (Sanchez-Moreno et al., 2008). It appears that predators such as carnivorous nematodes, mites, and tardigrades contribute to general suppression, and tillage practices that substantially reduce their numbers could reduce suppression of plant-parasitic nematodes.

In microplots, tillage reduced the percentage of *M. incognita* juveniles that acquired endospores of *P. penetrans* at planting from 47% in no-tillage plots to 34% in plots that were rotary tilled (Talavera et al., 2002). By harvest, the endospore levels had equalized in the two treatments. In support of these findings, I have observed lower endospore densities in conventional than in strip-tilled plots from a field study with cotton; densities were reduced by 40% and 36% in strip compared with conventional tillage in 2012 and 2013, respectively (unpub. data). Endospore densities in both the microplot study and my field study were assessed using a bioassay with greenhouse-cultured juveniles of *M. incognita* to avoid confounding effects of soil moisture and structure on nematode movement. It is not known if these reductions in endospore densities following tillage were sufficient to diminish biological control of *M. incognita*. In soybean, suppression of *H. glycines* by *Pasteuria nishizawae* was similar in conventional and no tillage plots; differences in endospore densities between tillage treatments were not determined (Noel et al., 2010).

When general suppression occurs, it is not always clear which antagonistic organisms are involved. Stirling et al. (2012) used soil collected from different treatments of a field experiment to determine whether there were differences in reproductive potential of *M. javanica*, which was not present in the field soil. Egg production by the nematode was lower in soil from no tillage than from conventional tillage. Compared with conventional tillage, reproduction was reduced in no tillage by 32%, 63%, and 80% in the first, second, and third years, respectively, of successive tillage. Simulated tillage also reduced egg production by *M. javanica*.

Pesticides: Broad spectrum pesticides have the potential to kill beneficial organisms, which keep pest populations low, leading to pest outbreaks (Debach and Rosen, 1991). However, there is scant evidence that pesticides are leading to outbreaks of plant-parasitic nematodes, in part, because there have been few studies evaluating the effect of pesticides on biological control of nematodes (Stirling, 1991). Commonly, populations of plant-parasitic nematodes are greater at the end of the season in nematicide-treated compared with control plots (Sipes and Schmitt, 1998). These greater populations are often attributed to larger root systems and better carrying capacity of plants protected from nematode damage; however, lower levels of biological control may also be involved. Nematicides are toxic to all nematodes, though some genera may be more sensitive than others. Moreover, larger predatory nematodes have longer life cycles and are less fecund than smaller bacterial feeders; therefore, their populations would take longer to recover from mass mortality (Bongers, 1990). Among the nematicides/insecticides tested by Smolik (1983), aldicarb was highly toxic to dorylaimid nematodes (many of which were carnivorous), suppressing populations for the entire growing season; carbofuran and terbufos were less toxic than aldicarb, but still caused significant mortality. Microbial-feeding nematodes were less sensitive than the dorylaimids to the nematicides, with aldicarb again ranking among the most toxic of the three. In a field study, application of 1,3-dichloropropene (1,3-D) plus aldicarb reduced the abundance of carnivorous nematodes by 75% compared with the no-nematicide control 2 wk after planting cotton (Timper et al., 2012). Populations of these nematodes recovered somewhat by midseason (43% reduction) and fully recovered by the next spring. The soil at the field site was suppressive throughout the growing season based on a survival bioassay using the reniform nematode. After planting and at midseason, suppression was significantly lower in plots treatment with the nematicides compared with control plots. Carnivorous nematodes were implicated in the nematode suppression; however, other organisms such as predatory arthropods and tardigrades may have also contributed to

suppression. In another study, fields never treated with 1,3-D showed a large increase in abundance of nematode-trapping fungi following incorporation of sunn hemp; whereas, fields recently treated with the fumigant did not show an increase in trapping fungi (Wang et al., 2003). Yardim and Edwards (1998) observed greater populations of plant-parasitic nematodes 2 wk after application of carbaryl than in field plots without the insecticide, but numbers of carnivorous nematodes were unaffected by carbaryl. Though not measured, the insecticide may have reduced abundance of predatory collembolans and mites allowing greater survival of plant-parasitic nematodes.

A few studies have demonstrated a reduction in nematode antagonists following application of fungicides. In a greenhouse study, the fungicide azoxystrobin suppressed populations of *P. chlamydosporia* in the rhizosphere of potato (Tobin et al., 2008). Colonization of roots by AM fungi was substantially reduced by carbendazim in greenhouse pots, but only slightly reduced in field plots (Ipsilantis et al., 2012). In vitro assays for fungicide inhibition of germination or growth of nematophagous fungi tend to overestimate the risk of fungal suppression. Pullen et al. (1990) tested seven fungicides used in peach orchards for inhibition of *H. rhossiliensis*; all the fungicides except sulfur inhibited the fungus in vitro. However, in soil infested with *H. rhossiliensis*, only benomyl, triforine, and chlorothalonil increased numbers of *Mesocriconema xenoplax* relative to the control in one trial out of three. The authors conclude that although some fungicides have the potential to reduce nematode suppression by *H. rhossileinsis*, their low residual levels in soil would limit their impact on the fungus.

Pasteuria penetrans is tolerant of many pesticides (Mankau and Prasad, 1972; Tzortzakakis and Gowen, 1994; Chen and Dickson, 1998). Chloropicrin is one of the few pesticides that is directly toxic to *P. penetrans*. In plots treated with the chemical, the percentage of *M. arenaria* females infected by *P. penetrans* was less than half the percentage in nonfumigated plots. Root galling by the nematode was also greater in plots treated with chloropicrin for two consecutive years than in nonfumigated plots. Although 1,3-D is not directly toxic to *Pasteuria* spp., several studies have shown that the nematicide can affect endospore production by reducing the number of hosts for the bacterium to infect (Kariuki and Dickson, 2007; Timper et al., 2012; Davis et al., 2013). Nevertheless, the nematicide likely has less of an effect on endospore production by *Pasteuria* spp. than rotations with nonhost crops because the 1,3-D does not suppress nematode populations the entire growing season.

Bioassays can be useful in determining the number of infectious spores of *Pasteuria* spp. or *Hirsutella* spp. in the soil because they do not rely on the depleted numbers of indigenous plant parasites remaining after pesticide application (Timper et al., 2012). Moreover, it is important to not only determine the immediate effects of a pesticide on biological control, but also when and if there is recovery. Timper et al. (2012) detected dramatic and immediate reductions in suppression of a bioassay nematode following the application of nematicides; however, the effects of the nematicides did not persist into the next spring. Unexpectedly, there was greater biological suppression in the spring in plots treated the previous year with nematicides than in plots without nematicide treatment.

Farming systems: A number of studies have evaluated extensive modifications in production practices on biological control of nematodes, such as the difference between organic and conventional production systems. The prediction is that antagonists of nematodes would cope better under organic than conventional systems because organic farms do not use synthetic pesticides or fertilizers. However, other organic practices may have positive or negative impacts on nematode antagonists. Organic farms tend to have longer rotations and less fallow periods than conventional farms; they also use either animal manure or legumes for crop fertilization and often employ tillage for weed management and incorporation of organic matter. Persmark (1997) found no difference in abundance of nematode-trapping fungi among 10 pairs of conventional and organically managed farms in Sweden. Similarly, in a California study, the abundance of nematode-trapping fungi did not differ between conventional and organic plots (established 8 yr before the study), though the number of species was greater in the organic plots (Jaffee et al., 1998). The soil in both organic and conventional plots was equally suppressive based on a bioassay with *M. javanica*, but there was no correlation between suppression and density of trapping fungi indicating that these antagonists were not responsible for the observed suppression. In another study on the same field site in California, abundance of carnivorous nematodes and mites was greatest in organically managed plots with minimal tillage than in conventionally managed plots with standard tillage (Sanchez-Moreno et al., 2009). Standard tillage in the organic plots also reduced numbers of carnivorous mites compared with minimum tillage. Kokalis-Burelle (2005) collected soil from a replicated field study to determine the effect of different production systems for tomato on reproduction of *M. incognita* and fungal parasitism of nematode eggs in greenhouse assays. Galling of cucumber was lower in organic, conventional (with 1,3-D), and bare fallow production systems than in weed fallow and bahiagrass (*Paspalum notatum*) production systems; these differences, however, may have been related to the initial populations of nematodes in the soil at the time of collection. There were no differences in egg parasitism and only small and inconsistent differences in egg mortality based on a bioassay. These production systems had only been initiated 1 yr before the

soil was collected; a longer period of time may be needed to develop nematode suppressive conditions under some of the systems. In Spain, 10 organic farms and 30 farms practicing integrated pest management were sampled for egg parasites of *Meloidogyne* spp. (Gine et al., 2013). Higher levels of egg parasitism were found in the organic compared with the integrated farms, with *P. chlamydosporia* being the dominant parasite in both farming systems. Parasitism was greater than 50% in 40% of the organic farms and 3% of the integrated farms. Soil organic matter and microbial biomass were also significantly greater in the organic than in the integrated farms.

Over the past several years, Graham Stirling in Australia has developed a working hypothesis for enhancing biological suppression of plant-parasitic nematodes in wheat, sugarcane, and ginger cropping systems. The central principle of this hypothesis is that soil carbon levels are strongly correlated with biological suppression of nematodes (Stirling et al., 2011b). Therefore, production practices such as minimum tillage, organic amendments, and mulches that increase soil carbon levels should increase biological control. In northern Australia, grain crops are grown with minimum tillage and the residue from previous crops are left on the soil surface. A wide range of soils from this region were bioassayed for suppression of *P. thornei* (Stirling, 2011b). Most of the soil collected from continuous wheat fields was suppressive, often more suppressive than noncultivated fields. In sugarcane soils, which contain surface residues from previous harvests, percentage suppression of *R. similis* based on a bioassay was greater near the surface (60%, 0 to 2 cm) than deeper (26%, 15 to 17 cm). Crop residue provides carbon inputs that sustain a diverse soil food web culminating in general suppression of plant-parasitic nematodes; this enrichment of the soil community should decline with distance from the source. Indeed, concentrations of total carbon, nitrogen, and labile carbon were greater near the soil surface than deeper, and were all correlated with nematode suppression. Identifying the organisms responsible for general suppression can be difficult. Populations of carnivorous nematodes were greater at 0 to 2 cm than at 15 to 17 cm; however, the level of *R. similis* suppression was only correlated with predatory and not omnivorous nematodes. The diversity of nematode-parasitic fungi belonging to the Orbiliales was also highly correlated with suppression of *R. similis*. In ginger, a bioassay was used to determine the effects of crop rotations, soil amendments, and tillage on suppression of *M. javanica* (Stirling et al., 2012). Nematode suppression was greater when ginger was rotated with other crop plants or pasture grass compared with 3 yr of fallow. Amending soil with a combination of chicken litter and sawdust enhanced suppression after 1 and 2 yr, but not after 3 yr. Tillage reduced suppression of *M. javanica* only in amended soil. Crop and pasture rotations with amendments and no tillage had the least reproduction of *M. javanica* in the bioassay, ranging from 18% to 38% that of crop rotation with tillage and without amendment.

Future Research and Challenges

This review has illustrated numerous ways that biological control of nematodes can either be diminished or enhanced in crop production systems. Most of the research in this area has focused on monitoring changes in abundance of specific antagonists or groups of antagonists. However, as we carry on this line of research in the future, greater use should be made of bioassays that measure nematode suppression. An increase or decrease in abundance of an antagonistic organism does not prove that biological control is enhanced or diminished. The organism may either not be involved in nematode suppression or differences in abundance may not be sufficient to affect nematode suppression. For example, Biggs et al. (1994) evaluated two crop rotations for managing nematodes before planting apple (*Malus domestica*): 2 yr of tall fescue (*Festuca arundinacea*) or 2 yr of maize with a nematicide (ethoprop). Although there was greater species diversity of nematophagous fungi and abundance of predatory nematodes in the fescue compared with the maize system, a survival bioassay with *Pratylenchus penetrans* revealed no differences in biological suppression. Additionally, the organisms involved in nematode suppression are not always known, particularly with general suppression. Focus on a particular antagonist or group of antagonists may result in erroneous conclusions about the effect of a management practice on biological control. For example, amendments of plant residue had no effect on predatory nematodes or nematode-trapping fungi in soil, yet resulted in biological suppression of *P. zeae* for up to 28 wk (Stirling et al., 2005). Other studies that have used bioassays to measure suppression of plant-parasitic nematodes have also concluded that organisms other than or in addition to the ones monitored were involved in suppression (Jaffee et al., 1998; Timper et al., 2012).

One of the challenges of conservation biological control is that practices intended to protect or enhance suppression of nematodes may not be effective in all field sites because they are dependent on resident antagonists and the susceptibility of the plant parasite present in the field. For example, when green manure crops were incorporated into soil from two field sites, parasitism of *Globodera pallida* eggs by the resident fungi was increased in one field site and decreased in the other (Pyrowolakis et al., 1999). Gu and Mazzola (2003) showed that the ability of a wheat rotation to enhance growth of apple was greater in orchard WVC than in orchard CV. Populations of fluorescent pseudomonads tended to be greater in WVC than in CV following

wheat, which may explain the improved apple growth. However, the primary apple pathogen also differed between the two sites, with *R. solani* dominant in WVC and *Cylindrocarpon* spp. dominant in CV. *Cylindrocarpon* spp. appears to be less sensitive to suppression from the bacterial community than *P. solani* (Gu and Mazzola, 2003). Although Stirling (2011b) showed that suppression of *P. thornei* was widespread in wheat fields in northern Australia, two field sites were not suppressive despite >50 yr of continuous cultivation. Ultimately, indicators will need to be identified, such as the presence of particular antagonists, which can guide decisions on when and where it is practical to use conservation practices to improve biological control of nematodes. Stirling et al. (2011b) suggests that soil carbon is a good indicator of general suppression, though others have identified general suppression in soil with very low organic content (Timper et al., 2012).

An obvious way to circumvent the lack of appropriate indigenous antagonists is to introduce antagonists in combination with conservation practices to establish and enhance the efficacy of the introduced organisms. In several instances, applying fungal antagonists with organic amendments has led to greater rates of parasitism or nematode suppression than applications of amendments only (Hoffmann and Sikora, 1993; Perez-Rodriguez et al., 2011; Khan et al., 2012). Rotations that include crop species supporting proliferation in the rhizosphere of an applied fungal parasite should also improve levels of biological control (Atkins et al., 2003). Likewise, rotations that sustain reproduction of root-knot nematodes should maintain higher densities of an introduced *P. penetrans* than rotations that limit nematode reproduction (Oostendorp et al., 1991). Ideally, conservation practices should be evaluated on both indigenous and introduced antagonists of nematodes. Shapiro-Ilan et al. (2012) found that planting a clover cover crop increased the persistence and efficacy of an indigenous population of the entomopathogen *Beauveria bassiana* compared with bare soil, but not an applied strain of the fungus; they speculated that the discrepancy between the indigenous and applied *B. bassiana* was because of differences in the biology or physiology of the fungal strains.

Another concern with some conservation practices is that they may exacerbate other pest problems. Symphylan damage to ginger was greater in crop rotations that received organic amendments and minimum tillage than in ginger after bare fallow and conventional tillage (Stirling et al., 2012). Continuous planting of the same crop in a field can lead to the buildup of plant-specific or nematode-specific antagonists; however, it can also lead to an increase in plant pathogens. While continuous cultivation has little negative impact on yield of some crops such as wheat, it can lead to very low yields in other crops because of diverse pest complexes. For instance, even though continuous peanut (*Arachis hypogaea*) increased endospore densities of *P. penetrans* to a level that maintained populations of *M. arenaria* below the damage threshold, peanut yields were lower in continuous peanut than in peanut rotated with other crops (Timper et al., 2001). Crop rotation is a key strategy for reducing several soilborne diseases of peanut. Rotating peanut with other hosts for *M. arenaria* increased the abundance of endospores compared with rotations with nonhosts while maintaining a low incidence of southern stem rot (*Sclerotium rolfsii*) compared with continuous peanut (Timper, 2009; unpub. data). The potential to increase other pests is not unique to conservation biological control; unforeseen pest problems can arise whenever crop production practices are changed. Adjusting production practices requires a comprehensive understanding of the pest complexes associated with a particular cropping system, and some trial and error.

Conservation biological control has a few advantages over traditional inundative applications of commercially-produced antagonists. With practices such as minimum tillage, residue retention, and planting antagonist-conducive cultivars, few additional production costs will be incurred. Moreover, minimum tillage and residue retention provide additional benefits such as reducing soil erosion and improving soil structure, organic matter content, and moisture retention (Bradford and Peterson, 2000). Conservation biological control also has the potential to improve the consistency, effectiveness, and duration of nematode suppression by introduced antagonists. Because so little research has been done on conservation biological control in nematology, there are numerous paths of research to explore. Plants are most vulnerable to nematode damage when they are young; therefore there is a need to identify strategies for encouraging early season activity of indigenous antagonists (e.g., winter cover crops and minimum tillage). Greater emphasis should also be placed on biological control that is operating over several seasons rather than just one season. Finally, there is mounting evidence that plants have evolved traits for recruiting beneficial organisms to help protect them from parasitism and herbivory; these traits have been largely overlooked in crop selection and breeding (Rasmann et al., 2005; Ling et al., 2011). Compatible plant-antagonist associations may be the foundation for improving biological control using indigenous and introduced antagonists of nematodes.

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