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

3
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14
15 **ABSTRACT**

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

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

31

32 **1. Introduction**

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

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

52 In past years, plant resistance and nematicides have been widely used to control
53 nematode attacks. Plant resistance is a very promising way of control, but has led, for many

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

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

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

79 2004) in order to propose efficient technical solutions to farmers that cannot continue to
80 depend on chemical solutions.

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

89

90 **2. Efficiency of individual alternative techniques**

91 *2.1. Sanitation methods*

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

94

95 *2.1.1. Prevention of new infestations*

96 Root-knot nematodes can be easily spread by human activities that provide
97 communication between contaminated and healthy areas; for example, the transport of
98 infested soil, plant debris or water. Research articles are rare and nematode advisory programs
99 do not rely on precise information. Because few experiments have been designed to quantify
100 the efficiency of sanitation methods, most information comes from farm surveys. At the farm
101 level, experts have recommended cleaning all agricultural machines and tools to avoid

102 transporting nematodes with the soil (Mateille et al., 2005; Djian-Caporalino et al., 2009). In
103 protected crops, most nematode damage appears to occur at the entrance of the greenhouse.
104 Those observations have led to the use of airlocks fitted with foot or wheel baths. Hugo and
105 Malan (2010) reviewed many situations with dissemination of nematodes (especially
106 *Meloidogyne* spp.) through irrigation water and pointed out the difficulties for controlling the
107 phenomenon. On the contrary, if nematodes can survive in plant materials (e.g. seeds, bulbs,
108 corms, tubers and cuttings), their spread can be prevented more easily by heating the plant
109 materials, by spraying or coating plant materials with natural nematicidal solutions, or using
110 *in vitro* grown, healthy plant materials (Bridge, 1996). Growers typically buy vegetable
111 seedlings; thus, it is essential to check that seedbeds and seedlings are free of nematodes.

112

113 2.1.2. Prevention of secondary infestations

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

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

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

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

145 **Weed control:** A wide range of weeds associated with vegetable crops are excellent
146 hosts for *Meloidogyne* species (Bélaïr and Benoit, 1996; Rich et al., 2009). Therefore,
147 exclusion of those weeds can efficiently prevent nematode infestation. Noling and Gilreath
148 (2002) considered that controlling *Amaranthus* spp. was essential for limiting a nematode
149 population, because that species is a very good host for root-knot nematodes. Schroeder et al.
150 (1993) showed that when weeds were not controlled in fallows, nematode population levels

151 increased. Kutuywayo and Been (2006) and Rich et al. (2009) indicated that inadequate weed
152 control may even counteract nematode control strategies, like fallows and resistant crops.

153 **Escape cropping:** Nematode damage can be reduced by growing crops at periods that
154 are not favorable for nematode growth (Bridge, 1996). Low temperatures increase nematode
155 life cycle duration and reduce reproduction and hatching; thus, sensitive vegetable species
156 have to be cropped in the coldest period tolerable. For example, in California, a delay in carrot
157 sowing for a few weeks enabled cropping in infected soils without yield losses (Roberts,
158 1993). In Spain, several lettuce transplanting dates were tested in fields infested by *M.*
159 *javanica* (Ornat et al., 2001). Delaying transplantation from September to October or
160 November caused reductions in both root-galling severity (from 2.2 to 0.5 or 0.2, respectively,
161 on a 1-10 scale) and nematode survival. Soil temperatures in November even prevented root
162 invasion. However, these techniques are not amenable to intensive crop rotations, particularly
163 when harvesting depends on market timing demand. Moreover, increased temperatures due to
164 climatic changes may reduce the efficacy of this technique, because nematodes, even
165 thermophil species, will be able to survive and reproduce in temperate winters.

166

167 2.2. Soil management

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

173

174 2.2.1. Tillage

175 In no tillage (NT) systems, the soil remains undisturbed, except the surface layer at
176 planting. This technique increases soil organic matter, with more residues in the upper layer,
177 and it improves the soil structure (Parmelee and Alston, 1986). In conventional tillage (CT)
178 systems, the soil is moldboard-plowed, disked and rotary-tilled after the crop harvest.
179 Compared to CT, NT or reduced tillage is often associated with higher microbial biomass and
180 activity in the upper soil layers (van Diepeningen et al., 2006). The different studies have
181 varied primarily in the crop sequences tested and in the number of years that the two tillage
182 systems were applied: 1 year by Baird and Bernard (1984); 5 years by Parmelee and Alston
183 (1986) and Gallaher et al. (1988); and 15 years by McSorley and Gallaher (1993). In all of
184 these studies, tillage had very little effect on the density of most nematode genera examined.
185 Thus, tillage effect was far less important than the effect of crop sequence. Furthermore, Lenz
186 and Eisenbeis (2000) observed that various tillage treatments (with a cultivator or a two-layer
187 plow) affected both the structural (taxonomic) and functional (trophic group, life strategy)
188 characteristics of nematode communities; the density of plant-parasitic nematodes was
189 reduced after tillage, and the populations of bacterivorous and fungivorous nematodes was
190 increased (Freckman and Ettema, 1993).

192 2.2.2. *Subsoiling*

193 Subsoiling is relatively disruptive. It is typically used for restoring water and nutrient
194 uptake of cropped plants, but its effects on nematode density is questionable. Rich et al.
195 (1986) examined whether it affected soils with a compacted layer that inhibited root
196 penetration to the deeper soil stratum. Because tillage pans limited root penetration into the
197 soil profile, plant-parasitic nematodes were confined mainly to the soil layer above the
198 compacted zone. Subsoiling slightly increased the total number of nematodes, but it changed
199 the distribution of plant roots and nematodes that moved deeper. Subsoiling had a positive

200 effect on plant growth, but this was attributed to improved root functions and water supply,
201 rather than to a reduction of nematode infection.

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

206 2.3. Organic amendments

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

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

220 - They release specific compounds that may be nematicidal.

221 - They stimulate microbial activities in the soil (including nematode antagonists), and
222 indirectly, they stimulate nematode predators and parasites that depend on microbial activities

223 (e.g., micro-arthropods, nematophagous fungi, parasitic bacteria). This topic is analyzed in
224 part 2.5 in relation to biological control.

225 Many previous reviews have focused on the use of organic amendments to control
226 plant-parasitic nematodes (Rodríguez-Kábana, 1986; D'Addabbo, 1995; Akhtar and Malik,
227 2000; Oka, 2010; Thoden et al., 2011). Farm manure trials have frequently involved poultry
228 or cattle litter. Poultry litter appeared to be an appropriate choice (Gamliel and Stapleton,
229 1993), especially when combined with sorghum cover crop (Everts et al., 2006), but it may be
230 phytotoxic at high dosages (Kaplan and Noe, 1993). Alternatively, Djian-Caporalino et al.
231 (2002) identified 39 species of green manures that belong to 22 botanical families, including
232 peanut (*Arachis hypogaeae*), basil (*Ocimum basilicum*), cotton (*Gossypium hirsutum*), sesame
233 (*Sesamum orientale*), oat (*Avena sativa*), and rye (*Secale cereale*). But the most efficient were
234 sudangrass and sorghum (*Sorghum sudanense*), cruciferae, like oil radish (*Raphanus sativus*)
235 and rapeseed (*Brassica napus*), ricin (*Ricinus communis*), marigold (*Tagetes erecta*, *T. patula*,
236 *T. minuta*), and velvet bean (*Mucuna deeringiana*) (Crow et al., 1996; Bridge, 1996;
237 Al-Rehiayani and Hafez, 1998; Widmer and Abawi, 2002; Everts et al., 2006). The use of
238 yard waste compost gave contradictory results: McSorley and Gallaher (1995) found no effect
239 on nematode density, but Chellemi (2006) found significant inhibiting effects. Oil cakes are
240 usually considered good for controlling nematodes. Akhtar and Malik (2000) repeatedly
241 tested neem (*Azadirachta indica*) oil cake, and found that it is particularly efficient against
242 root-knot nematodes even at low dosages (1 to 2 t/ha). Several studies reported that neem oil
243 cake applications reduced the *Meloidogyne* spp. population to half the density (Akhtar, 1998);
244 this was associated with an increase of predator and free-living nematodes. Chen et al. (2000)
245 observed that, when industrial wastes, like brewery compost or wheat mash, were added to
246 field microplot tests, it caused a sharp decrease in lettuce root galling and in *M. hapla* egg
247 production.

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

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

258

259 *2.3.1. Dosages of organic amendment and number of application years*

260 In the literature, the tested dosages of organic amendment varied from 1 to 269 t/ha
261 (McSorley and Gallaher, 1995), but most dosages ranged from 1 to 20 t/ha. Increasing
262 dosages of organic amendment typically increased its efficiency in nematode control, up to a
263 level where phytotoxicity was observed. Kaplan and Noe (1993) tested five dosages of
264 poultry litter (10 to 45 t/ha), and found an inverse relationship between dosage and both the
265 total number of *M. arenaria* in tomato roots and the quantity of eggs in soil. Crow et al.
266 (1996) compared three dosages of rapeseed green manure. A 14 t/ha dosage (dry weight)
267 reduced root galling on the subsequent squash crop, without any effect on yield. At higher
268 dosages (21 and 28 t/ha), root-galling was suppressed, but yield was decreased due to
269 phytotoxicity. These phytotoxic effects were obviated when a two-week delay was applied
270 between green manure application and squash planting. But Everts et al. (2006) comparing 2

271 dosages of poultry litter (2.8 and 8.2 t/ha) and 2 dosages of poultry litter compost (11.7 and 35
272 t/ha) did not find a systematically improved control for high dosages.

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

280

281 2.3.2. Chemical characteristics of different products

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

289 The highly variable results of these compounds may be explained, in part, by the
290 relative efficacy of the different compounds; but also, by the variations in concentration
291 during the decomposition process. For example, green manures based on cyanogenic plants
292 (like sudangrass) showed a negative relationship between the concentration of hydrogen
293 cyanide (HCN) and root galling. However, the soil and plant concentration ratios were not
294 constant (Widmer and Abawi, 2002), probably due to the cultivars used and the burying

295 conditions of the green manure. The sudangrass cultivar frequently used by market-gardeners
296 in European areas (Piper) was first selected for animal fodder, with a low level of HCN
297 (American Genetics, 2000; Myers and Fry, 1978). Because HCN is volatile, the slow release
298 of HCN may be insufficient, in some cases, to affect nematode eggs.

299 Similarly, Brassica green manures are known for limiting reproduction of nematodes,
300 because once chopped and incorporated into the soil they produce glucosinolates, a process
301 called biofumigation (Ploeg, 2007). But a large variability in efficiency is observed. Zasada et
302 al. (2003) consider it is due to several agronomical factors such as the variability in cultivars
303 and their relative concentration in glucosinolates, the stage of development of the crop when
304 chopped, soil type, temperature and moisture when incorporated into the soil. Monfort et al.
305 (2007) also identified a great variability among and within Brassica species on *Meloidogyne*
306 control effects under plastic shelters. They clearly demonstrated that net efficiency of a
307 Brassica cover crop depends on the difference between (i) the decrease in *Meloidogyne*
308 population due to the biofumigation process and (ii) its increase while Brassica species is
309 cropped because most of them are host for nematodes.

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

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

320 products may result in concentrations that are too low to be effective (Akhtar and Malik,
321 2000). Therefore, less stable composts would probably be more efficient, because toxic
322 compounds could quickly reach the toxicity threshold required to control nematodes. Nahar et
323 al. (2006) proposed that raw manures may be more effective than composted manures,
324 because they could reduce nematode populations and simultaneously increase beneficial
325 species and microbial activities. The drawback to that approach is that fresh organic matter
326 may introduce pathogens (especially fungi) and temporarily increase other soil-borne diseases
327 (van Bruggen and Termorshuizen, 2003).

328 **C/N ratios of the organic amendment.** Mian and Rodríguez-Kábana (1982) reported
329 that the nematode management potential of an organic amendment is directly related to its
330 nitrogen (N) content. Soil amendments with low carbon:nitrogen (C/N) ratios (e.g., animal
331 manures, oilcakes, and green manures) exhibit high nematicidal activity (Lazarovits et al.,
332 2001; Oka, 2010). This phenomenon is attributed to the release of ammonia during the
333 decomposition of the amendment in soil (Rodríguez-Kábana, 1986; Rodríguez-Kábana et al.,
334 1987; Spiegel et al., 1987; Oka et al., 1993). But for very low C/N amendments, phytotoxicity
335 problems occur and may be responsible for subsequent limited crop growth. On the other
336 hand, composts with C/N ratios above 20 (grassy hay, stubbles, and cellulosic materials, like
337 paper and sawdust) enhance N immobilization by enhancing microflora growth (Akhtar and
338 Malik, 2000; Widmer and Abawi, 2002). Therefore Rodríguez-Kábana et al. (1987)
339 considered that organic amendments with C/N ratios between 12 and 20, would both enable
340 nematicidal activity and avoid phytotoxicity. The incorporation of chicken litter with urban
341 plant debris (Chellemi, 2006) and olive pomace (Marull et al., 1997; D'Addabbo et al., 2003)
342 limited the phytotoxicity, enhanced microbial activity and controlled the nematode population
343 better than any treatment alone.

344

345 2.3.3. Soil infestation level and nematode community structures

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

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

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

364 365 2.4. Fertilization

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

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

375 376 *2.5. Biological control*

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

389 390 *2.5.1. Nematophagous fungi*

391 Several fungi have been identified and classified according to their nematophagous
392 properties. They include trappers, endoparasites, egg-parasites and toxin producers (Liu et al.,

393 2009). The most frequently studied nematode-trapping fungi are *Arthrobotrys* spp. and
394 *Monacrosporium* spp., which trap nematodes in constricting rings and adhesive nets,
395 respectively (Duponnois et al., 1998; Stirling and Smith, 1998; Stirling et al., 1998; Viaene
396 and Abawi, 1998a; Duponnois et al., 2001; Kumar and Singh, 2006; Thakur and Devi, 2007).
397 These fungi naturally occur in soils at low concentrations, and they predate only very specific
398 nematode species, which limits their potential use. The recognition mechanism involves the
399 association between a lectin secreted by the fungus and a carbohydrate secreted by the
400 nematode cuticle (Nordbring-Hertz and Mattiasson, 1979). They have been shown to predate
401 the root-knot nematode species that most frequently affects vegetable crops, including *M.*
402 *incognita* (Duponnois et al., 1996; Kumar and Singh, 2006; Thakur and Devi, 2007), *M.*
403 *javanica* (Khan et al., 2006), and *M. hapla* (Viaene and Abawi, 1998a).

404 Egg-parasitic fungi include *Paecilomyces*, *Pochonia* and *Verticilium* genera.
405 *Paecilomyces lilacinus* and *Pochonia chlamydosporia* are probably the most effective egg-
406 parasites. *Paecilomyces lilacinus* has been proven to successfully control root-knot
407 nematodes, *M. javanica* and *M. incognita* on tomato, egg-plant and other vegetable crops
408 (Verdejo-Lucas et al., 2003; Goswami and Mittal, 2004; van Damme et al., 2005; Goswami et
409 al., 2006; Haseeb and Kumar, 2006; Kumar et al., 2009). *Paecilomyces lilacinus* formulations
410 have been homologated in many countries for vegetables and other crops, including coffee
411 and banana. However, *P. lilacinus* appears to be more suited to tropical conditions
412 (Krishnamoorthi and Kumar, 2007) and acid soils close to pH 6 (Krishnamoorthi and Kumar,
413 2008) than to temperate or cold conditions. *Pochonia chlamydosporia* prefers mild climate
414 and soil conditions (Atkins et al., 2003), where it occurs naturally (Bent et al., 2008).
415 However, *P. chlamydosporia* had no effect in greenhouse experiments with tomato rotations
416 (Tzortzakakis and Petsas, 2003) or lettuce-tomato rotations (Verdejo-Lucas et al., 2003).
417 Those authors noted that the fungus did not colonize well and did not control the nematode

418 population inoculated in the soil. They concluded that *P. chlamydosporia* did not hold
419 promise as a biocontrol agent in the Mediterranean region.

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

425

426 2.5.2. Antagonistic bacteria

427 *Pasteuria penetrans* and *Pseudomonas fluorescens* are the two most studied
428 antagonistic bacteria. *Pasteuria penetrans* effectively parasitized *M. incognita* in rotations
429 that included tomato, egg-plant, and beans or cabbage (Amer-Zareen et al., 2004), but its
430 efficacy depended on cropping techniques and soil conditions. Both soil porosity and water
431 flow (hence irrigation practices) directly affected the efficacy of *P. penetrans* by modifying
432 the probability that the bacteria met the nematodes and attached to their cuticles. High
433 irrigation loads or frequencies tended to wash away spores (Dabiré et al., 2005; Mateille et al.,
434 2009). Soil texture and structure also influenced spore attachment to the nematode; sandy
435 soils were more favorable than clay soils (Mateille et al., 1995). *Pseudomonas fluorescens*
436 also provide effective control of root-knot nematodes on vegetable crops (Haseeb and Kumar,
437 2006; Krishnaveni and Subramanian, 2004; Stalin et al., 2007). *Bacillus firmus* has also
438 shown good results; it is available as a trade product in some countries (Giannakou et al.,
439 2007; Terefe et al., 2009). In some cases, nematophagous fungi or parasitic bacteria are
440 associated with vesicular or arbuscular mycorrhiza (most of the *Glomus* genus), which

441 improves their effects (Jaizme-Vega et al., 2006; Verma and Nandal, 2006; Siddiqui and
442 Akhtar, 2008).

443 2.5.3. Interactions among biocontrol agents and with other soil organisms

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

453 Biocontrol agent combinations have also shown varied results. For example, Rao (2007)
454 showed that combining *P. chlamydosporia* and *P. fluorescens* improved nematode control.
455 Several other combinations are reported in the literature, but the inconsistent results prevent
456 drawing any strong conclusions. Interactions between biocontrol agents and organic fertilizers
457 (green or cattle manure, compost, etc.) have also been explored. Combining neem cake or
458 dried neem leaves amendments with *P. penetrans* gave encouraging results (Javed et al.,
459 2008). In addition, combining the rhizobacterium, *Pseudomonas putida*, with the arbuscular
460 mycorrhizal fungus, *Glomus intraradices*, and neem leaf litter provided good control of *M.*
461 *incognita* on tomato crops (Siddiqui and Akhtar, 2008). Replacing neem leaf litter with horse
462 manure reduced the effects. Animal manure, particularly poultry and, to a lesser extent goat,
463 combined with *P. fluorescens* also gave good results on tomatoes (Siddiqui, 2004). In order to
464 increase biocontrol efficiency, Dong and Zhang (2006) advocate integrating biocontrol with
465 other cultural methods through multidisciplinary studies.

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

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

476

477 *2.6. Heat-based methods*

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

481

482 *2.6.1. Steaming*

483 Steaming the soil is similar to sterilization, rather than disinfestation. It kills most of the
484 microorganisms in the heated layers of the soils, including pests and beneficial agents (Katan,
485 2000). The efficiency depends on soil preparation. The soil must achieve high porosity to
486 allow deep penetration of the steam (20 cm or more). Steam application requires a boiler and
487 an injection device. Steam can be injected under a fleece placed on the soil, which allows
488 large areas to be treated at once (up to 400 m²); with 4 to 5-h applications, the 20 to 30-cm
489 soil layer can be heated to over 80 °C (Le Bohec et al., 1999). An alternative to fleece is

490 injecting steam under a solid hood placed on the soil. Smaller areas are treated in each
491 application with the hood, but it is not necessary to lock down the sides of the hood with
492 weights or soil to ensure sealing (Gay et al., 2010). A negative pressure technique provides
493 better results; this forces the steam to enter into the soil (Runia, 1984). Negative pressure is
494 achieved by sucking the air out of the soil through perforated pipes that are connected to a
495 fan. The pipes are permanently installed under the field, at about 60 cm deep for protection
496 from plowing damage. With this method, the heat penetrates to a deeper layer, close to the
497 depth at which the pipes are buried. Finally, sandwich steaming is a recent technique, where
498 the steam is injected from both above and within the soil. It requires a large device which is
499 unsuitable for greenhouses.

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

514 2.6.2. Solarization

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

533 Solarization generally holds promise for controlling root-knot nematodes (Gamliel and
534 Stapleton, 1993; Ozores-Hampton et al., 2004; Ozores-Hampton et al., 2005), but failures
535 have also been reported (Chellemi, 2002). Failures are primarily due to (i) the higher
536 resistance of nematode eggs to heat treatments, (ii) the dependence of soil temperatures on
537 both the state of the soil and the climate conditions during the solarization period, and (iii) the
538 fact that the soil can be re-infested after solarization. In the latter case, nematodes may

539 migrate from deeper layers, either due to deep tillage practices, which inverts the soil layers,
540 or due to the gradual, long-term movement of nematodes.

541

542 **3. Towards a systemic agro-ecological approach**

543 Our analysis found that most techniques listed had a partial effect on nematode control.

544 Currently, these alternative techniques are difficult to promote in intensive western
545 agriculture, because farmers can and do compare it to chemical efficiency. Moreover, there is
546 great variability in efficiency among studies, due to several factors. Those that depend on
547 practical modalities (e.g., organic amendment rates, maximum temperatures achieved in
548 solarization, etc.) have been highlighted above. Others include soil and climate conditions.

549 For example, clay soils offer poor conditions for the development of nematodes (Mateille et
550 al., 1995; Barker and Koenning, 1998). Consequently, the effect of any particular technique
551 probably depends on the ratio between clay and sand in the soil, which is not always reported.
552 In addition, soil types differ among regions. For example, African soil differs from Indian or
553 Pakistanese soil, in part due to climate differences, but also due to the cultivation history and
554 the micro-organisms promoted by those cropping systems. Moreover, temperature and
555 humidity greatly affect the development of nematodes. This should be taken into account
556 when comparing results reported in tropical, Mediterranean, and temperate areas.

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

560

561 *3.1. Interactions between techniques: a key factor in nematode management*

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

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

587 combination of solarization and green manure. Blok et al. (2000) showed that it combined the
588 thermal effects of solarization and the anaerobic reducing effects of organic amendment. They
589 demonstrated that these synergistic effects were quite efficient against soil-borne fungi.
590 Gamliel and Stapleton (1993) and Oka et al. (2007) found that the combination reduced
591 nematode populations and galling indices in conditions that were not effectively controlled by
592 solarization or organic amendment alone. Another approach is to organize the actions of
593 different techniques by combining short and long-term effects (Roberts, 1993). The short term
594 aim should be to limit plant infestation by temporarily reducing nematode numbers in the soil
595 before planting and reducing their infectivity before growing with resistant or tolerant
596 cultivars. The long term aim should be to reduce the multiplication rate of nematodes on each
597 crop, even partially; this will have beneficial effects on the succeeding crops, and therefore, in
598 the long-term.

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

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

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

617

618 *3.2. Soil biodiversity and trophic networks: another key factor for nematode management*

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

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

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

644 Soil biodiversity may not systematically confer protection against soil-borne diseases,
645 but it is always associated with better soil health, and therefore, it provides stability against
646 stress and disturbances. It may be possible to manage soil biodiversity (Brussaard et al.,
647 2007), as proposed for above-ground biodiversity (Altieri, 1999), to control pathogenic
648 populations. Mateille et al. (2008) advised that studies on plant-nematode relationships should
649 extend to ecological investigations on nematode communities for biodiversity management.

650 651 3.3. Towards more sustainable systems

652 The alternative methods we have reviewed focused on nematode control. However,
653 many of these techniques also modify soil functions that affect soil fertility, nutrient supply,
654 soil structure, soil health, etc. Therefore, when these techniques are introduced into a cropping
655 system these interactions should be taken into consideration throughout the cropping system
656 cycle. Fig. 2 shows a typical crop sequence for market garden vegetable production in the
657 Mediterranean. As can be seen, organic amendment (whether green manure or not) interacts
658 with fertilization, but also with heat-based techniques because of the increased organic matter
659 decomposition induced by the increase in soil temperature. Fig. 2 also shows that escape
660 cropping, if implemented by delaying the plantation date of crop 2, is incompatible with crop
661 3 unless the spring crop (crop 1) plantation date can be postponed. Management techniques

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

667

668 *3.3.1. Nutrient cycle*

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

682

683 *3.3.2. Soil health*

684 Plant production is directly related to soil quality, which is defined by its functional capacity
685 within an ecosystem in terms of biological productivity, environmental quality, and plant
686 health (Doran et al., 1996). Soil quality is based on its physical, chemical, and biological

687 properties. Soil biological properties include (Doran and Zeiss, 2000) fertility, health,
688 environmental impact, and resilience. Soil health is related to its ecological characteristics
689 (Doran and Zeiss, 2000) and deals with agronomy (Doran and Safley, 1997). Good soil health
690 is usually correlated with fast nutrient cycles, strong stability (high resistance or resilience),
691 and broad biodiversity. Based on these complex soil properties and interactions, the
692 development of sustainable management strategies must move to a systemic approach that can
693 lead to global nematode suppression indicators (Ferris et al., 2001; Neher, 2001; Nahar et al.,
694 2006). Thus, the future challenge for nematode management is to link above-ground effect
695 traits to below-ground response traits. From an experimental point of view, this will require
696 the establishment of (1) observation plots in crop production systems with specific ecological
697 and agronomical characteristics and specific crop practices. Then, (2) appropriate trials and
698 comparisons of different practices can be performed.

699

700 *3.3.3. New cropping systems: substitution or system redesign?*

701 Alternative techniques for cropping systems can be classified according to their
702 consequences on the design of the cropping systems, along the conceptual framework
703 proposed by Hill and MacRae (1995). According to these authors, transitions towards
704 sustainable agriculture can be categorized by three levels: Efficiency (increases over current
705 practices), Substitution (replacement of chemicals by natural products), and Redesign
706 (modifying the cropping system to confer resistant properties). Less disruptive methods
707 include replacements for fumigants and other nematicide formulations that were or are
708 currently available. This category includes thermal disinfection by steam, organic amendment,
709 nematicidal plant fungus and bacterium extracts, and biological control. It can be completed
710 with the use of plant resistance, which may then be used less systematically, a possible way to
711 lessen the probability of resistance breakdown by pathogens. These methods are not too

712 complicate to introduce because the applications are instantaneous. In contrast, many other
713 techniques would create new constraints within the cropping system. Some have
714 consequences on the rotation design because they replace a cash crop, like nematicidal green
715 manure or solarization, which are typically applied instead of planting summer crops. Other
716 techniques change the organization of the rotation, but not the range of the species cropped;
717 for example, escape cropping or selecting non-susceptible, resistant, or tolerant rootstocks.
718 However, these constraints may be more or less troublesome depending on the type of farm.
719 Replacing or shortening the cultivation of a spring cash crop with a green manure or thermal
720 disinfection by solarization is less disruptive than altering the cultivation of a summer crop. In
721 that case, Navarrete et al. (2006) showed that solarization led to summer crop abandonment
722 and increased farm specialization. In contrast, a redesign of the whole rotation to introduce a
723 combination of techniques and increased crop diversity with various sensitivities or
724 resistances to pests and diseases will cause much larger changes at the farm scale because new
725 markets must be found (Navarrete, 2009).

726 The complexity of these interactions and the multidimensional nature of their
727 consequences suggest that models will be required to support the redesign of sustainable
728 cropping systems. These models can simulate population dynamics or directly perform a
729 multiple criteria evaluation. Therefore, we have initiated a research project with the aim of
730 promoting the introduction of these techniques into the redesign of cropping systems
731 (Navarrete et al., 2010). Two steps are necessary; first, designing a model to assess the
732 resistance or resilience of a given cropping system to soil-borne pests (Tchamitchian et al.,
733 2009); second, using the model in cooperation with advisers and farmers in order to build
734 alternative cropping and farming systems that take into account a new nematode management
735 paradigm and the farm constraints (resource availability, marketing environment, etc.).
736 Furthermore, this cooperation will promote new ways of thinking that do not require

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

739

740 **4. Conclusion**

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

762

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764

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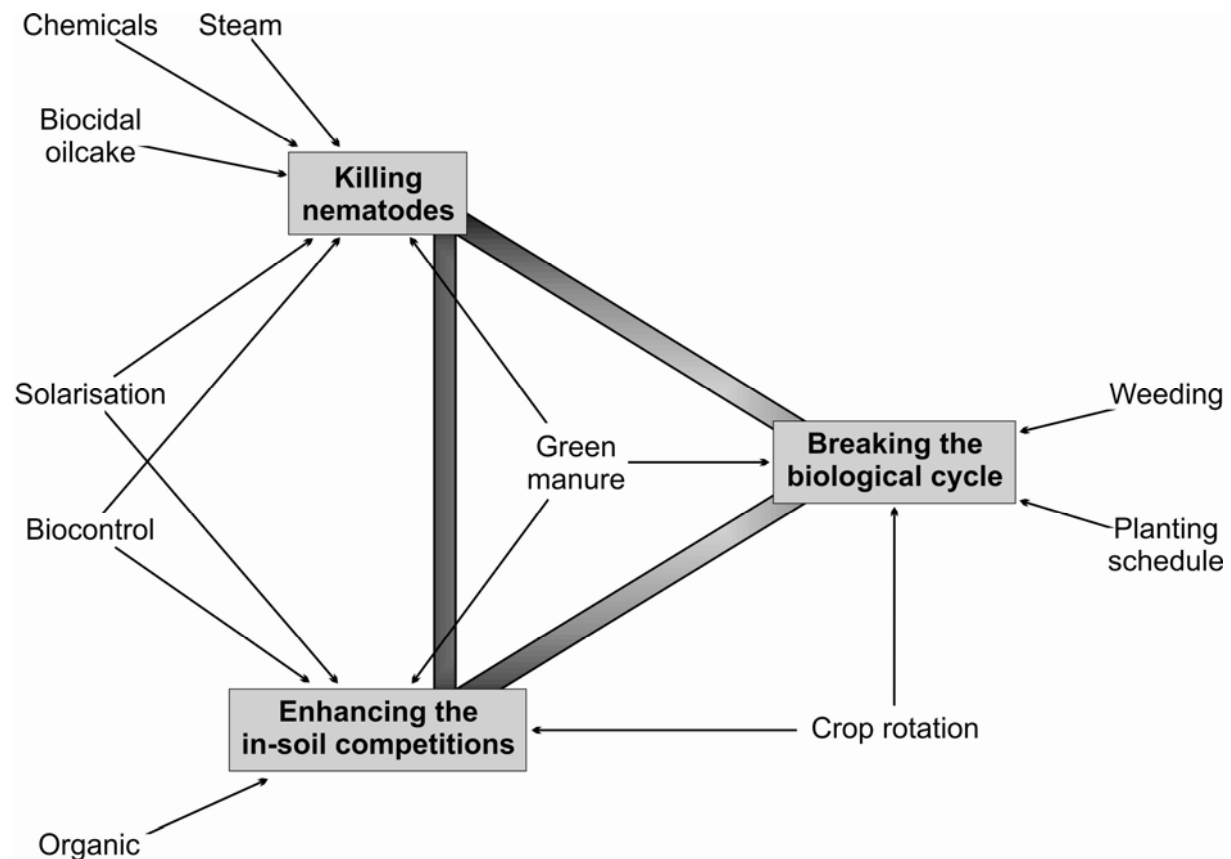
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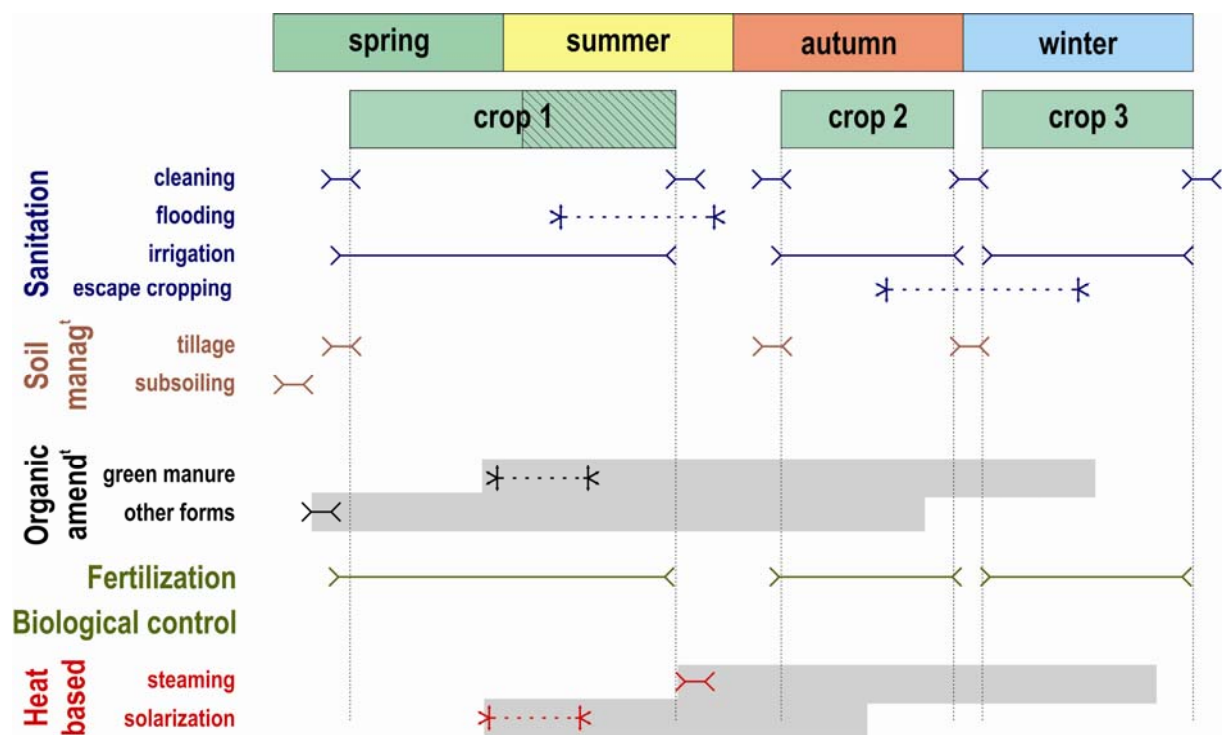
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1149 **Figure Captions**



151 **Fig. 1.** Interactions between techniques (free text) and processes (boxed bold text) for
 152 controlling nematodes. The types of nematode control include killing nematodes, competition
 153

1154 with other micro-organisms in the soil, and breaking the reproduction cycle (grey
 1155 components); a fourth type of control, limiting nematode dissemination, is not represented
 1156 here. The grey triangle represents the soil matrix altered by the techniques and in which the
 1157 processes occur. Only the main contributions are mentioned here, so steaming for example
 1158 contributes first to killing nematodes (represented) while its indirect effect on competition
 1159 through the changes in the pattern of microorganism species resulting from this lethal action
 1160 is not represented. On the contrary, solarization which is a softer technique, directly
 1161 contributes to both these processes, by killing free nematodes and by increasing the biological
 1162 activity in the soil through the increase in organic matter decomposition. Interactions between
 1163 these processes themselves take place within the soil matrix represented by the triangle
 1164 linking these processes.



165
 166
 167 **Fig. 2.** Schematic representation of the time sequence of a simple cropping system and
 168 position of the nematode management techniques. The upper part of the figure shows a typical
 169 temporal sequence of crops in the Mediterranean region (the dashed part of crop 1 shows the

1170 variability in the duration of this spring crop). The lower part of the figure places the different
1171 management techniques that are reviewed. Lines indicate the duration of the technique: solid
1172 if they do not conflict with the crop sequence, dashed if they do (conflicts arise from temporal
1173 concomitance of two reciprocally exclusive operations). Grey boxes indicate the duration of
1174 the effects of techniques influencing the nutrient availability and their vertical overlapping
1175 indicates that interactions between these techniques must be taken into account.

1176