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Soil Organic Matter and Management of Plant-Parasitic Nematodes[1]

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Abstract: Organic matter and its replenishment has become a major component of soil health management programs. Many of the soil's physical, chemical, and biological properties are a function of organic matter content and quality. Adding organic matter to soil influences diverse and important biological activities. The diversity and number of free-living and plant-parasitic nematodes are altered by rotational crops, cover crops, green manures, and other sources of organic matter. Soil management programs should include the use of the proper organic materials to improve soil chemical, physical, and biological parameters and to suppress plant-parasitic nematodes and soilborne pathogens. It is critical to monitor the effects of organic matter additions on activities of major and minor plant-parasitic nematodes in the production system. This paper presents a general review of information in the literature on the effects of crop rotation, cover crops, and green manures on nematodes and their damage to economic crops.
Key words: cover crops, crop rotation, green manure, nematode control.

The soil is practically a nonrenewable resource, and the economics of agricultural production depend on how well the soil is maintained. Recently, a great deal of attention has been paid to soil management practices that promote sustainable soil quality and productivity (Doran and Jones, 1996; Magdoff and van Es, 2000; Pankhurst et al., 1997). The employment of various sources of organic materials has been promoted as one of the principal sustainable management options for improving soil quality and productivity. Organic matter is one of the most important components of soil (Magdoff and van Es, 2000), and many physical, chemical, and biological properties of soil are a function of soil organic matter. The functions and interactions of soil organic matter are complex. Some of the benefits of organic matter include the improvement of soil structure, erosion control, water relations, availability of plant nutrients, ion exchange, chelation, buffering capacity, energy for soil organisms, and suppression of plant pathogens (Hodges, 1991).

Soil density affects not only root growth but also the penetration of water as well as air permeability. The addition of organic matter significantly changes soil density. Compost incorporation significantly decreases soil density (Mays et al., 1973; Turner et al., 1994; Widmer et al., 1997) by the formation and stabilization of soil aggregates (Allison, 1968; Biswas and Khosla, 1971; Pagliai et al., 1981; Rose, 1991) and increases soil pore size (Gallardo-Lara and Nogales, 1987), thus improving soil structure. Soil structure is of paramount importance in soil productivity and can become the limiting factor of crop yield (Low, 1973). One method of studying soil structure is measuring porosity and pore size distribution (Lawrence, 1977). Total porosity, expressed as a percentage of the total area occupied by pores, increases significantly after the incorporation of aerobic and anaerobic sludge, composted sludge, farmyard manure, and urban refuse (Pagliai et al., 1981; Rose, 1991). Pore size distribution, the main aspect of soil porosity, is related to crop yield through ease of root penetration and the storage and movement of water and gases. Pores larger than 500 µm, called fissures, are considered an index of poor soil structure, although they can have some useful effects on root penetration. Pagliai et al. (1981) found that the addition of organic matter decreased the proportion of very large pores while increasing the proportion of storage (0.5–50 µm) and transmission (50–500 µm) pores. Another improvement of the physical characteristics of soil is an increase in moisture-holding capacity (Epstein et al., 1976; Mays et al., 1973; Rose, 1991; Turner et al., 1994). This is observed most dramatically in well-drained sandy soils where the addition of organic matter can increase available water and so decrease irrigation requirements. When composted municipal waste was applied to mature citrus trees, visual observations of a denser canopy and less water stress of the foliage were noted (Widmer et al., 1997).

Different sources of organic matter affect the chemical properties of soils in different ways. One important change resulting from the addition of organic matter is a potential increase in available nutrients, including an increase in organic carbon (Guidi et al., 1983), potassium, calcium, and magnesium (Bengston and Cornette, 1973; Duggan and Wiles, 1976; Hortenstine and Rothwell, 1969; Mays et al., 1973). Organic matter also can change the level of available nitrogen in the soil. Nitrogen availability depends on the C/N ratio of the organic source. The addition of compost with a C/N ratio above 30 produces N^- immobilization, a reduction of available nitrogen for plants caused by the accelerated growth of microflora that use nitrogen. The supply of plant nutrients from organic matter depends on the rate of biological breakdown. Some sources of organic residues, such as well-decomposed compost and humus, are stable and mineralize slowly, thus releasing nutrients gradually (Hodges, 1991). This slow release may be beneficial because it supplies nutrients over a long period (Keeling et al., 1991). The addition of or-

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ganic matter also has been shown to increase ion exchange and buffering capacity and neutralize the soil pH. Soil organic matter can retain cations because of its negative charged sites. This is especially important where nutrient leaching, through rainfall or irrigation, is a problem. Poor soils also may have a low pH, which can be detrimental to plant growth, especially to plants sensitive to acidic conditions. The incorporation of organic matter can neutralize soil acidity and provide a buffer against drastic changes.

Organic matter addition affects the diverse and important biological activities of soils. The incorporation of organic materials provides soil organisms with a new energy source that results in the increased diversity and activities of soil microbes. The effects of organic matter on soil microorganisms vary depending on soil type, source of organic matter, and decomposition status, but the populations of most soil organisms increase (Gallardo-Lara and Nogales, 1987; Kuter et al., 1983; N'Dayegamiye and Isfan, 1991; Pera et al., 1983; You and Sivasithamparam, 1995). A recent study by Widmer and Abawi (2000) showed that the incorporation of sundangrass increased populations of total bacteria, fungi, and nematodes. Many of these organisms or their metabolites are beneficial for plant growth (Kloepper and Schroth, 1981; Schippers et al., 1987) or antagonistic toward plant pathogens, including nematodes (Chen et al., 1999; Viaene and Abawi, 2000).

Almost all crop production practices have a direct or indirect impact on root disease incidence and severity. Of particular influence are cover crops, mulches and composts, tillage systems, cropping sequences, and planting systems (Abawi and Thurston, 1994; Abawi and Widmer, 2000; Allmaras et al., 1988; Cook and Baker, 1983; Cook et al., 1978; Sumner et al., 1981). Often, suppression of plant diseases by these cultural practices can be attributed to an increase or change in microbial activity (Broadbent and Baker, 1974; Cook and Baker, 1983). Studying the population dynamics and changes due to the addition of organic matter in relation to disease suppression can help decide which cultural practice to use to promote a specific beneficial organism. Populations and diversity of nematode communities also are affected by the addition of organic matter. Several studies have shown that populations of plant-parasitic nematodes have decreased and saprophytic nematodes increased with organic matter additions (Barker and Koenning, 1998; Bird, 2000; Hunt et al., 1973; McSorley and Gallaher, 1996; Mojtahedi et al., 1991).

The objective of this paper is to present a general review of information available in the literature on the effects of organic matter from rotational crops, cover crops, and green manures on nematodes and their damage to economic crops. No attempt is made to fully review the literature but to present only available recent evidence on demonstrated effects of organic matter toward nematodes.

Rotational crops: Crop rotation is one of the oldest and most important methods for managing plant disease (Curl, 1963; Nusbaum and Ferris, 1973). When a plant disease becomes severe and damaging, planting a nonhost crop in intervening years can dramatically reduce disease and damage on the primary crop, as can planting a resistant cultivar. Crop rotations not only keep the overall level of disease relatively low but also generally increase the diversity and stability of microorganisms associated with the rhizosphere, as compared to monocultures (Cook and Baker, 1983). A number of crops used in rotations can improve soil structure and increase nutrient cycling, which results in higher yield for the main economic crop and thus provides a greater return for growers. Although appropriate crop-rotation schemes are well suited to controlling plant-parasitic nematodes, care is necessary when selecting crops because many nematodes have a wide host range. This can also make it difficult to design effective rotations. Therefore, it is essential to know a nematode's host range before an effective crop rotation can be deployed. *Meloidogyne hapla,* for instance, has a host range consisting of more than 550 crop and weed species (Jepson, 1987). In vegetable production systems it can parasitize onions, carrots, lettuce, celery, beans, and many other important crops. Consequently, developing rotational management strategies in these systems is difficult and complex when resistant varieties do not exist and the inclusion of nonhost crops such as grains is not an option. In contrast, rotations are effective for management of the sugar beet cyst nematode, *Heterodera schachtii* (Mai and Abawi, 1980). Although this nematode has a host range including 218 plant species, most of these hosts are in the Chenopodiaceae and Cruciferae (Steele, 1965).

Essentially two types of rotational crops are commonly used—nonhosts and resistant hosts. Nonhost crops are immune to a particular nematode or are not efficient hosts under typical field conditions. Nonhosts are usually plants of a different species than the primary crop. They are good at reducing disease and nematode levels but may not produce a marketable commodity or sufficient economic return. Resistant crops are usually the same species as the primary crop but are not susceptible to a particular disease or nematode. Resistant varieties are the most economical means of managing plant-parasitic nematodes (Barker and Koenning, 1998), as they allow production of the desirable commodity. A common concern with resistant varieties is that their intensive use may select for more aggressive biotypes of a pathogen. Unfortunately, nematode-resistant cultivars are unavailable for most major agronomic crops (Young, 1998). This requires that most rotations be designed with nonhosts or poor hosts.

The soybean cyst nematode, *Heterodera glycines*, is a significant problem in soybean-growing regions of the United States (Wang et al., 2000). One of the most effective methods of controlling this nematode is by use of resistant varieties, and a number of race-specific sources of resistance to *H. glycines* exist (Noel and Edwards, 1996; Wang et al., 1995). Therefore, it is necessary to know which nematode race is present in a field before a resistant variety is planted. Nonhosts also have been used in soybean rotational programs. Researchers who have incorporated maize into a soybean-cropping sequence frequently observe significant nematode control when used with or without resistant varieties (Koenning et al., 1995; Noel and Edwards, 1996; Sasser and Uzzell, 1991). Rotations with soybean and sorghum or wheat also have been demonstrated to suppress soybean cyst nematode, populations of *Fusarium solani*, and the severity of soybean sudden death syndrome (Rupe et al., 1997). Weaver et al. (1995) concluded that rotations with a sorghum-sudangrass hybrid or fallow were effective in increasing soybean yield in the presence of a mixed population of soybean cyst and root-knot nematodes. They also observed that the highest yield was obtained using a crop rotation and soybean cultivars with the highest resistance to both nematodes.

Crop rotation also has been effective at reducing nematode levels in vegetable production systems. An experiment on rotation crops such as radish, spinach, and oats significantly decreased *M. hapla* damage to carrots. In addition, a rotation of carrot-onion-oat-carrot not only reduced nematode levels and increased the marketable yield of carrots by as much as 282% but was economically feasible for most growers (Belair, 1992). In a separate experiment it was demonstrated that a barley rotation in a carrot cropping system was also extremely effective at reducing *M. hapla* levels (Belair, 1996). Crop rotation also can be successful at controlling nematode damage to fruit crops. LaMondia (1999) has recently shown that Saia oat may be a potentially effective rotation crop for managing multiple nematodes on strawberry. In Georgia, it was shown that a wheat-sorghum rotation could be used as a preplant strategy to control *Criconemella xenoplax* on peach trees (Nyczepir et al., 1996).

Rotations can positively affect soil quality. Studies have demonstrated that numerous changes can occur in soils as a result of crop rotation. The most important factor that influences changes in soil conditions (such as microbial community structure, density, and distribution) is nutrient supply (Nusbaum and Barker, 1971). The nutrient supply can be manipulated by changing the crops grown, which change the exudates being released into the soil and consequently microbial activity and diversity within the soil. In some instances, the indirect manipulation of microbial communities may generate suppressive soils, which will be antagonistic toward plant-parasitic nematodes (Kloepper et al., 1991, 1992). It is also possible to enhance or change these soil communities by type of crop debris incorporated into the soil (Cook and Baker, 1983; Kloepper and Schroth, 1981).

The use of velvetbean, *Mucuna deeringiana*, in a soybean rotation enhanced the activity of the rhizosphere bacteria antagonistic to the soybean cyst nematode and the southern root-knot nematode *Meloidogyne incognita* (Kloepper et al., 1991, 1992). A study by Sohlenius et al. (1987) demonstrated that different cropping systems affected the abundance and taxa of nematode feeding groups. They found that the influence of cropping practices on specific taxa was greatest among plant feeders. For example, in fescue (*Festuca pratensis* Huds. cv. Mimer), *Pratylenchus* spp. were increased by almost 10 times in comparison to alfalfa (*Medicago sativa* L. cv. Suerre).

The complexity of developing a rotation is significantly increased if more than one parasitic nematode is present. A cropping system should be selected so that one crop does not produce a population of nematodes larger than the economic threshold density on the succeeding crop (Nusbaum and Ferris, 1973). Developing a crop rotation strategy requires considerable knowledge of the disease organism(s), the hosts involved, and the environment in which they interact. Burt and Ferris (1996) dealt with the decision-making process involved in developing such a strategy. Crop rotation is widely applicable for numerous types of crops and diseases, not only nematodes. Crop rotation will continue to be a mainstay of nematode and disease management for years to come.

Cover crops: The use of cover crops has been widely implemented to reduce plant-parasitic nematodes in agricultural soils. A cover crop is planted in between the cultivation of an annual cash crop, typically but not always outside of the usual growing season. Cover crops include species such as vetch, cowpea, crotaleria, sudangrass, sorghum, marigold, rye, wheat, and others. There are many reasons for growing cover crops, but they are typically planted to increase soil quality, control erosion, or address perennial disease problems. Mechanisms of disease control can vary but frequently rely upon the resistance of the cover crop to the nematode. While many plant-parasitic nematodes have a wide host range, several are limited to a small group of plant families or even a few plant species. In these cases, nonhosts can be planted between primary crop cycles to reduce the numbers of plant-parasitic nematodes. Because nematodes that encounter nonhosts are unable to reproduce, their numbers decline. The term allelopathy is frequently used to describe antagonistic interactions between plants and microorganisms or between plants that are facilitated by chemical signals or toxins (Halbrendt, 1996). In some instances, a cover crop or rotational crop that produces allelopathic nematicidal chemicals may be used (Patrick et al., 1965;

Rodríguez-Kábana and Canullo, 1992). Marigold is a commonly studied cover crop that produces nematicidal allelochemicals (Uhlenbroek and Bijloo, 1958).

Currently, many researchers are examining the use of cover crops for managing nematode damage. In an experiment using several cover crops, it was recently demonstrated that the levels of *Meloidogyne* on marigold, sesame, cowpea, and crotalaria were dramatically below those of the control host (tomato) (McSorley, 1999). *Meloidogyne hapla* has a wide host range but typically will not reproduce on members of the Poaceae. Cover crops such as sudangrass and oat have been shown to be highly resistant to the nematode (Viaene and Abawi, 1998). *Pratylenchus penetrans* also has a wide host range, but potential resistant cover crops have been identified from plant families including Asclepiadaceae, Asteraceae, Poaceae, and Fabaceae (McKeown et al., 1994). In the Netherlands, *Meloidogyne chitwoodi* is a problem on potatoes, sugarbeet, carrots, maize, and other economically important crops. Investigations using a number of cover crops have found that perennial ryegrass results in very low levels of *M. chitwoodi* reproduction (Korthals et al., 2000). Nematode control may not always increase crop yields. Pedersen and Rodríguez-Kábana (1991) demonstrated that although annual ryegrass was able to reduce the numbers of *Pratylenchus* spp., *Heterodera glycines*, and *Tylenchorhynchus claytoni* in soybean fields, soybean yields were actually higher in fields that had been only fallowed.

As with rotations, it is important to recognize the host range of the plant-parasitic nematode under consideration. Even if a cover crop is found that is resistant to the nematode species being targeted, it may actually prove to be a suitable host for other plant-parasitic nematodes, which may affect the primary crop. The use of crotolaria as a cover crop was shown to decrease the levels of *Meloidogyne* when maize was continuously cropped, but an increase in the levels of *Pratylenchus zeae* resulted. As a result of the high *Pratylenchus* levels, fields implementing this strategy were soon unsuitable for maize production, but *Meloidogyne* levels were reduced enough so that bean cultivation was feasible (Desaeger and Rao, 2000). Hairy vetch has been promoted and used as a cover crop for controlling erosion and improvement of soil quality parameters in general. While vetch has several beneficial effects as a cover crop, it is an excellent host for *Pratylenchus penetrans* (Abawi and Ludwig, 1995). This can be problematic for growers interested in primary crops highly susceptible to the lesion nematode.

Different types of fallow also can be used in between primary crop cycles, but suffer from a number of limitations. Fallowing a field exposes it to increased rates of erosion and runoff. Many nematodes will hatch in the presence of root exudates, regardless of whether those exudates are from a host plant. If a nonhost stimulates egg hatching, juvenile nematodes will not have a suitable food source and will eventually perish. In a fallow field, there is no stimulus to hatch juvenile nematodes and many of them may remain viable in the soil for the next crop cycle. In a "weed fallow," in which no effort at weed control is made, nematode numbers may actually increase as many plant-parasitic nematodes survive on weed hosts (Schroeder et al., 1993).

Green manures: The efficacy of cover crops is frequently increased when they are incorporated into the soil as manures. Incorporating cover crop biomass helps to add nutrients into the soil and can positively impact soil quality by increasing organic matter and improving soil structure (Allison, 1973; Magdoff and van Es, 2000). Green manures and other amendments also can be effective at controlling diseases and nematodes. Their mode of action can be either chemical or biological, but some incorporate both aspects. Chemical control mechanisms typically affect plant-pathogenic nematodes through the release of compounds into the soil that are toxic or antagonistic to the nematodes. Biological control mechanisms typically affect plant-pathogenic nematodes by providing an environment suitable for the increase of microorganisms antagonistic or parasitic to the nematodes, including those that may produce allelochemicals.

Sudangrass is an excellent example of a cover crop that is also useful as a green manure. When sudangrass is grown and incorporated into the soil as a green manure, the released decomposition products act as a potent nematicide (Widmer and Abawi, 2000). In experiments using lettuce grown in field microplots previously amended with sudangrass residues and infested with high levels of *Meloidogyne hapla*, an increase of at least 20% in the head weight of lettuce over that of control plots was observed (Chen et al., 1999; Viaene and Abawi, 1998). In a similar experiment marketable yields of carrots increased by 18% when sudangrass residues were added to the soil (Widmer and Abawi, 1998). Sudangrass cultivars contain in their cell walls the cyanogenic glucoside dhurrin, which is enzymatically degraded in soil resulting in the release of hydrogen cyanide (Widmer and Abawi, 2000). Exposure of eggs of *M. hapla* to as low as 0.01 ppm of CN^- was enough to affect egg hatching and reduce infection of lettuce roots.

In greenhouse experiments, sudangrass, oil radish, buckwheat, rapeseed, horsebean, velvetbean, castorbean, and maize residues were incorporated into sterile soil and inoculated with *Meloidogyne chitwoodi.* It was demonstrated that all of the treatments significantly reduced the levels of *M. chitwoodi* as compared to control treatments, with some residues reducing populations by as much as 94% (Al Rehiayani and Hafez, 1998). In the same experiment, oil radish and rapeseed were used as green manures in conjunction with crop rotation in field trials with potato. Not only were *M. chitwoodi* numbers significantly reduced in the green manure treatments as compared to the fallow controls but marketable yields were increased by as much as 185%. Levels of *Pratylenchus neglectus*, however, were unaffected by the green manure treatments. In an earlier experiment, Mojthahedi et al. (1993) obtained similar results in the field using rapeseed as an amendment to soils infested with *M. chitwoodi* on which potatoes were grown. *Heterodera cajani* on Pigeonpea has been managed using green manures of mung, cowpea, sunhemp, and dhaincha (Devi and Gupta, 1995). Reproduction of *M. arenaria* and *M. incognita* was reduced on squash through incorporation of velvetbean and rapeseed green manures with the application of supplemental urea (Crow et al., 1996). In an experiment designed to identify nematode control measures for vineyards, McLeod and Steele (1999) incorporated chopped leaves from 15 different brassicaceous species into the soil to reduce the levels of *M. javanica*. Green manures also can be useful on tropical crops. For example, green manures from a number of different crops, including marigold, greatly increased yields of taro (Sipes and Arakaki, 1997).

Conclusion

The annual introduction of organic matter as a disease management option has become a major component in the overall sustainable management of soil health and productivity. It is well known and well documented that the addition and maintenance of high levels of organic matter, especially the active fraction, will greatly improve the physical, chemical, and biological properties of soil, thus increasing productivity. However, various sources of organic materials have different effects on the general biological activities in soil and more so against specific pathogens and their resultant diseases. Total soil nematodes and plant-parasitic nematodes are especially affected by organic materials added in the form of rotational and cover crop debris, green manures, composts, or other soil amendments. Soil management programs should include the proper source and quality of organic amendments to improve soil quality and to suppress soilborne pathogens, including nematodes. It is critical to monitor the effects of organic matter additions on the activities of major and minor plant-parasitic nematodes and other soilborne pathogens in the production system.

Crop disease management is a complex and challenging science. In general, management strategies are influenced by numerous factors that vary by both time and location. When choosing an appropriate management strategy, one must consider not only the disease in question but also those factors directly and indirectly affecting disease. For example, choosing a rotational crop that limits one disease but promotes another may not be a viable option in one location but may provide suitable disease control elsewhere. Crop varieties may respond unpredictably under different climatic conditions, soil conditions, or levels of disease pressure. Frequently, pathotypes or races of a pathogen may easily be controlled by one variety but not another. In some cases, high fertilization may be needed to achieve a crop performance goal, but the additional nitrogen may increase a crop's susceptibility to one or more diseases or insects. Ultimately, economics and grower concerns must be considered. These are just a few of the many factors that must be considered in developing an effective disease management strategy as a component of a sustainable soil management program.

Successful management strategies usually have multiple components and employ the principles of integrated pest management (IPM). Such a soil-IPM strategy uses a combination of different disease control methods to decrease disease, increase yield, minimize environmental damage, prevent buildup of resistant pathogen strains, and produce high-quality products. However, IPM programs can be expensive, as they require more intensive knowledge of pest biology and more management efforts. Nematode management can benefit greatly from the use of alternative control methods employing IPM strategies. Choosing nematode-resistant varieties, using appropriate cover crops, and applying antagonistic green manures and residues can contribute to the development of suppressive soils and sustainable agricultural practices. Suppressive soils can keep nematode levels below the damage threshold density without excessive use of chemicals and with less cost to the grower. Nematode control imparted by the development of suppressive soils is generally longer lived than that provided by chemicals, is safer for the environment, and poses less risk of contamination of the food supply.

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