Root-knot nematode (Meloidogyne) management in vegetable crop production: the challenge of an agronomic system analysis

Béatrice Collange, Mireille Navarrete, Gaëlle Peyre, Thierry Mateille, Marc Tchamitchian

To cite this version:

Béatrice Collange, Mireille Navarrete, Gaëlle Peyre, Thierry Mateille, Marc Tchamitchian. Root-knot nematode (Meloidogyne) management in vegetable crop production: the challenge of an agronomic system analysis. Crop Protection, Elsevier, 2011, 30 (10), pp.1251-1262. <10.1016/j.cropro.2011.04.016>. <hal-00767386>

HAL Id: hal-00767386
https://hal.archives-ouvertes.fr/hal-00767386

Submitted on 19 Dec 2012

Version définitive du manuscrit publié dans / Final version of the manuscript published in : Crop Protection, 2011, In Press. DOI: 10.1016/j.cropro.2011.04.016

Root-knot nematode (*Meloidogyne*) management in vegetable crop production: the challenge of an agronomic system analysis

Béatrice Collange [a], Mireille Navarrete [a], Gaëlle Peyre [a], Thierry Mateille [b], Marc Tchamitchian [a,]*

[a] *INRA, Ecodéveloppement Unit, 84914 Avignon cedex 09, France*
[b] *IRD, UMR CBGP, Campus de Baillarguet, CS30016, 34988 Montferrier-sur-Lez Cedex, France*

* Corresponding author. Tel.: +33 (0)4 32 72 25 61; fax: +33 (0)4 32 72 25 62
E-mail address: marc.tchamitchian@avignon.inra.fr (M. Tchamitchian)

ABSTRACT

Root-knot nematodes are a growing concern for vegetable producers, because chemical nematicides are gradually disappearing. Alternative techniques based on agronomic practices are needed to solve the problem. This review analyzes the most recent studies related to these techniques and their combinations and identifies the most effective ones. Based on an agronomic point of view, the analysis focuses on a description of agricultural factors and practices, rather than on biological processes. Several alternative techniques are considered, including sanitation, soil management, organic amendments, fertilization, biological control and heat-based methods. We analyzed the effects of each practice and interactions among techniques and found large variations among studies. Many practices are only partially effective for nematode control; thus, combining control methods in a systemic analysis presents a challenge. We outline such an ongoing systemic approach and identify key future research studies.

Keywords: Nematode; *Meloidogyne*; Pest management; Alternative technique; Interaction; System

1. Introduction

Root-knot nematodes (*Meloidogyne* spp.) are the most frequently observed and damaging plant-parasitic nematodes in vegetable production (Koenning et al., 1999). Most of the *Meloidogyne* species are easily diagnosed by farmers by the presence of galls on the roots. Galls are formed as a consequence of physiological disturbances in the root tissues caused by the trophic interactions of female nematodes. But the identification of a particular nematode species is difficult, and typically requires taxonomic analysis, which is rarely feasible for most farmers. Nevertheless, four species are mainly related to vegetable production: *Meloidogyne arenaria* (Neal) Chitwood, *M. javanica* (Treub) Chitwood and *M. incognita* (Kofoid & White) Chitwood which are thermophil species and *M. hapla* Chitwood which is a cryophil species (Moens et al., 2009). *M. arenaria*, *M. javanica* and *M. incognita* are found worldwide, typically in tropical and subtropical areas but are also present in more temperate areas especially in protected cultivation. *M. hapla* is typically observed in temperate areas and at higher altitude in the tropics (Hunt and Handoo, 2009).

Root-knot nematodes cause considerable economic losses. An average 10% of loss in yield is frequently cited for vegetables (Barker and Koenning, 1998; Koenning et al., 1999; Regnault-Roger et al., 2002). However, much higher percentages have been recorded in local regions, depending on the genus, population level (Ornat and Sorribas, 2008), and crop species. For example, Sikora and Fernandez (2005) reported yield losses of over 30% in three highly susceptible vegetable crops (egg-plant, tomato and melon).

In past years, plant resistance and nematicides have been widely used to control nematode attacks. Plant resistance is a very promising way of control, but has led, for many other pathogens, to resistance breakdown due to the severe selection pressure exerted by the resistant plants (Aubertot et al., 2006). Designing sustainable control management methods based on plant resistance only remains a challenge (Thakur, 2007). Nematicides are highly toxic to both human health and the environment (Abawi and Widmer, 2000). Most nematicides are being progressively banned or highly restricted for protecting vegetable production (e.g., methyl bromide, a very common fumigant, has been totally banned in developed countries for environmental reasons since 2005). Thus the development of alternative control strategies and long-term integrative approaches is urgently needed in order to replace chemical nematicides (Martin, 2003).

This review aims to analyze alternative cropping techniques and identify techniques and combinations of techniques that can be effectively used for sustainable farming systems. The literature on nematodes is abundant; therefore, we chose to focus on controversial techniques and interactions or soil conditions that might explain discrepancies among reports. Taking an agronomic point of view, we focused on descriptions of agricultural factors and practices, rather than biological processes. Similarly, we gave priority to field trials, because they represent farmers' conditions better than trials conducted under controlled conditions (pots or cylinder cells).

Several alternative techniques were considered, including sanitation, soil management, organic amendments, fertilization, biological control, and heat-based methods. Many studies were located in developing tropical countries, particularly those regarding cost-effective ways to control plant-parasitic nematodes, including organic manure, biocontrol agents, and plant extracts (D'Addabbo, 1995). More recently, in the United States and Europe, several long-term experiments were conducted that combined various techniques and/or compared the effects of several organic and conventional cropping systems. Currently, it is a challenge to evaluate and optimize alternative techniques in temperate cropping systems (Litterick et al.,

2004) in order to propose efficient technical solutions to farmers that cannot continue to depend on chemical solutions.

It is particularly challenging to combine and integrate control methods based on cropping techniques that are only partially effective (Katan, 2000). The first part of this review will cover the effects of individual practices and the main factors that might explain the variability in efficiency. The second part will cover interactions between techniques and between micro-organisms. The biological, physical and chemical mechanisms involved are then used to understand the positive or negative interactions previously highlighted. Finally, we will outline an ongoing systemic approach we are involved in and we will recommend key future research studies.

2. Efficiency of individual alternative techniques

2.1. Sanitation methods

There are two forms of sanitation, (i) prevent nematode introduction into fields, and (ii) reduce or eliminate inoculum, once nematodes are present.

2.1.1. Prevention of new infestations

Root-knot nematodes can be easily spread by human activities that provide communication between contaminated and healthy areas; for example, the transport of infested soil, plant debris or water. Research articles are rare and nematode advisory programs do not rely on precise information. Because few experiments have been designed to quantify the efficiency of sanitation methods, most information comes from farm surveys. At the farm level, experts have recommended cleaning all agricultural machines and tools to avoid transporting nematodes with the soil (Mateille et al., 2005; Djian-Caporalino et al., 2009). In protected crops, most nematode damage appears to occur at the entrance of the greenhouse. Those observations have led to the use of airlocks fitted with foot or wheel baths. Hugo and Malan (2010) reviewed many situations with dissemination of nematodes (especially *Meloidogyne* spp.) through irrigation water and pointed out the difficulties for controlling the phenomenon. On the contrary, if nematodes can survive in plant materials (e.g. seeds, bulbs, corms, tubers and cuttings), their spread can be prevented more easily by heating the plant materials, by spraying or coating plant materials with natural nematicidal solutions, or using *in vitro* grown, healthy plant materials (Bridge, 1996). Growers typically buy vegetable seedlings; thus, it is essential to check that seedbeds and seedlings are free of nematodes.

2.1.2. Prevention of secondary infestations

Once the nematodes have contaminated the soil, sanitation methods involve the reduction or elimination of inoculum.

Soil flooding: Flooding creates anaerobic conditions that reduce the density of *M. incognita*; but the optimal duration of flooding depends on air temperature (Rhoades, 1982). Four weeks appeared to be insufficient for reducing nematode infestations in any air temperature. In contrast, an 8-week flooding could suppress the nematode population in air temperatures above 20 °C. Moreover, alternating flooding and drying cycles appeared to be more effective than prolonged flooding (Noling and Becker, 1994). Duncan (1991) reported that flooding was an effective option for suppressing root-knot nematodes in irrigated rice cultivation; furthermore, after paddy rice, vegetables could often be grown successfully without damage. However, typically, flooding in vegetable production is not very convenient and difficult to apply due to water consumption, the nature of the soil and the agronomic consequences on soil (lack of oxygen, soil structure degradation) that might reduce yield.

Irrigation management: Nematodes move most easily in wet soils (Djian-Caporalino et al., 2009), offering them the best conditions to achieve their life cycle. Soil moisture enhances egg hatching; dryness leads to resistance forms (van Gundy, 1985). Thus, vegetable crops are particularly susceptible in greenhouse conditions, where the soils offer both high temperature and humidity. This suggests that irrigation should be reduced, but water is critical for yield and quality; consequently, it is difficult to apply optimal water management for nematode control.

Plant residue cleaning: As root-knot nematodes are obligate parasites of plants, they can survive in residues of infected plants for only short periods, until they consume their own reserves (Ornat and Sorribas, 2008). Therefore, contaminated cropped plants and root elimination will prevent nematodes from multiplying after harvest. Bridge (1996) advised uprooting plants after each harvest and exposing the roots to sun radiation to kill nematodes in root tissues. This has become a common practice for some tropical crops, but its efficiency has rarely been quantified. Barker and Koenning (1998) considered that taking this precaution could reduce *Meloidogyne* populations by 90% compared to leaving residual roots in the soil. Ornat et al. (1999) observed a slighter decline in the *Meloidogyne* populations (about 25%) after pulling out the roots of French beans and allowing a two-month fallow, compared to leaving the crop roots in place during the same fallow.

Weed control: A wide range of weeds associated with vegetable crops are excellent hosts for *Meloidogyne* species (Bélair and Benoit, 1996; Rich et al., 2009). Therefore, exclusion of those weeds can efficiently prevent nematode infestation. Noling and Gilreath (2002) considered that controlling *Amaranthus* spp. was essential for limiting a nematode population, because that species is a very good host for root-knot nematodes. Schroeder et al. (1993) showed that when weeds were not controlled in fallows, nematode population levels increased. Kutywayo and Been (2006) and Rich et al. (2009) indicated that inadequate weed control may even counteract nematode control strategies, like fallows and resistant crops.

Escape cropping: Nematode damage can be reduced by growing crops at periods that are not favorable for nematode growth (Bridge, 1996). Low temperatures increase nematode life cycle duration and reduce reproduction and hatching; thus, sensitive vegetable species have to be cropped in the coldest period tolerable. For example, in California, a delay in carrot sowing for a few weeks enabled cropping in infected soils without yield losses (Roberts, 1993). In Spain, several lettuce transplanting dates were tested in fields infested by *M. javanica* (Ornat et al., 2001). Delaying transplantation from September to October or November caused reductions in both root-galling severity (from 2.2 to 0.5 or 0.2, respectively, on a 1-10 scale) and nematode survival. Soil temperatures in November even prevented root invasion. However, these techniques are not amenable to intensive crop rotations, particularly when harvesting depends on market timing demand. Moreover, increased temperatures due to climatic changes may reduce the efficacy of this technique, because nematodes, even thermophil species, will be able to survive and reproduce in temperate winters.

2.2. Soil management

A disturbance of soil structure may have strong, long-term consequences on biological trophic networks. Three types of tillage practices have been tested and compared: conventional tillage, subsoiling and no tillage (or conservation systems). The effects were studied on specific nematode taxa and on whole communities (including global density and sometimes structure).

2.2.1. Tillage

Version définitive du manuscrit publié dans / Final version of the manuscript published in : Crop Protection, 2011, In Press. DOI: 10.1016/j.cropro.2011.04.016

In no tillage (NT) systems, the soil remains undisturbed, except the surface layer at planting. This technique increases soil organic matter, with more residues in the upper layer, and it improves the soil structure (Parmelee and Alston, 1986). In conventional tillage (CT) systems, the soil is moldboard-plowed, disked and rotary-tilled after the crop harvest. Compared to CT, NT or reduced tillage is often associated with higher microbial biomass and activity in the upper soil layers (van Diepeningen et al., 2006). The different studies have varied primarily in the crop sequences tested and in the number of years that the two tillage systems were applied: 1 year by Baird and Bernard (1984); 5 years by Parmelee and Alston (1986) and Gallaher et al. (1988); and 15 years by McSorley and Gallaher (1993). In all of these studies, tillage had very little effect on the density of most nematode genera examined. Thus, tillage effect was far less important than the effect of crop sequence. Furthermore, Lenz and Eisenbeis (2000) observed that various tillage treatments (with a cultivator or a two-layer plow) affected both the structural (taxonomic) and functional (trophic group, life strategy) characteristics of nematode communities; the density of plant-parasitic nematodes was reduced after tillage, and the populations of bacterivorous and fungivorous nematodes was increased (Freckman and Ettema, 1993).

2.2.2. Subsoiling

Subsoiling is relatively disruptive. It is typically used for restoring water and nutrient uptake of cropped plants, but its effects on nematode density is questionable. Rich et al. (1986) examined whether it affected soils with a compacted layer that inhibited root penetration to the deeper soil stratum. Because tillage pans limited root penetration into the soil profile, plant-parasitic nematodes were confined mainly to the soil layer above the compacted zone. Subsoiling slightly increased the total number of nematodes, but it changed the distribution of plant roots and nematodes that moved deeper. Subsoiling had a positive effect on plant growth, but this was attributed to improved root functions and water supply, rather than to a reduction of nematode infection.

In conclusion, tillage does not appear to efficiently control plant-parasitic nematodes. Most of the experiments showed a limited impact of tillage on nematode densities, or the effects were temporary and varying over time.

2.3. Organic amendments

A long tradition of research studies have evaluated whether plant-parasitic nematodes could be controlled by adding organic matter to soil. However, “organic amendment” is polysemic; it covers several sources and products, including animal manures (poultry, cattle), green manures from cover crops or crop residues, industrial wastes (oil seed cakes), or town wastes; they have or have not been composted, and they have or do not have a particular biocide activity; some are applied on top of the soil as mulches and others are incorporated into the soil. For example, neem (*Azadirachta indica*) can be used either as a green manure, by incorporating the leaf into the soil, as an oil cake or as an extract for biological control (Akhtar and Malik, 2000; Oka, 2010). The mechanisms of action for these products are not always clear, and application modalities are often empirical. Three major biological processes are involved in their mechanism of action against nematodes (Bridge, 1996; Oka, 2010):

- They improve the soil capacity for holding nutrients and water, which improves plant vigor and therefore, increases plant tolerance to nematodes.

- They release specific compounds that may be nematicidal.

- They stimulate microbial activities in the soil (including nematode antagonists), and indirectly, they stimulate nematode predators and parasites that depend on microbial activities (e.g., micro-arthropods, nematophagous fungi, parasitic bacteria). This topic is analyzed in part 2.5 in relation to biological control.

Many previous reviews have focused on the use of organic amendments to control plant-parasitic nematodes (Rodríguez-Kábana, 1986; D'Addabbo, 1995; Akhtar and Malik, 2000; Oka, 2010; Thoden et al., 2011). Farm manure trials have frequently involved poultry or cattle litter. Poultry litter appeared to be an appropriate choice (Gamliel and Stapleton, 1993), especially when combined with sorghum cover crop (Everts et al., 2006), but it may be phytotoxic at high dosages (Kaplan and Noe, 1993). Alternatively, Djian-Caporalino et al. (2002) identified 39 species of green manures that belong to 22 botanical families, including peanut (*Arachis hypogeae*), basil (*Ocimum basilicum*), cotton (*Gossypium hirsutum*), sesame (*Sesamum orientale*), oat (*Avena sativa)*, and rye (*Secale cereale*). But the most efficient were sudangrass and sorghum (*Sorghum sudanense*), cruciferae, like oil radish (*Raphanus sativus*) and rapeseed (*Brassica napus*), ricin (*Ricinus communis*), marigold (*Tagetes erecta*, *T. patula,* *T. minuta*), and velvet bean (*Mucuna deeringiana*) (Crow et al., 1996; Bridge, 1996; Al-Rehiayani and Hafez, 1998; Widmer and Abawi, 2002; Everts et al., 2006). The use of yard waste compost gave contradictory results: McSorley and Gallaher (1995) found no effect on nematode density, but Chellemi (2006) found significant inhibiting effects. Oil cakes are usually considered good for controlling nematodes. Akhtar and Malik (2000) repeatedly tested neem (*Azadirachta indica*) oil cake, and found that it is particularly efficient against root-knot nematodes even at low dosages (1 to 2 t/ha). Several studies reported that neem oil cake applications reduced the *Meloidogyne* spp. population to half the density (Akhtar, 1998); this was associated with an increase of predator and free-living nematodes. Chen et al. (2000) observed that, when industrial wastes, like brewery compost or wheat mash, were added to field microplot tests, it caused a sharp decrease in lettuce root galling and in *M. hapla* egg production.

Although the efficacy of these products under controlled conditions is commonly recognized, results in field conditions are rather inconsistent (Abawi and Widmer, 2000); for example, some experiments showed no significant effect of compost on nematode control (Szczech et al., 1993; McSorley et al., 1997). Thoden et al. (2011) even reviewed several studies in which root-knot nematode populations were increased after the application of organic amendment. This gave rise to the hypothesis that the interactions between several factors may contribute to the results, including:

- The dosages of organic amendment and the number of application years,
- The chemical characteristics of different products,
- The soil infestation level and the nematode community structures.

2.3.1. Dosages of organic amendment and number of application years

In the literature, the tested dosages of organic amendment varied from 1 to 269 t/ha (McSorley and Gallaher, 1995), but most dosages ranged from 1 to 20 t/ha. Increasing dosages of organic amendment typically increased its efficiency in nematode control, up to a level where phytotoxicity was observed. Kaplan and Noe (1993) tested five dosages of poultry litter (10 to 45 t/ha), and found an inverse relationship between dosage and both the total number of *M. arenaria* in tomato roots and the quantity of eggs in soil. Crow et al. (1996) compared three dosages of rapeseed green manure. A 14 t/ha dosage (dry weight) reduced root galling on the subsequent squash crop, without any effect on yield. At higher dosages (21 and 28 t/ha), root-galling was suppressed, but yield was decreased due to phytotoxicity. These phytotoxic effects were obviated when a two-week delay was applied between green manure application and squash planting. But Everts et al. (2006) comparing 2 dosages of poultry litter (2.8 and 8.2 t/ha) and 2 dosages of poultry litter compost (11.7 and 35 t/ha) did not find a systematically improved control for high dosages.

Moreover, some trials indicated that the nematicidal effects were cumulative over time. For example, a single sudangrass cover crop cycle did not control *M. hapla* populations, while two and three annual crop cycles provided efficient control (Viaene and Abawi, 1998b). McSorley and Gallaher (1996) tested the long-term effects of yard waste composts on nematode populations in maize. They confirmed that the nematotoxicity produced by the first amendment was insufficient to suppress the *Meloidogyne* population, but after several amendment applications, a significant control effect was observed.

2.3.2. Chemical characteristics of different products

Release of nematotoxic compounds. Nematode suppressive effects have been attributed to the release of nematicidal products during amendment decomposition in soil. For example, decomposition of sudangrass, castor bean, neem, sunn hemp and *Tagetes* spp. released the cyanoglycoside dhurrin, which can be hydrolyzed to hydrogen cyanide (Widmer and Abawi, 2000); ricin molecule (Rich et al., 1989); limonoids, phenols, and tannins (Viaene and Abawi, 1998b; Akhtar and Malik, 2000); monocrotaline and pyrrolizidine alkaloids (Rich and Rahi, 1995); and α-terthienyl (Barker and Koenning, 1998), respectively.

The highly variable results of these compounds may be explained, in part, by the relative efficacy of the different compounds; but also, by the variations in concentration during the decomposition process. For example, green manures based on cyanogenic plants (like sudangrass) showed a negative relationship between the concentration of hydrogen cyanide (HCN) and root galling. However, the soil and plant concentration ratios were not constant (Widmer and Abawi, 2002), probably due to the cultivars used and the burying conditions of the green manure. The sudangrass cultivar frequently used by market-gardeners in European areas (Piper) was first selected for animal fodder, with a low level of HCN (American Genetics, 2000; Myers and Fry, 1978). Because HCN is volatile, the slow release of HCN may be insufficient, in some cases, to affect nematode eggs.

Similarly, Brassica green manures are known for limiting reproduction of nematodes, because once chopped and incorporated into the soil they produce glucosinolates, a process called biofumigation (Ploeg, 2007). But a large variability in efficiency is observed. Zasada et al. (2003) consider it is due to several agronomical factors such as the variability in cultivars and their relative concentration in glucosinolates, the stage of development of the crop when chopped, soil type, temperature and moisture when incorporated into the soil. Monfort et al. (2007) also identified a great variability among and within Brassica species on *Meloidogyne* control effects under plastic shelters. They clearly demonstrated that net efficiency of a Brassica cover crop depends on the difference between (i) the decrease in *Meloidogyne* population due to the biofumigation process and (ii) its increase while Brassica species is cropped because most of them are host for nematodes.

Physiological stages of the incorporated plant tissues. Viaene and Abawi (1998b) compared the effects of three sudangrass amendments produced from 1-3-month old crops. All plant parts of sudangrass, except for the seeds, contained nematotoxic compounds, but the amount of hydrogen cyanide due to dhurrin decomposition was reported to decrease with plant-growth and maturity. That explained the finding that the incorporation of young sudangrass crops (< 2-months old) was more effective than the incorporation of older crops for suppressing nematode disease (*M. hapla*) on subsequent lettuce plants.

Compost maturity and decomposition stage of organic matter. Well-decomposed composts are stable and mineralize slowly. This provides a regular supply of nutrients over a long period of time (Widmer and Abawi, 2002). However, this slow release of nematicidal

Version définitive du manuscrit publié dans / Final version of the manuscript published in : Crop Protection, 2011, In Press. DOI: 10.1016/j.cropro.2011.04.016

products may result in concentrations that are too low to be effective (Akhtar and Malik, 2000). Therefore, less stable composts would probably be more efficient, because toxic compounds could quickly reach the toxicity threshold required to control nematodes. Nahar et al. (2006) proposed that raw manures may be more effective than composted manures, because they could reduce nematode populations and simultaneously increase beneficial species and microbial activities. The drawback to that approach is that fresh organic matter may introduce pathogens (especially fungi) and temporarily increase other soil-borne diseases (van Bruggen and Termorshuizen, 2003).

C/N ratios of the organic amendment. Mian and Rodríguez-Kábana (1982) reported that the nematode management potential of an organic amendment is directly related to its nitrogen (N) content. Soil amendments with low carbon:nitrogen (C/N) ratios (e.g., animal manures, oilcakes, and green manures) exhibit high nematicidal activity (Lazarovits et al., 2001; Oka, 2010). This phenomenon is attributed to the release of ammonia during the decomposition of the amendment in soil (Rodríguez-Kábana, 1986; Rodríguez-Kábana et al., 1987; Spiegel et al., 1987; Oka et al., 1993). But for very low C/N amendments, phytotoxicity problems occur and may be responsible for subsequent limited crop growth. On the other hand, composts with C/N ratios above 20 (grassy hay, stubbles, and cellulosic materials, like paper and sawdust) enhance N immobilization by enhancing microflora growth (Akhtar and Malik, 2000; Widmer and Abawi, 2002).Therefore Rodríguez-Kábana et al. (1987) considered that organic amendments with C/N ratios between 12 and 20, would both enable nematicidal activity and avoid phytotoxicity. The incorporation of chicken litter with urban plant debris (Chellemi, 2006) and olive pomace (Marull et al., 1997; D'Addabbo et al., 2003) limited the phytotoxicity, enhanced microbial activity and controlled the nematode population better than any treatment alone.

2.3.3. Soil infestation level and nematode community structures

Wang et al. (2004) observed that sunn hemp (*Crotalaria juncea*) residues, applied just before planting, could effectively reduce soil populations of *M. incognita* and yellow squash root-galling at low inoculum levels. However, the organic amendment had no effect at higher levels of nematode populations, and actually resulted in higher numbers of juveniles than in soils without amendments. Furthermore, it was observed that the efficiency of green manures depended on either the *Crotalaria* species or the plant tissue from which they were derived (Jourand et al., 2004a, 2004b).

Thoden et al. (2011) assume that the variability in control efficiency of organic amendments could be mainly due to interactions with the microbial populations preexisting in the soil, and in particular free-living nematodes: they could foster plant growth and vitality, and plants would in turn become less susceptible to root-knot nematodes.

In conclusion, organic amendments may have nematode suppressive effects, depending on many interactions, including the type of compounds released, the dosages, the soil characteristics, and the level of nematode population. Moreover, nematode control requires a large amount of organic amendment (several t/ha), and therefore, it is quite expensive (Noling and Becker, 1994). Thus, this technique is relatively difficult to implement, and is probably best used as a preventive measure in global strategies to maintain soil fertility and soil health, rather than as a curative technique to control existing nematodes.

2.4. Fertilization

Fertilization includes both organic and inorganic amendments. Organic amendments have been reviewed previously; thus, here, we have mainly focused on inorganic fertilizers. Those that contain or release ammoniacal nitrogen are liable to control nematodes

(Rodríguez-Kábana, 1986). However, the effective dosage exceeds by far that required for fertilization, and it has negative consequences on plant growth, disease sensitivity, and even on the environment. Urea additives for soil can also be converted to ammonia by ureases present in the soil (Akhtar and Malik, 2000); however, the high dosages required for consistent efficiencies on nematodes (300 kg N/ha; Rodríguez-Kábana, 1986) result in nitrate accumulation and phytotoxicity.

2.5. Biological control

Control of root-knot nematodes by natural enemies is a promising method of control. Suppressive soils are made by inoculation with specialized antagonists. High level inoculations provide immediate control (inundation strategy). Long term effects are achieved with antagonists that can colonize the soil and remain active. Nematode antagonists include fungi or bacteria that feed on or parasitize nematodes, and compounds released by organisms, like fungi and nematicidal plants. Their isolation requires, first, assessing whether the suppressive property of the soil has a biological origin. Then, the biological agents are identified and isolated from the soil. Finally, they are screened to assess their potential for nematode control (Bent et al., 2008; Kumar and Singh, 2006). This review only takes into account biological control provided by live agents applied to the soil, leaving apart the case of biological nematicides and plant extracts, for which a great number of studies are available (for example Dong and Zhang, 2006; Khan et al., 2008).

2.5.1. Nematophagous fungi

Several fungi have been identified and classified according to their nematophagous properties. They include trappers, endoparasites, egg-parasites and toxin producers (Liu et al., 2009). The most frequently studied nematode-trapping fungi are *Arthrobotrys* spp. and *Monacrosporium* spp., which trap nematodes in constricting rings and adhesive nets, respectively (Duponnois et al., 1998; Stirling and Smith, 1998; Stirling et al., 1998; Viaene and Abawi, 1998a; Duponnois et al., 2001; Kumar and Singh, 2006; Thakur and Devi, 2007). These fungi naturally occur in soils at low concentrations, and they predate only very specific nematode species, which limits their potential use. The recognition mechanism involves the association between a lectin secreted by the fungus and a carbohydrate secreted by the nematode cuticle (Nordbring-Hertz and Mattiasson, 1979). They have been shown to predate the root-knot nematode species that most frequently affects vegetable crops, including *M. incognita* (Duponnois et al*.*, 1996; Kumar and Singh, 2006; Thakur and Devi, 2007), *M. javanica* (Khan et al., 2006), and *M. hapla* (Viaene and Abawi, 1998a).

Egg-parasitic fungi include *Paecilomyces*, *Pochonia* and *Verticilium* genera. *Paecilomyces lilacinus* and *Pochonia chlamydosporia* are probably the most effective egg-parasites. *Paecilomyces lilacinus* has been proven to successfully control root-knot nematodes, *M. javanica* and *M. incognita* on tomato, egg-plant and other vegetable crops (Verdejo-Lucas et al., 2003; Goswami and Mittal, 2004; van Damme et al., 2005; Goswami et al., 2006; Haseeb and Kumar, 2006; Kumar et al., 2009). *Paecilomyces lilacinus* formulations have been homologated in many countries for vegetables and other crops, including coffee and banana. However, *P. lilacinus* appears to be more suited to tropical conditions (Krishnamoorthi and Kumar, 2007) and acid soils close to pH 6 (Krishnamoorthi and Kumar, 2008) than to temperate or cold conditions. *Pochonia chlamydosporia* prefers mild climate and soil conditions (Atkins et al., 2003), where it occurs naturally (Bent et al., 2008). However, *P. chlamydosporia* had no effect in greenhouse experiments with tomato rotations (Tzortzakakis and Petsas, 2003) or lettuce-tomato rotations (Verdejo-Lucas et al., 2003). Those authors noted that the fungus did not colonize well and did not control the nematode population inoculated in the soil. They concluded that *P. chlamydosporia* did not hold promise as a biocontrol agent in the Mediterranean region.

Other fungi that have toxic effects on nematodes include *Aspergillus* spp. and *Trichoderma* spp. Several *Aspergillus* species (*A. niger*, *A. fumigates*, *A. terreus*) showed high toxicity against *M. incognita* juveniles (Goswami and Tiwari, 2007; Tripathi et al., 2006). *Trichoderma viride* reduced egg-hatching (Goswami and Mittal, 2004); trade formulations have also proven to be efficacious in tropical greenhouse conditions (Cuadra et al., 2008).

2.5.2. Antagonistic bacteria

Pasteuria penetrans and *Pseudomonas fluorescens* are the two most studied antagonistic bacteria. *Pasteuria penetrans* effectively parasitized *M. incognita* in rotations that included tomato, egg-plant, and beans or cabbage (Amer-Zareen et al., 2004), but its efficacy depended on cropping techniques and soil conditions. Both soil porosity and water flow (hence irrigation practices) directly affected the efficacy of *P. penetrans* by modifying the probability that the bacteria met the nematodes and attached to their cuticles. High irrigation loads or frequencies tended to wash away spores (Dabiré et al., 2005; Mateille et al., 2009). Soil texture and structure also influenced spore attachment to the nematode; sandy soils were more favorable than clay soils (Mateille et al., 1995). *Pseudomonas fluorescens* also provide effective control of root-knot nematodes on vegetable crops (Haseeb and Kumar, 2006; Krishnaveni and Subramanian, 2004; Stalin et al., 2007). *Bacillus firmus* has also shown good results; it is available as a trade product in some countries (Giannakou et al., 2007; Terefe et al., 2009). In some cases, nematophagous fungi or parasitic bacteria are associated with vesicular or arbuscular mycorrhiza (most of the *Glomus* genus), which improves their effects (Jaizme-Vega et al., 2006; Verma and Nandal, 2006; Siddiqui and Akhtar, 2008).

2.5.3. Interactions among biocontrol agents and with other soil organisms

Most studies were conducted *in vitro*, in pots, or in microcosm conditions; field trials are scarce and efficiency often inconsistent (Dong and Zhang, 2006). Field experiments are hindered by the difficulties in producing a stable, viable biocontrol formulation and achieving consistent control results across different soil and cropping conditions. For example, *P. fluorescens* showed different nematicidal activities in the presence of different *Aspergillus* species. Its activity was enhanced by *A. Niger* and reduced by *A. quadrilineatus* (Siddiqui et al., 2004). Because *Aspergillus* species are commonly found in agricultural soils, they often impede the development of bacterial biocontrol agents. Finally, fungi introduction and adaptation in soil is a challenging prospect (Cayrol et al., 1992; Stirling and Smith, 1998).

Biocontrol agent combinations have also shown varied results. For example, Rao (2007) showed that combining *P. chlamydosporia* and *P. fluorescens* improved nematode control. Several other combinations are reported in the literature, but the inconsistent results prevent drawing any strong conclusions. Interactions between biocontrol agents and organic fertilizers (green or cattle manure, compost, etc.) have also been explored. Combining neem cake or dried neem leaves amendments with *P. penetrans* gave encouraging results (Javed et al., 2008). In addition, combining the rhizobacterium, *Pseudomonas putida*, with the arbuscular mycorrhizal fungus, *Glomus intraradices*, and neem leaf litter provided good control of *M. incognita* on tomato crops (Siddiqui and Akhtar, 2008). Replacing neem leaf litter with horse manure reduced the effects. Animal manure, particularly poultry and, to a lesser extent goat, combined with *P. fluorescens* also gave good results on tomatoes (Siddiqui, 2004). In order to increase biocontrol efficiency, Dong and Zhang (2006) advocate integrating biocontrol with other cultural methods through multidisciplinary studies.

It should be noted that most studies on nematode biocontrol with single or combined agents, alone or associated with other cropping techniques, were carried out in warm countries (India, Pakistan, Israel), where soil conditions (physico-chemical and climatic) differ from those encountered in temperate regions (Europe, Northern America). This may contribute to the high variability in the results.

Currently, very few bacterial control agents have been registered as plant protection products, partly due to their variable efficacy, but also due to different national regulations concerning the use of living organisms. Most are registered as fertilizers or plant growth promoters, with the argument that they enhance crop growth and yield (either by depleting root-knot nematodes or by associating with mycorrhiza).

2.6. Heat-based methods

Heat can efficiently kill nematodes (and other pests or pathogens). There are two main heat-based techniques. First, soil can be injected with steam; second, solar heat can be captured to increase the soil temperature (solarization).

2.6.1. Steaming

Steaming the soil is similar to sterilization, rather than disinfestation. It kills most of the microorganisms in the heated layers of the soils, including pests and beneficial agents (Katan, 2000). The efficiency depends on soil preparation. The soil must achieve high porosity to allow deep penetration of the steam (20 cm or more). Steam application requires a boiler and an injection device. Steam can be injected under a fleece placed on the soil, which allows large areas to be treated at once (up to 400 m²); with 4 to 5-h applications, the 20 to 30-cm soil layer can be heated to over 80 °C (Le Bohec et al., 1999). An alternative to fleece is injecting steam under a solid hood placed on the soil. Smaller areas are treated in each application with the hood, but it is not necessary to lock down the sides of the hood with weights or soil to ensure sealing (Gay et al., 2010). A negative pressure technique provides better results; this forces the steam to enter into the soil (Runia, 1984). Negative pressure is achieved by sucking the air out of the soil through perforated pipes that are connected to a fan. The pipes are permanently installed under the field, at about 60 cm deep for protection from plowing damage. With this method, the heat penetrates to a deeper layer, close to the depth at which the pipes are buried. Finally, sandwich steaming is a recent technique, where the steam is injected from both above and within the soil. It requires a large device which is unsuitable for greenhouses.

Few experiments have been conducted to assess the specific effects on nematodes, most of them dealing on weeds and fungi. Reuven et al. (2005) applied steam at 100 °C for 1 h with a negative pressure system. They observed a moderate decrease in root galling on flower crops (carnation), but largely insufficient to limit yield decrease. On the contrary, nematode population decrease was higher in Dutch experiments, where steam at 160 °C was blown in the soil until 25-30 cm (Runia and Greenberger, 2005). These authors also compared steam and hot air application treatment, for which temperature was sublethal and therefore less efficient that steam itself. Moreover as steaming indifferently kills micro-organisms (including non-pathogen ones), it is likely to reduce natural biocontrol processes, as shown by McSorley et al. (2006). Steaming results in water-saturated soil; this may promote soil compaction, increases nitrogen mineralization, and added water may result in nutrient washing. Organic manure or amendments must be incorporated into the soil long before the application of steam.

2.6.2. Solarization

Solarization traps solar radiation with transparent plastic films placed on the soil to maximize conversion and conservation of heat. First reported by Katan et al. (1976), solarization has been widely studied. Solarization increases soil temperature by 2 to 15 °C in warm climate conditions. Its efficacy depends on the combination of soil temperature and duration. *M. incognita* second-stage juveniles were completely killed in a water bath heated above 38 °C; it took 48 h at 39 °C, but only 14 h at 42 °C (Wang and McSorley, 2008). However, temperature alone is an inappropriate measure for efficacy. The degree-day is the appropriate measure. Over 75 degree-days were needed to kill all nematodes at 39 or 40 °C, but only 24 degree-days were needed at 43 °C. Furthermore, killing eggs was equivalent to killing juveniles at 42 or 43 °C, but eggs were more resistant to low temperatures; thus, eggs required 267 degree-days at 39°C (Wang and McSorley, 2008). To achieve the required combinations of soil temperature and duration, solarization must be applied for several weeks during the period of maximum solar radiation. In a Mediterranean climate, solarization should be started in mid-June to July and maintained for at least 5-6 weeks. These conditions can achieve soil temperatures above 45 °C for long time periods. It is important to use film with the appropriate physical properties, and to enhance soil thermal conductivity prior to solarization, with irrigation and tillage to avoid compaction (Scopa et al., 2008; Le Bohec et al., 1999).

Solarization generally holds promise for controlling root-knot nematodes (Gamliel and Stapleton, 1993; Ozores-Hampton et al., 2004; Ozores-Hampton et al., 2005), but failures have also been reported (Chellemi, 2002). Failures are primarily due to (i) the higher resistance of nematode eggs to heat treatments, (ii) the dependence of soil temperatures on both the state of the soil and the climate conditions during the solarization period, and (iii) the fact that the soil can be re-infested after solarization. In the latter case, nematodes may migrate from deeper layers, either due to deep tillage practices, which inverts the soil layers, or due to the gradual, long-term movement of nematodes.

3. Towards a systemic agro-ecological approach

Our analysis found that most techniques listed had a partial effect on nematode control. Currently, these alternative techniques are difficult to promote in intensive western agriculture, because farmers can and do compare it to chemical efficiency. Moreover, there is great variability in efficiency among studies, due to several factors. Those that depend on practical modalities (e.g., organic amendment rates, maximum temperatures achieved in solarization, etc.) have been highlighted above. Others include soil and climate conditions. For example, clay soils offer poor conditions for the development of nematodes (Mateille et al., 1995; Barker and Koenning, 1998). Consequently, the effect of any particular technique probably depends on the ratio between clay and sand in the soil, which is not always reported. In addition, soil types differ among regions. For example, African soil differs from Indian or Pakistanese soil, in part due to climate differences, but also due to the cultivation history and the micro-organisms promoted by those cropping systems. Moreover, temperature and humidity greatly affect the development of nematodes. This should be taken into account when comparing results reported in tropical, Mediterranean, and temperate areas.

However, the main problems arise from underestimating the interactions within a soil system, among techniques, and among micro-organisms (pathogenic and otherwise) and consequently the lack of studies conducted to assess them.

3.1. Interactions between techniques: a key factor in nematode management

There are four main processes for controlling root-knot nematodes (Fig. 1):

- Killing nematodes in the soil with thermal or chemical agents
- Breaking the nematode biological cycle to limit female reproduction potential or delay reproduction sequences
- Enhancing the competitions from other micro-organisms in the soil to reduce nematode populations by predation, trophic competition, or parasitism
- Limiting dissemination from a contaminated to an uncontaminated area.

Understanding the variability among studies is difficult, because, as shown in Fig. 1, several techniques may contribute to the same process, and a single technique may contribute to several different processes. As an example of the first case, killing nematodes can be achieved by different techniques, alone or concurrently (Fig. 1): solarization or steaming (thermal effects), biocontrol or nematicidal products (nematicidal oil-cakes, chemicals, natural or not). Conversely, green manure affects multiple processes; it may have a biocidal effect once buried, it may break the biological cycle of the nematodes if a non-host or resistant species is chosen and it enhances the competition by providing new organisms and feeding those present in soil (Fig. 1). However, green manure may also have a negative effect on nematode levels by enabling root-galling during cropping. For example, sorghum, generally considered as non-host, can increase root-gall occurrences in heavily infested soils. Therefore, the resultant effects will depend on the balance between the intensity of these contradictory processes. It can be noted that while many techniques contribute to killing nematodes, fewer are available for alternative ways of control (Fig. 1).

Numerous authors have recognized the advantages of combining several cropping techniques or biological processes to improve results (Lewis et al., 1997; Chellemi, 2002; Litterick et al., 2004). A typical example of additive effects between two techniques is the combination of solarization and green manure. Blok et al. (2000) showed that it combined the thermal effects of solarization and the anaerobic reducing effects of organic amendment. They demonstrated that these synergistic effects were quite efficient against soil-borne fungi. Gamliel and Stapleton (1993) and Oka et al. (2007) found that the combination reduced nematode populations and galling indices in conditions that were not effectively controlled by solarization or organic amendment alone. Another approach is to organize the actions of different techniques by combining short and long-term effects (Roberts, 1993). The short term aim should be to limit plant infestation by temporarily reducing nematode numbers in the soil before planting and reducing their infectivity before growing with resistant or tolerant cultivars. The long term aim should be to reduce the multiplication rate of nematodes on each crop, even partially; this will have beneficial effects on the succeeding crops, and therefore, in the long-term.

Combining techniques does not necessarily lead to synergistic effects, and complex interactions can occur. Therefore, it may be appropriate to rethink the whole system instead of trying to control it with a single action. Along these lines, we advocate systemic agronomic research (Lewis et al., 1997), which aims to rebuild cropping systems as a whole and formulate cropping systems that naturally limit the increase of pathogens, rather than sticking to the therapeutic paradigm.

Identifying the most promising combinations is the key. To date, few operational propositions have been made that efficiently control nematodes in vegetable production. Most rely on advisory services and local experimentation. For example, Melton (1995), in North Carolina, built an efficient cropping system based on host resistance, crop rotation, residual root destruction immediately after harvest, and cover cropping; Arrufat and Dubois (2006) in Southeast France, found satisfying long-term nematode control with a cropping system based on diversified crop sequence and solarization. But those studies appeared to be sensitive to

Version définitive du manuscrit publié dans / Final version of the manuscript published in : Crop Protection, 2011, In Press. DOI: 10.1016/j.cropro.2011.04.016

local soil or climate characteristics. It would be interesting to compare all the "success stories" and assess their generalizability; i.e. identify the soil, climate, cropping history, etc. that would respond to those combinations. To that end, the French PicLeg initiative (http://www.picleg.fr/) formed an experimental network, which aims to organize and analyze several experiments on cropping systems in various regions and soil types.

3.2. Soil biodiversity and trophic networks: another key factor for nematode management

Recently, Mateille et al. (2008) pointed out that control practices, included or not in integrated pest management strategies, all target some nematode species (population approach), and then involve changes in nematode communities, but do not necessarily modify their overall pathogenicity. They induce biotic gaps, community rearrangements, insurgence of virulent races, increased aggressiveness of minor species, etc. However, in practice, the elimination of root-knot nematodes does not prevent another nematode species from becoming pathogenic. Thus, "soil cleaning" strategies do not appear to be sustainable.

Brussaard et al. (2007) studied the different agricultural management practices that affect soil and noted their effects on soil microbial and fauna activities. They showed that most beneficial practices, i.e. organic amendments, green manure, fertilization, tillage, crop rotation and crop sequences, could directly and/or indirectly influence soil animal populations positively and/or negatively. Van Diepeningen et al. (2006) compared soils in 27 Dutch farms, half organic and half conventional, and concluded that most soil chemical and physical characteristics were not significantly different; however, greater biological activity was observed in organically managed compared to conventionally managed soils, especially nematode diversity. Nevertheless, van Bruggen and Termorshuizen (2003) suggested that increased microbial activity in organic systems did not necessarily provide control of root-knot nematodes.

Version définitive du manuscrit publié dans / Final version of the manuscript published in : Crop Protection, 2011, In Press. DOI: 10.1016/j.cropro.2011.04.016

Some variability in the effects of different techniques (e.g. organic amendment) may arise from differences in micro-organism competition. Thus, despite quite good efficiency under controlled conditions, biocontrol may not operate in the field. The added micro-organisms may not survive in field soil, they may be unable to adequately reproduce, or the competition may be too strong. For example, Siddiqui et al. (2004) showed that a potential cause of variability in nematode control at the field level was due to interactions between *P. fluorescens* and *Aspergillus* species.

Soil biodiversity may not systematically confer protection against soil-borne diseases, but it is always associated with better soil health, and therefore, it provides stability against stress and disturbances. It may be possible to manage soil biodiversity (Brussaard et al., 2007), as proposed for above-ground biodiversity (Altieri, 1999), to control pathogenic populations. Mateille et al. (2008) advised that studies on plant-nematode relationships should extend to ecological investigations on nematode communities for biodiversity management.

3.3. Towards more sustainable systems

The alternative methods we have reviewed focused on nematode control. However, many of these techniques also modify soil functions that affect soil fertility, nutrient supply, soil structure, soil health, etc. Therefore, when these techniques are introduced into a cropping system these interactions should be taken into consideration throughout the cropping system cycle. Fig. 2 shows a typical crop sequence for market garden vegetable production in the Mediterranean. As can be seen, organic amendment (whether green manure or not) interacts with fertilization, but also with heat-based techniques because of the increased organic matter decomposition induced by the increase in soil temperature. Fig. 2 also shows that escape cropping, if implemented by delaying the plantation date of crop 2, is incompatible with crop 3 unless the spring crop (crop 1) plantation date can be postponed. Management techniques

Version définitive du manuscrit publié dans / Final version of the manuscript published in : Crop Protection, 2011, In Press. DOI: 10.1016/j.cropro.2011.04.016

requiring time (flooding, 8 weeks; green manure, about 8 weeks; solarization, at least 6 weeks) often conflict with the crop sequence too (Fig. 2). The introduction of the management techniques reviewed here in the current cropping system therefore requires to analyze these potential conflicts and may lead to drastic changes in the cropping system, which we analyze now.

3.3.1. Nutrient cycle

In particular, soil nutrient cycle is strongly affected by organic amendments, green manure incorporation, and heat treatments. Organic amendments and green manure enrich the soil in organic compounds, and mineralization provides necessary nutrients (N, among others) to the crop. However, mineralization results from microorganisms feeding on organic compounds; therefore, it depends on the abundance and activity of microorganisms. Heat treatments have a double effect; they modify the total biotic population (and its composition), and they increase the microbial activity (mineralization doubles with every 10 °C increase, Dessureault-Rompre et al., 2010). Therefore, it is necessary to consider these effects when planning crop fertilization after organic amendments, green manure, and heat treatments. Because mineralization depends on soil temperature, climate also plays a role by modifying soil temperature. Organic amendment and green manure also modify the structure of the soil (as do tillage and subsoiling); thus, they can alter soil porosity and water transfer properties. Therefore, they should be taken into account when designing irrigation.

3.3.2. Soil health

Plant production is directly related to soil quality, which is defined by its functional capacity within an ecosystem in terms of biological productivity, environmental quality, and plant health (Doran et al., 1996). Soil quality is based on its physical, chemical, and biological properties. Soil biological properties include (Doran and Zeiss, 2000) fertility, health, environmental impact, and resilience. Soil health is related to its ecological characteristics (Doran and Zeiss, 2000) and deals with agronomy (Doran and Safley, 1997). Good soil health is usually correlated with fast nutrient cycles, strong stability (high resistance or resilience), and broad biodiversity. Based on these complex soil properties and interactions, the development of sustainable management strategies must move to a systemic approach that can lead to global nematode suppression indicators (Ferris et al., 2001; Neher, 2001; Nahar et al., 2006). Thus, the future challenge for nematode management is to link above-ground effect traits to below-ground response traits. From an experimental point of view, this will require the establishment of (1) observation plots in crop production systems with specific ecological and agronomical characteristics and specific crop practices. Then, (2) appropriate trials and comparisons of different practices can be performed.

3.3.3. New cropping systems: substitution or system redesign?

Alternative techniques for cropping systems can be classified according to their consequences on the design of the cropping systems, along the conceptual framework proposed by Hill and MacRae (1995). According to these authors, transitions towards sustainable agriculture can be categorized by three levels: Efficiency (increases over current practices), Substitution (replacement of chemicals by natural products), and Redesign (modifying the cropping system to confer resistant properties). Less disruptive methods include replacements for fumigants and other nematicide formulations that were or are currently available. This category includes thermal disinfection by steam, organic amendment, nematicidal plant fungus and bacterium extracts, and biological control. It can be completed with the use of plant resistance, which may then be used less systematically, a possible way to lessen the probability of resistance breakdown by pathogens. These methods are not too complicate to introduce because the applications are instantaneous. In contrast, many other techniques would create new constraints within the cropping system. Some have consequences on the rotation design because they replace a cash crop, like nematicidal green manure or solarization, which are typically applied instead of planting summer crops. Other techniques change the organization of the rotation, but not the range of the species cropped; for example, escape cropping or selecting non-susceptible, resistant, or tolerant rootstocks. However, these constraints may be more or less troublesome depending on the type of farm. Replacing or shortening the cultivation of a spring cash crop with a green manure or thermal disinfection by solarization is less disruptive than altering the cultivation of a summer crop. In that case, Navarrete at al. (2006) showed that solarization led to summer crop abandonment and increased farm specialization. In contrast, a redesign of the whole rotation to introduce a combination of techniques and increased crop diversity with various sensitivities or resistances to pests and diseases will cause much larger changes at the farm scale because new markets must be found (Navarrete, 2009).

The complexity of these interactions and the multidimensional nature of their consequences suggest that models will be required to support the redesign of sustainable cropping systems. These models can simulate population dynamics or directly perform a multiple criteria evaluation. Therefore, we have initiated a research project with the aim of promoting the introduction of these techniques into the redesign of cropping systems (Navarrete et al., 2010). Two steps are necessary; first, designing a model to assess the resistance or resilience of a given cropping system to soil-borne pests (Tchamitchian et al., 2009); second, using the model in cooperation with advisers and farmers in order to build alternative cropping and farming systems that take into account a new nematode management paradigm and the farm constraints (resource availability, marketing environment, etc.). Furthermore, this cooperation will promote new ways of thinking that do not require

Version définitive du manuscrit publié dans / Final version of the manuscript published in : Crop Protection, 2011, In Press. DOI: 10.1016/j.cropro.2011.04.016

pesticides or similar eradication techniques, but rather, are based on the prevention of the appearance, expansion, or dissemination of pests.

4. Conclusion

This review covers the findings and controversies surrounding the effects of alternative pest control techniques, including sanitation, soil management, organic amendments, fertilization, biological control and heat-based methods. Most of these alternative techniques only partially control nematode infestations, and they have consequences on other soil functions or services (fertility, structure, water retention, etc.). We identified two directions for controlling nematodes in the future. First, improving the current conception of pest management, which relies on external inputs to control pest population. This method depends on finding new nematicidal products, preferably of natural origin or inspiration (plant extracts; biological control). The second method, although more complicated, is probably more promising; it consists of designing cropping systems with intrinsic properties that maintain the nematode population below a threshold of acceptable impact. It will take advantage of interactions between different techniques, and different organisms to address the aims of the cropping systems, including pathogen control, soil health and the nutrient cycle. Adapting cropping systems to each soil type (in particular its chemical and biological characteristics, its level of inoculum) will become a key question, which requires systemic studies to build soil health indicators. Unfortunately, western agriculture is probably not currently ready for this approach. However, interest in this method may increase as chemical solutions disappear and synergistic combinations are discovered that increase their efficiency. This holistic approach is required to redesign the cropping systems according to the goals of production, pest management, and other services, like environmental preservation.

Acknowledgements

This work has been supported by 1/INRA with a project on integrated production of vegetable crops (PIClég_), acronym Neoleg2, and 2/ the French National Research Agency with a project on Ecosystems, living resources, landscapes and agriculture (Systerra), acronym Sysbiotel (01/2009-01/20013).

References

Abawi, G.S., Widmer, T.L., 2000. Impact of soil health management practices on soilborne pathogens, nematodes and root diseases of vegetable crops. Appl. Soil Ecol. 15, 37-47.

Akhtar, M., 1998. Biological control of plant-parasitic nematodes by neem products in agricultural soil. Appl. Soil Ecol. 7, 219-223.

Akhtar, M., Malik, A., 2000. Roles of organic soil amendments and soil organisms in the biological control of plant-parasitic nematodes: a review. Bioresour. Technol. 74, 35-47.

Al-Rehiayani, S., Hafez, S., 1998. Host status and green manure effect of selected crops on *Meloidogyne chitwoodi* race 2 and *Pratylenchus neglectus*. Nematropica 28, 213-230.

Altieri, M.A., 1999. The ecological role of biodiversity in agroecosystems. Agric. Ecosyst. Environ. 74, 19-31.

Amer-Zareen, Z.M.J., Abid, M., Gowen, S.R., Kerry, B.R., 2004. Management of root knot nematode (*Meloidogyne javanica*) by biocontrol agents in two crop rotations. Int. J. Biol. Biotechnol. 1, 67-73.

American Genetics Inc., 2000. Piper Sudangrass. http://www.americangeneticsinc.com/54304F3A.en.aspx (Last visit on Dec. 2010).

Arrufat, A., Dubois, M., 2006. Prévention contre les pathogènes du sol en culture sous abris : rotations, engrais verts, solarisation. Alter. Agri. 77, 13-15.

Atkins, S.D., Hidalgo-Diaz, L., Kalisz, H., Mauchline, T.H., Hirsch, P.R., Kerry, B.R., 2003. Development of a new management strategy for the control of root-knot nematodes (Meloidogyne spp) in organic vegetable production. Pest Manag. Sci. 59, 183-189.

Aubertot, J.-N., West, J.S., Bousset-Vaslin, L., Salam, M.U., Barbetti, M.J., Diggle, A.J., 2006. Improved resistance management for durable disease control: A case study of phoma stem canker of oilseed rape (*Brassica napus*). Eur. J. Plant Pathol. 114, 91-106.

Baird, S.M., Bernard, E.C., 1984. Nematode population and community dynamics in soybean wheat cropping and tillage regimes. J. Nematol. 16, 379-386.

Barker, K.R., Koenning, S.R., 1998. Developing sustainable systems for nematode management. Annu. Rev. Phytopathol. 36, 165-205.

Bélair, G., Benoit, D.L., 1996. Host suitability of 32 common weeds to *Meloidogyne hapla* in organic soils of southwestern Quebec. J. Nematol. 28, 643-647.

Bent, E., Loffredo, A., McKenry, M.V., Becker, J.O., Borneman, J., 2008. Detection and investigation of soil biological activity against *Meloidogyne incognita*. J. Nematol. 40, 109-118.

Blok, W.J., Lamers, J.G., Termorshuizen, A.J., Bollen, G.J., 2000. Control of soilborne plant pathogens by incorporating fresh organic amendments followed by tarping. Phytopathology 90, 253-259.

Bridge, J., 1996. Nematode management in sustainable and subsistence agriculture. Annu. Rev. Phytopathol. 34, 201-225.

Brussaard, L.J., de Ruiter, P.C., Brown, G.G., 2007. Soil biodiversity for agricultural sustainability. Agric. Ecosyst. Environ. 121, 233-244.

Cayrol, J.-C., Djian-Caporalino, C., Panchaud-Mattei, E., 1992. La lutte biologique contre les Nématodes phytoparasites. Courrier Environ. 17, 31-44.

Chellemi, D.O., 2002. Nonchemical management of soilborne pests in fresh market vegetable production systems. Phytopathology 92, 1367-1372.

Chellemi, D.O., 2006. Effect of urban plant debris and soil management practices on plant parasitic nematodes, Phytophthora blight and Pythium root rot of bell pepper. Crop Prot. 25, 1109-1116.

Chen, J., Abawi, G.S., Zuckerman, B.M., 2000. Efficacy of *Bacillus thuringiensis*, *Paecilomyces marquandii* and *Streptomyces costaricanus* with and without organic amendments against *Meloidogyne hapla* infecting lettuce. J. Nematol. 43, 70-77.

Crow, W.T., Guertal, E.A., Rodríguez-Kábana, R., 1996. Responses of *Meloidogyne arenaria* and M-*incognita* to green manures and supplemental urea in glasshouse culture. J. Nematol. 28, 648-654.

Cuadra, R., Ortega, J., Morfi, O.L., Soto, L., Zayas, M. d. l.A., Perera, E., 2008. Effect of the biological controls Trifesol and Nemacid on root-knot nematodes in sheltered vegetable production. Rev. Protección Veg. 23, 59-62.

Dabiré, K.R., Ndiaye, S., Chotte, J.L., Fould, S., Diop, M.T., Mateille, T., 2005. Influence of irrigation on the distribution and control of the nematode *Meloidogyne javanica* by the biocontrol bacterium *Pasteuria penetrans* in the field. Biol. Fertil. Soils 41, 205–211.

D'Addabbo, T., 1995. The nematicidal effect of soil amendments: a review of the literature. Nematol. Medit. 23, 121-127.

D'Addabbo, T., Sasanelli, N., Lamberti, F., Greco, P., Carella, A., 2003. Olive pomace and chicken manure amendments for control of *Meloidogyne incognita* over two crop cycles. Nematropica 33, 1-7.

Dessureault-Rompre, J., Zebarth, B.J., Georgallas, A., Burton, D.L., Grant, C.A., Drury, C.F., 2010. Temperature dependence of soil nitrogen mineralization rate: Comparison of mathematical models, reference temperatures and origin of the soils. Geoderma 157, 97-108.

Djian-Caporalino, C., Bourdy, G., Cayrol, J.-C., 2002. Plantes nématicides et plantes résistantes aux nématodes. In: Regnault-Roger, C., Philogène, B.J.R., Vincent, C. (Eds.), Biopesticides d'origine végétale. Tec et Doc, Paris (FRA), pp. 187-241.

Djian-Caporalino, C., Védie, H., Arrufat, A., 2009. Gestion des nématodes à galles : lutte conventionnelle et luttes alternatives. L'atout des plantes pièges. Phytoma 624, 21-25.

Dong, L.Q., Zhang, K.Q., 2006. Microbial control of plant-parasitic nematodes: a five-party interaction. Plant Soil 288, 31-45.

Doran, J.W., Safley, M., 1997. Defining and assessing soil health and sustainable productivity, in: Pankhurst, C., Doube, B., Gupta, V. (Eds.), Biological indicators of soil health. CABI International, Wallingford, Oxon (UK), pp. 1-28.

Doran, J.W., Sarrantonio, M .and Liebig, M.A., 1996. Soil health and sustainability. Adv. Agron. 56, 1-54.

Doran, J.W., Zeiss, M.R., 2000. Soil health and sustainability: managing the biotic component of soil quality. Appl. Soil Ecol. 15, 3-11.

Duncan, L.W., 1991. Current options for nematode management. Annu. Rev. Phytopathol. 29, 469–490.

Duponnois, R., Bâ, A.M., Mateille, T., 1998. Effects of some rhizosphere bacteria for the biocontrol of nematodes of the genus *Meloidogyne* with *Arthrobotrys oligospora*. Fund. Appl. Nematol. 21, 157-163.

Duponnois, R., Chotte, J.-L., Sall, S., Cadet, P., 2001. The effects of organic amendments on the interactions between a nematophagous fungus *Arthrobotrys oligospora* and the root-knot nematode *Meloidogyne mayaguensis* parasitizing tomato plants. Biol. Fertil. Soils 34, 1-6.

Duponnois, R., Mateille, T., Sene, V., Sawadogo, A., Fargette, M., 1996. Effect of different west African species and strains of *Arthrobotrys* nematophagous fungi on *Meloidogyne* species. Entomophaga 41, 475-483.

Everts, K.L., Sardanelli, S., Kratochvil, R.J., Armentrout, D.K., Gallagher, L.E., 2006. Root-knot and root-lesion nematode suppression by cover crops, poultry litter, and poultry litter compost. Plant Dis. 90, 487-492.

Ferris, H., Bongers, T., de Goede, R.G.M., 2001. A framework for soil food web diagnostics: extension of the nematode faunal analysis concept. Appl. Soil Ecol. 18, 13-29.

Freckman, D.W., Ettema, C.H., 1993. Assessing nematode communities in agroecosystems of varying human intervention. Agric. Ecosyst. Environ. 45, 239-261.

Gallaher, R.N., Dickson, D.W., Corella, J.F., Hewlett, T.E., 1988. Tillage and multiple cropping systems and population-dynamics of phytoparasitic nematodes. Ann. Appl. Nematol. 2, 90–94.

Gamliel, A., Stapleton, J.J., 1993. Effect of chicken compost or ammonium phosphate and solarization on pathogen control, rhizosphere microorganisms, and lettuce growth. Plant Dis. 77, 886-891.

Gay, P., Piccarolo, P., Aimonino, D.R., Tortia, C., 2010. A high efficacy steam soil disinfestation system, part II: Design and testing. Biosyst. Eng. 107, 194-201.

Giannakou, I.O., Anastasiadis, I.A., Gowen, S.R., Prophetou-Athanasiadou, D.A., 2007. Effects of a non-chemical nematicide combined with soil solarization for the control of root-knot nematodes. Crop Prot. 26, 1644-1654.

Goswami, B.K., Mittal, A., 2004. Management of root-knot nematode infecting tomato by *Trichoderma viride* and *Paecilomyces lilacinus*. Indian Phytopathol. 57, 235-236.

Goswami, B.K., Pandey, R.K., Rathour, K.S., Bhattacharya, C., Singh, L., 2006. Integrated application of some compatible biocontrol agents along with mustard oil seed cake and furadan on *Meloidogyne incognita* infecting tomato plants. J. Zhejiang Univ. Sci. B 7, 873-875.

Goswami, J., Tiwari, D.D., 2007. Management of *Meloidogyne incognita* and *Fusarium oxysporum* f. sp lycopersici disease complex on tomato by *Trichoderma harzianum*, *Tinospora longifolia* and *Glomus fasciculatum*. Pestic. Res. J. 19, 51-55.

Haseeb, A., Kumar, V., 2006. Management of *Meloidogyne incognita-Fusarium solani* disease complex in brinjal by biological control agents and organic additives. Ann. Plant Protect. Sci. 14, 519-521.

Hill, S.B., MacRae, R.J., 1995. Conceptual framework for the transition from conventional to sustainable agriculture. J. Sustain. Agric. 7, 81-87.

Hugo, H.J., Malan, A.P., 2010. Occurrence and control of plant-parasitic nematodes in irrigation water – A review. S. Afr. J. Enol. Vitic. 31, 169-180.

Hunt, D.J., Handoo, Z.A., 2009. Taxonomy, identification and principal species. In: Perry, R.N., Moens, M., Starr, J.L. (Eds.), Root-knot nematodes. CABI International, Cambrige, MA (USA), pp. 55-97.

Jaizme-Vega, M.C., Rodríguez-Romero, A.S., Barroso-Nunez, L.A., 2006. Effect of the combined inoculation of arbuscular mycorrhizal fungi and plant growth-promoting rhizobacteria on papaya (*Carica papaya* L.) infected with the root-knot nematode *Meloidogyne incognita*. Fruits (Paris) 61, 151-162.

Javed, N., El-Hassan, S., Gowen, S., Pemproke, B., Inam-Ul-Haq, M., 2008. The potential of combining *Pasteuria penetrans* and neem (*Azadirachta indica*) formulations as a management system for root-knot nematodes on tomato. Eur. J. Plant Pathol. 120, 53-60.

Jourand, P., Rapior, S., Fargette, M., Mateille, T., 2004a. Nematostatic activity of aqueous extracts of West African Crotalaria species. Nematology 6, 765-771.

Jourand, P., Rapior, S., Fargette, M., Mateille, T., 2004b. Nematostatic effects of a leaf extract from *Crotalaria virgulata* subsp grantiana on *Meloidogyne incognita* and its use to protect tomato roots. Nematology 6, 79-84.

Kaplan, M., Noe, J.P., 1993. Effects of chicken-excrement amendments on *Meloidogyne arenaria*. J. Nematol. 25, 71-77.

Katan, J., 2000. Physical and cultural methods for the management of soil-borne pathogens. Crop Prot. 19, 725-731.

Katan, J., Greenberger, A., Alon, H., Grinstein, A., 1976. Solar heating by polyethylene mulching for control of diseases caused by soil-borne pathogens. Phytopathology 66, 683-688.

Khan, A., Williams, K.L., Nevalainen, H.K.M., 2006. Infection of plant-parasitic nematodes by *Paecilomyces lilacinus* and *Monacrosporium lysipagum*. Biocontrol 51, 659-678.

Khan, S.A., Javed, N., Khan, M.A., Kamran, M., Atif, H.M., 2008. Management of root knot nematode *Meloidogyne incognita* through the use of plant extracts. Pak. J. Phytopathol. 20, 214-217.

Koenning, S.R., Overstreet, C., Noling, J.W., Donald, P.A., Becker, J.O., Fortnum, B.A., 1999. Survey of crop losses in response to phytoparasitic nematodes in the United States for 1994. J. Nematol. 31, 587-618.

Krishnamoorthi, R., Kumar, S., 2007. Management of root-knot nematode, *Meloidogyne incognita* by *Paecilomyces lilacinus* - influence of soil moisture and soil temperature. Indian J. Nematol. 37, 135-137.

Krishnamoorthi, R., Kumar, S., 2008. Management of *Meloidogyne incognita* by *Paecilomyces lilacinus* - influence of soil pH and soil types. Ann. Plant Protect. Sci. 16, 263-265.

Krishnaveni, M., Subramanian, S., 2004. Evaluation of biocontrol agents for the management of *Meloidogyne incognita* on cucumber (*Cucumis sativus* L.). Curr. Nematol. 15, 33-37.

Kumar, D., Singh, K.P., 2006. Assessment of predacity and efficacy of *Arthrobotrys dactyloides* for biological control of root knot disease of tomato. J. Phytopathol. 154, 1-5.

Kumar, V., Haseeb, A., Sharma, A., 2009. Integrated management of *Meloidogyne incognita*-*Fusarium solani* disease complex of brinjal cv. Pusa Kranti. Ann. Plant Protect. Sci. 17, 192-194.

Kutywayo, V., Been, T.H., 2006. Host status of six major weeds to *Meloidogyne chitwoodi* and *Pratylenchus penetrans*, including a preliminary field survey concerning other weeds. Nematology 8, 647-657.

Lazarovits, G., Tenuta, M., Conn, K.L., 2001. Organic amendments as a disease control strategy for soilborne diseases of high-value agricultural crops. Australas. Plant Pathol. 30, 111-117.

Le Bohec, J., Giraud, M., 1999. Désinfecter les sols autrement. Ctifl, Paris (FRA).

Lenz, R., Eisenbeis, G., 2000. Short-term effects of different tillage in a sustainable farming system on nematode community structure. Biol. Fertil. Soils 31, 237-244.

Lewis, W.J., van Lenteren, J.C., Phatak, S.C., Tumlinson, J.H., 1997. A total system approach to sustainable pest management. Proc. Natl. Acad. Sci. USA 94, 12243-12248.

Litterick, A.M., Harrier, L., Wallace, P., Watson, C.A., Wood, M., 2004. The role of uncomposted materials, composts, manures, and compost extracts in reducing pest and disease incidence and severity in sustainable temperate agricultural and horticultural crop production – A review. Crit. Rev. Plant Sci. 23, 453-479.

Liu, X.-Z., Xiang, M.-C., Che, Y.-S., 2009. The living strategy of nematophagous fungi. Mycoscience 50, 20-25.

Martin, F.N., 2003. Development of alternative strategies for management of soilborne pathogens currently controlled with methyl bromide. Annu. Rev. Phytopathol. 41, 325-350.

Marull, J., Pinochet, J., Rodríguez-Kábana, R., 1997. Agricultural and municipal compost residues for control of root-knot nematodes in tomato and pepper. Compost Sci. Util. 5, 6-15.

Mateille, T., Cadet, P., Fargette, M., 2008. Control and management of plant-parasitic nematode communities in a soil conservation approach. In: Cianco, A., Mukerji, K.G. (Eds.), Integrated management and biocontrol of vegetable and grain crops nematodes. Springer, Dordrecht (NLD), (Integrated management of plant pests and diseases, vol. 2), pp. 79-97.

Mateille, T., Duponnois, R., Diop, M.T., 1995. Influence of abiotic soil factors and the host plant on the infection of photoparasitic nematodes of the genus *Meloidogyne* by the actinomycete parasitoid *Pasteuria penetrans*. Agronomie 15, 581-591.

Mateille, T., Fould, S., Dabiré, K.R., Diop, M.T., Ndiaye, S., 2009. Spatial distribution of the nematode biocontrol agent *Pasteuria penetrans* as influenced by its soil habitat. Soil Biol. Biochem. 41, 303-308.

Mateille, T., Schwey, D., Amazouz, S., 2005. Sur tomates, la cartographie des indices de galles. Phytoma 584, 40-43.

McSorley, R., Gallaher, R.N., 1993. Effect of crop-rotation and tillage on nematode densities in tropical corn. J. Nematol. 25, 814-819.

McSorley, R., Gallaher, R.N., 1995. Cultural-practices improve crop tolerance to nematodes. Nematropica 25, 53-60.

McSorley, R., Gallaher, R.N., 1996. Effect of yard waste compost on nematode densities and maize yield. J. Nematol. 28, 655-660.

McSorley, R., Stansly, P.A., Noling, J.W., Obreza, T.A., Conner, J.M., 1997. Impact of organic soil amendments and fumigation on plant-parasitic nematodes in a southwest Florida vegetable field. Nematropica 27, 181-189.

McSorley, R., Wang, K.H., Kokalis-Burelle, N., Church, G., 2006. Effects of soil type and steam on nematode biological control potential of the rhizosphere community. Nematropica 36, 197-214.

Melton, T.A., 1995. Disease management. In: 1995 Flue-cured Information. NC Agric. Ext. Serv. AG-187, Raleigh, NC (USA), pp. 85-111.

Mian, I.H., Rodríguez-Kábana, R., 1982. Organic amendments with high tannin and phenolic contents for control of *Meloidogyne arenaria* in infested soil. Nematropica 12, 221-234.

Moens, M., Perry, R.N., Starr, J.L., 2009. *Meloidogyne* species – A diverse group of novel and important plant parasites. In: Perry, R.N., Moens, M., Starr, J.L. (Eds.), Root-knot nematodes. CABI International, Cambrige, MA (USA), pp. 1-17.

Monfort, W.S., Csinos, A.S., Desaeger, J., Seebold, K., Webster, T.M., Diaz-Perez, J.C., 2007. Evaluating *Brassica* species as an alternative control measure for root knot nematode (*M. incognita*) in Georgia vegetable plasticulture. Crop Prot. 26, 1359-1368.

Myers, D.F., Fry, W.E., 1978. Hydrogen cyanide potential during pathogenesis of sorghum by *Gloeocercospora sorghi* or *Helminthosporium sorghicola*. Phytopathology 68, 1037-1041.

Nahar, M.S., Grewal, P.S., Miller, S.A., Stinner, D., Stinner, B.R., Kleinhenz, M.D., Wszelaki, A., Doohan, D., 2006. Differential effects of raw and composted manure on nematode community, and its indicative value for soil microbial, physical and chemical properties. Appl. Soil Ecol. 34, 140-151.

Navarrete, M., 2009. How do farming systems cope with marketing channel requirements in organic horticulture? The case of market-gardening in southeastern France. J. Sustain. Agric. 33, 552-565.

Navarrete, M., Le Bail, M., Papy, F., Bressoud, F., Tordjman, S., 2006. Combining leeway on farm and supply basin scales to promote technical innovations in lettuce production. Agron. Sustain. Dev. 26, 77-87.

Navarrete, M., Tchamitchian, M., Aissa Madani, C., Collange, C., Taussig, C., 2010. Elaborating innovative solutions with experts using a multicriteria evaluation tool. The case of soil borne disease control in market-gardening cropping systems, in: Coudel, É.., Devautour, H., Soulard, C. (Eds.), ISDA, Innovation & Sustainable Development in Agriculture. Montpellier (FRA).

Neher, D.A., 2001. Role of nematodes in soil health and their use as indicators. J. Nematol. 33, 161-168.

Noling, J.W., Becker, J.O., 1994. The challenge of research and extension to define and implement alternatives to methyl-bromide. J. Nematol. 26, 573-586.

Noling, J.W., Gilreath, J.P., 2002. Weed and nematode management: Simultaneous considerations. In: Gobenauf, G.L. (Ed.), Annu. Int. Res. Conf. on Methyl Bromide Alternatives and Emissions Reductions. Orlando, FL (USA).

Nordbring-Hertz, B., Mattiasson, B., 1979. Action of a nematode-trapping fungus shows lectin-mediated host-microorganism interaction. Nature 281, 477-479.

Oka, Y., 2010. Mechanisms of nematode suppression by organic soil amendments—A review. Appl. Soil Ecol. 44, 101-115.

Oka, Y., Chet, I., Spiegel, Y., 1993. Control of the root knot nematode *Meloidogyne javanica* by *Bacillus cereus*. Biocontrol Sci. Technol. 3, 115-126.

Oka, Y., Shapira, N., Fine, P., 2007. Control of root-knot nematodes in organic farming systems by organic amendments and soil solarization. Crop Prot. 26, 1556-1565.

Ornat, C., Sorribas, F.J., 2008. Integrated management of root-knot nematodes in mediterranean horticultural crops. In: Cianco, A., Mukerji, K.G. (Eds.), Integrated Management and Biocontrol of Vegetable and Grain Crops Nematodes. Springer, Dordrecht (NLD), (Integrated management of plant pests and diseases, vol. 2), pp. 295-319.

Ornat, C., Sorribas, F.J., Verdejo-Lucas, S., Galeano, M., 2001. Effect of planting date on development of *Meloidogyne javanica* on lettuce in northeastern Spain, in: XXXIII Annual Meeting of ONTA. Varadero, Cuba.

Ornat, C., Verdejo-Lucas, S., Sorribas, F.J., Tzortzakakis, E.A., 1999. Effect of fallow and root destruction on survival of root-knot and root-lesion nematodes in intensive vegetable cropping systems. Nematropica 29, 5-16.

Ozores-Hampton, M., McSorley, R., Stansly, P.A., Roe, N.E., Chellemi, D.O., 2004. Long term large scale soil solarization as low-input production system for Florida vegetables. Acta Hortic. 638, 177–188.

Ozores-Hampton, M., Stansly, P.A., McSorley, R., Obreza, T.A., 2005. Effects of long-term organic amendments and soil solarization on pepper and watermelon growth, yield, and soil fertility. HortScience 40, 80-84.

Parmelee, R.W., Alston, D.G., 1986. Nematode trophic structure in conventional and no-till agroecosystem. J. Nematol. 18, 403-407.

Ploeg, A., 2007. Biofumigation to manage plant-parasitic nematodes. In: Ciancio, A., Mukerji, K.G. (Eds.), Integrated Management and Biocontrol of Vegetable and Grain Crops Nematodes. Springer, Dordrecht (NLD), (Integrated Management of Plant Pests and Diseases, vol. 2), pp. 239-248.

Rao, M.S., 2007. Management of root-knot nematode, *Meloidogyne incognita* (Kofoid & White) Chitwood, on crossandra (*Crossandra undulaefolia* Salisb.) using *Pochonia chlamydosporia* and *Pseudomonas fluorescens*. J. Ornam. Hortic. 10, 110-114.

Regnault-Roger, C., Philogène, B.J.R., Vincent, C., 2002. Biopesticides d'origine végétale. Tec et Doc, Paris (FRA).

Reuven, M., Szmulewich, Y., Kolesnik, I., Gamliel, A., Zilberg, V., Mor, M., Cahlon, Y., Ben-Yephet, Y., 2005. Methyl bromide alternatives for controlling fusarium wilt and root knot nematodes in carnations. Acta Hortic. 698, 99-104.

Rhoades, H.L., 1982. Effect of temperature on survival of *Meloidogyne incognita* in flooded and fallow muck soil. Nematropica 12, 33-37.

Rich, J.R., Brito, J.A., Kaur, R., Ferrell, J.A., 2009. Weed species as hosts of *Meloidogyne*: a review. Nematropica 39, 157-185.

Rich, J.R., Hodge, C., Robertson, W.K., 1986. Distribution of field corn roots and parasitic nematodes in subsoiled and nonsubsoiled soil. J. Nematol. 18, 203-207.

Rich, J.R., Rahi, G.S., 1995. Suppression of *Meloidogyne javanica* and *M. incognita* on tomato with ground seed of castor, crotalaria, hairy indigo, and wheat. Nematropica 25, 159-164.

Rich, J.R., Rahi, G.S., Opperman, C.H., Davis, E.L., 1989. Influence of the castor bean (*Ricinus communis*) lectin (ricin) on motility of *Meloidogyne incognita*. Nematropica 19, 99-103.

Roberts, P.A., 1993. The future of nematology – Integration of new and improved management strategies. J. Nematol. 25, 383-394.

Rodríguez-Kábana, R., 1986. Organic and inorganic nitrogen amendments to soil as nematode suppressants. J. Nematol. 18, 129-135.

Rodríguez-Kábana, R., Morgan-Jones, G., Chet, I., 1987. Biological-control of nematodes – soil amendments and microbial antagonists. Plant Soil 100, 237-247.

Runia, W.T., 1984. A recent development in steam sterilisation. Acta Hortic. 152, 195-200.

Runia, W., Greenberger, A., 2005. Preliminary results of physical soil disinfestation by hot air. Acta Hortic. 698, 251-256.

Schroeder, J., Thomas, S.H., Murray, L., 1993. Yellow and purple nutsedge and chile peppers host southern root-knot nematode. Weed Sci. 41, 150-156.

Scopa, A., Candido, V., Dumontet, S., Miccolis, V., 2008. Greenhouse solarization: effects on soil microbiological parameters and agronomic aspects. Sci. Hortic. 116, 98-103.

Siddiqui, I.A., Shaukat, S.S., Khan, A., 2004. Differential impact of some *Aspergillus* species on *Meloidogyne javanica* biocontrol by *Pseudomonas fluorescens* strain CHA0. Lett. Appl. Microbiol. 39, 74-83.

Siddiqui, Z.A., 2004. Effects of plant growth promoting bacteria and composed organic fertilizers on the reproduction of *Meloidogyne incognita* and tomato growth. Bioresour. Technol. 95, 223-227.

Siddiqui, Z.A., Akhtar, M.S., 2008. Effects of organic wastes, *Glomus intraradices* and *Pseudomonas putida* on the growth of tomato and on the reproduction of the root-knot nematode *Meloidogyne incognita*. Phytoparasitica 36, 460-471.

Sikora, R.A., Fernández, E., 2005. Nematodes parasites of vegetables. In: Liuc, M., Sikora, R.A., Bridge, J. (Eds.), Plant Parasitic Nematodes in Subtropical and Tropical Agriculture. CAB International, Wallingford (GBR), pp. 319-392.

Spiegel, Y., Chet, I., Cohn, E., 1987. Use of chitin for controlling plant plant-parasitic nematodes .2. Mode of action. Plant Soil 98, 337-345.

Stalin, C., Ramakrishnan, S., Jonathan, E.I., 2007. Management of root knot nematode *Meloidogyne incognita* in bhumyamalaki (*Phyllanthus amarus*) and makoy (*Solanum nigrum*). Biomed 2, 119-122.

Stirling, G.R., Smith, L.J., 1998. Field tests of formulated products containing either *Verticillium chlamydosporium* or *Arthrobotrys dactyloides* for biological control of root-knot nematodes. Biol. Control 11, 231-239.

Stirling, G.R., Smith, L.J., Licastro, K.A., Eden, L.M., 1998. Control of root-knot nematode with formulations of the nematode-trapping fungus *Arthrobotrys dactyloides*. Biol. Control 11, 224-230.

Szczech, M., Rondomanski, W., Brzeski, M.W., Smolinska, U., Kotowski, J.F., 1993. Suppressive effect of a commercial earthworm compost on some root infecting pathogens of cabbage and tomato. Biol. Agric. Hortic. 10, 47-52.

Tchamitchian, M., Collange, B., Navarrete, M., Peyre, G., 2009. Multicriteria evaluation of the pathological resilience of in-soil vegetable protected cropping systems, in: Gosselin, A., Dorais, M. (Eds.), GreenSys 2009. Québec City, Québec (CAN).

Terefe, M., Tefera, T., Sakhuja, P.K., 2009. Effect of a formulation of *Bacillus firmus* on root-knot nematode *Meloidogyne incognita* infestation and the growth of tomato plants in the greenhouse and nursery. J. Invertebr. Pathol. 100, 94-99.

Thakur, N.S.A., Devi, G., 2007. Management of *Meloidogyne incognita* attacking okra by nematophagous fungi, *Arthrobotrys oligospora* and *Paecilomyces lilacinus*. Agric. Sci. Digest 27, 50-52.

Thakur, R.P., 2007. Host plant resistance to diseases: potential and limitations. Indian. J. Plant. Protect. 35, 17-21.

Thoden T. C., Korthals G. W., Termorshuizen A. J. 2011. Organic amendments and their influences on plant-parasitic and free-living nematodes: a promising method for nematode management? Nematology 13, 133-153.

Tripathi, P.K., Singh, C.S., Prasad, D., Singh, O.P., 2006. Use of fungal bio-agents for the management of *Meloidogyne incognita* infecting tomato. Ann. Plant Protect. Sci. 14, 194-196.

Tzortzakakis, E.A., Petsas, S.E., 2003. Investigation of alternatives to methyl bromide for management of *Meloidogyne javanica* on greenhouse grown tomato. Pest Manag. Sci. 59, 1311-1320.

van Bruggen, A.H.C., Termorshuizen, A.J., 2003. Integrated approaches to root disease management in organic farming systems. Australas. Plant Pathol. 32, 141-156.

van Damme, V., Hoedekie, A., Viaene, N., 2005. Long-term efficacy of *Pochonia chlamydosporia* for management of *Meloidogyne javanica* in glasshouse crops. Nematology 7, 727-736.

van Diepeningen, A.D., de Vos, O.J., Korthals, G.W., van Bruggen, A.H.C., 2006. Effects of organic versus conventional management on chemical and biological parameters in agricultural soils. Appl. Soil Ecol. 31, 120-135.

van Gundy, S.D., 1985. Ecology of *Meloidogyne* spp. Emphasis on environmental factors affecting survival and pathogenicity. In: Sasser, J.N., Caryer, C.C. (Eds.), An advanced treatise on Meloidogyne. Vol. 1: Biology and control. North Carolina State University Graphics, Raleigh, NC (USA), pp. 77-182.

Verdejo-Lucas, S., Sorribas, F.J., Ornat, C., Galeano, M., 2003. Evaluating *Pochonia chlamydosporia* in a double-cropping system of lettuce and tomato in plastic houses infested with *Meloidogyne javanica*. Plant Pathol. 52, 521-528.

Verma, K.K., Nandal, S.N., 2006. Comparative efficacy of VAM, *Glomus fasciculatum* and *G. mosseae* for the management of *Meloidogyne incognita* in tomato at different phosphorus levels. Nat. J. Plant Improv. 8, 174-176.

Viaene, N.M., Abawi, G.S., 1998a. Fungi parasitic on juveniles and egg masses of *Meloidogyne hapla* in organic soils from New-York. J. Nematol. 40, 632-638.

Viaene, N.M., Abawi, G.S., 1998b. Management of *Meloidogyne hapla* on lettuce in organic soil with sudangrass as a cover crop. Plant Dis. 82, 945-952.

Wang, K.H., McSorley, R., 2008. Exposure time to lethal temperatures for *Meloidogyne incognita* suppression and its implication for soil solarisation. J. Nematol. 40, 7-12.

Wang, K.H., McSorley, R., Gallaher, R.N., 2004. Effect of *Crotalaria juncea* amendment on squash infected with *Meloidogyne incognita*. J. Nematol. 36, 290-296.

Widmer, T.L., Abawi, G.S., 2000. Mechanism of suppression of *Meloidogyne hapla* and its damage by a green manure of Sudan grass. Plant Dis. 84, 562-568.

Widmer, T.L., Abawi, G.S., 2002. Relationship between levels of cyanide in sudangrass hybrids incorporated into soil and suppression of *Meloidogyne hapla*. J. Nematol. 34, 16-22.

Zasada, I.A., Ferris, H., Elmore, C.L., Roncoroni, J.A., MacDonald, J.D., Bolkan, L.R., Yakabe, L.E., 2003. Field application of brassicaceous amendments for control of soilborne pests and pathogens. Online. Plant Health Progress. doi:10.1094/PHP-2003-1120-01-RS.

Figure Captions

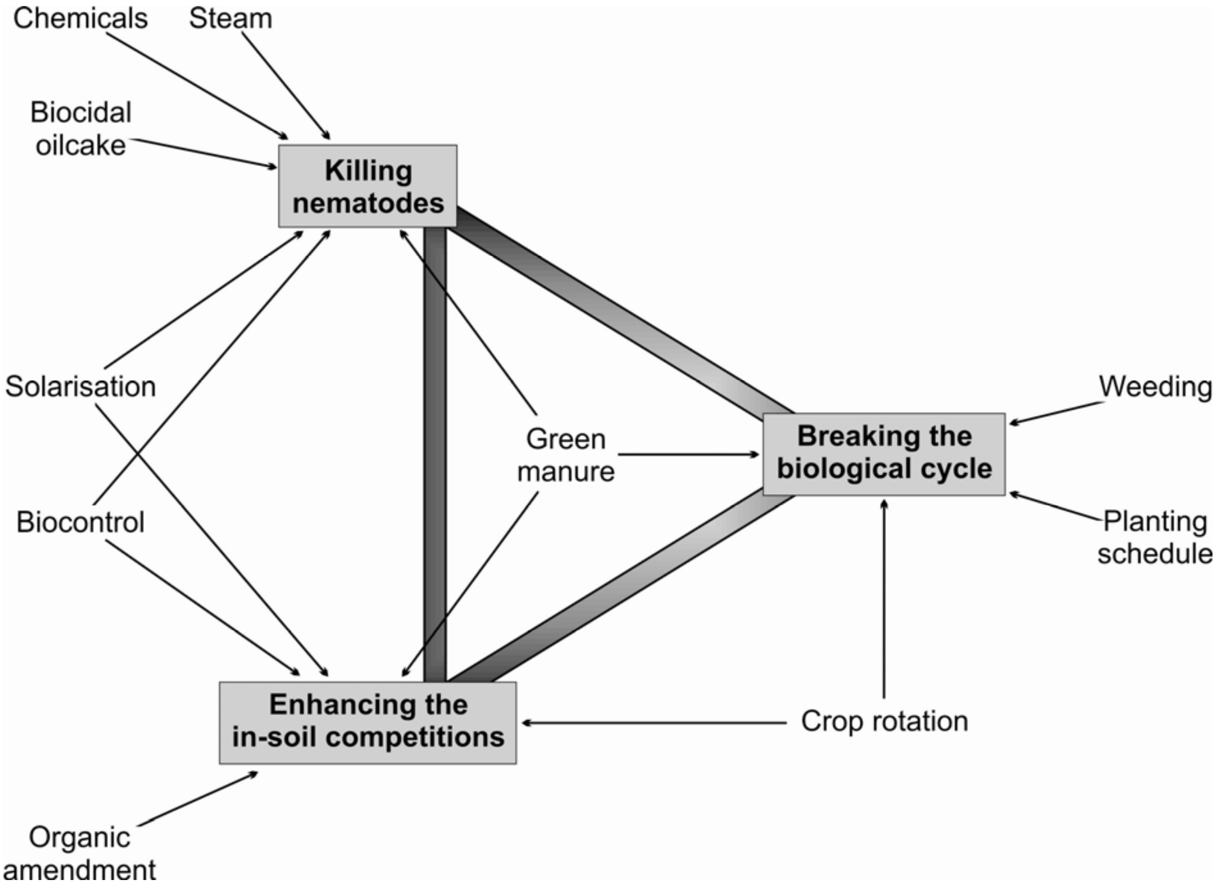

Fig. 1. Interactions between techniques (free text) and processes (boxed bold text) for controlling nematodes. The types of nematode control include killing nematodes, competition

with other micro-organisms in the soil, and breaking the reproduction cycle (grey components); a fourth type of control, limiting nematode dissemination, is not represented here. The grey triangle represents the soil matrix altered by the techniques and in which the processes occur. Only the main contributions are mentioned here, so steaming for example contributes first to killing nematodes (represented) while its indirect effect on competition through the changes in the pattern of microorganism species resulting from this lethal action is not represented. On the contrary, solarization which is a softer technique, directly contributes to both these processes, by killing free nematodes and by increasing the biological activity in the soil through the increase in organic matter decomposition. Interactions between these processes themselves take place within the soil matrix represented by the triangle linking these processes.

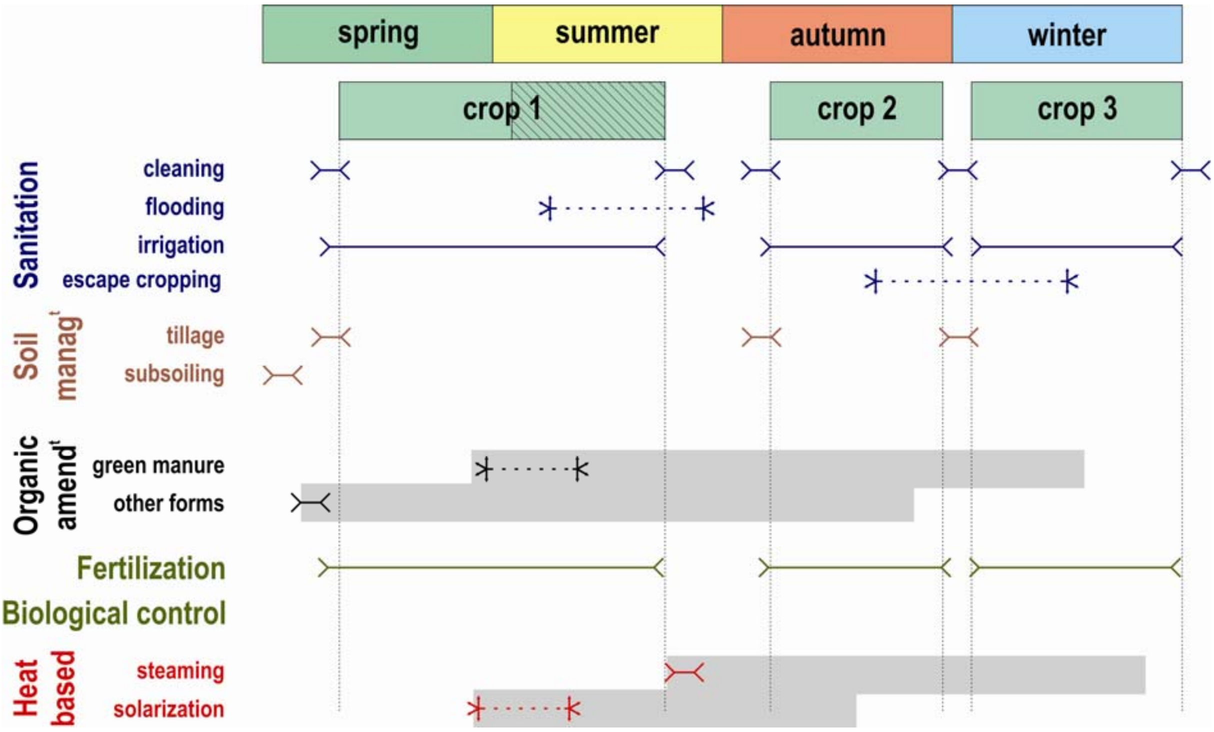

Fig. 2. Schematic representation of the time sequence of a simple cropping system and position of the nematode management techniques. The upper part of the figure shows a typical temporal sequence of crops in the Mediterranean region (the dashed part of crop 1 shows the

Version définitive du manuscrit publié dans / Final version of the manuscript published in : Crop Protection, 2011, In Press. DOI: 10.1016/j.cropro.2011.04.016

variability in the duration of this spring crop). The lower part of the figure places the different management techniques that are reviewed. Lines indicate the duration of the technique: solid if they do not conflict with the crop sequence, dashed if they do (conflicts arise from temporal concomitance of two reciprocally exclusive operations). Grey boxes indicate the duration of the effects of techniques influencing the nutrient availability and their vertical overlapping indicates that interactions between these techniques must be taken into account.