

Meloidogyne enterolobii (= *M. mayaguensis*): profile of an emerging, highly pathogenic, root-knot nematode species

Philippe CASTAGNONE-SERENO *

INRA UMR1301/UNSA/CNRS UMR6243, 400 route des Chappes, 06903 Sophia Antipolis, France

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Summary – *Meloidogyne enterolobii* (= *M. mayaguensis*), the root-knot nematode of the pacara earpod tree, belongs to the group of tropical root-knot nematodes and is considered as one of the most damaging species, due to its wide host range, pathogenicity and ability to develop and reproduce on several crops carrying resistance genes. Moreover, recent reports indicate that the geographic distribution of the parasite tends to extend beyond tropical areas, and the risk of its establishment and spread in Mediterranean regions and southern Europe is now highly probable. Recently, molecular markers have been developed that allow the specific identification of this pest, a prerequisite for the implementation of efficient control strategies. In that respect, plant resistance and biological control are currently being actively investigated but a huge amount of research and development is still required to ensure the successful use of such methods in the field.

Keywords – control, host range, invasive species, pacara earpod tree, taxonomy.

Originally considered as a damaging pest distributed in tropical areas, the pacara earpod tree (*Enterolobium contortisiliquum*) root-knot nematode, *Meloidogyne enterolobii* Yang & Eisenback, 1983, has become economically important and has emerged as a major parasite in many crops worldwide (Moens *et al.*, 2009; Wesemael *et al.*, 2011). The purpose of this profile is not to perform an exhaustive review of the literature available, but rather to provide a general overview of the existing knowledge on this species, and to summarise the current and ongoing research aiming to broaden our basic understanding of the plant-nematode interaction and opening new perspectives for the management of this damaging pest.

Meloidogyne enterolobii, from misidentification to synonymisation

Meloidogyne enterolobii was originally described from a population that caused severe damage on the pacara earpod tree on Hainan Island in China (Yang & Eisenback, 1983). Based on female perineal patterns it was preliminary identified as *M. incognita*, and further analysis (*i.e.*, response to the North Carolina differential host test, chromosome number and mitotic mode of reproduction) in-

dicated some resemblance to the latter species; however, from a morphological point of view, the population was very different from *M. incognita* and any other described species of root-knot nematode (Yang & Eisenback, 1983). Since the original description, *M. enterolobii per se* has been the topic of very few published studies (four papers recorded in Web of Science® from 1983 to 2008), which gave the impression that it was a very minor species.

A few years later, a new species of root-knot nematode was described from specimens recovered from galled roots of eggplant in Puerto Rico, and named *M. mayaguensis* (Rammah & Hirschmann, 1988). In their original description, the authors indicated that “*M. mayaguensis* superficially resembles *M. enterolobii* but differs distinctly from it in (some) morphological features” (Rammah & Hirschmann, 1988). In addition, the esterase phenotype of *M. mayaguensis* (VS1-S1) was identical to that of *M. enterolobii* (Esbenshade & Triantaphyllou, 1985; Rammah & Hirschmann, 1988). Also, a possible confusion and misidentification of *M. mayaguensis* as *M. incognita* has been reported on a number of occasions (Fargette *et al.*, 1994; Carneiro *et al.*, 2001; Brito *et al.*, 2004). However, in contrast to *M. enterolobii*, the importance of *M. mayaguensis* as a crop pest is well doc-

* E-mail: Philippe.Castagnone@sophia.inra.fr

umented, as indicated by the abundant literature available on this species.

More recently, the taxonomic relationship of *M. enterolobii* and *M. mayaguensis* was further questioned based on molecular data. Indeed, Xu *et al.* (2004) demonstrated sequence identity of an mtDNA region between these two nominal species, and suggested that *M. mayaguensis* should be considered as a junior synonym of *M. enterolobii*. Since then, and although no 'official' synonymisation has been published, it is generally accepted that *M. enterolobii* and *M. mayaguensis* are the same species, with *M. enterolobii* as valid name (Hunt & Handoo, 2009). In the text below, most of the references cited take this synonymisation into account.

Host range and pathogenicity

Meloidogyne enterolobii is considered to be a highly polyphagous species with a host range similar to that of *M. incognita* (Yang & Eisenback, 1983). The most frequently recorded hosts include many vegetables, *e.g.*, tomato, pepper, watermelon (Yang & Eisenback, 1983; Rammah & Hirschmann, 1985), but also guava tree (Gomes *et al.*, 2011), ornamental plants (Brito *et al.*, 2010) and weeds (Rich *et al.*, 2009). Although few detailed studies are available, *M. enterolobii* is referred to as a highly aggressive species (*i.e.*, a very successful parasitic species with high infestation rate on the roots of host plants), and induces more severe root galling than other species of root-knot nematodes. In a microplot experiment, tomato yield losses of up to 65% have been observed (Cetintas *et al.*, 2007). In heavily infested areas, cultivation may become unviable, as exemplified for guava in Brazil (Carneiro *et al.*, 2007). In addition, a particular concern is the ability of *M. enterolobii* to develop on crop genotypes carrying resistance to the major species of *Meloidogyne*, including resistant cotton, sweet potato, tomatoes (*Mi-1* gene), potato (*Mh* gene), soybean (*Mir1* gene), bell pepper (*N* gene), sweet pepper (*Tabasco* gene) and cowpea (*R_k* gene) (Yang & Eisenback, 1983; Fargette & Braaksma, 1990; Berthou *et al.*, 2003; Brito *et al.*, 2007a; Cetintas *et al.*, 2008). Very few crop species have been recorded as non-hosts for *M. enterolobii*, including grapefruit, sour orange, garlic and peanut (Rodriguez *et al.*, 2003; Brito *et al.*, 2004).

Meloidogyne enterolobii as an invasive species

Until recently, it has been generally admitted that the distribution of *M. enterolobii* was restricted to regions with typical tropical climatic conditions, *i.e.*, Africa, South and Central America, the Caribbean and Asia. In 2004, in the course of regulatory sampling at ornamental nurseries, the nematode was detected in Florida (Brito *et al.*, 2004), where the climate is similar to that of southern Europe. Also, apart from a few interceptions in imported plant material, the presence of *M. enterolobii* has been reported in glasshouses in France (Didier Mugniéry, pers. commun.) and Switzerland (Kiewnick *et al.*, 2008). In addition, the possibility that its distribution has been underestimated due to misidentification in different regions of the world, including Europe, should not be excluded. Since it is probable that *M. enterolobii* can survive in the warmer parts of Europe and in glasshouses throughout the region, the risk of its establishment and spread in this area is quite likely. Moreover, although it is difficult to predict how global environmental changes such as climate change will affect biological invasions, the establishment of exotic invasive species into new geographic areas is regarded as a realistic hypothesis (Hellmann *et al.*, 2008), and *M. enterolobii* appears to be a good candidate for such a process. Consequently, in 2010 *M. enterolobii* was added to the European and Mediterranean Plant Protection Organization (EPPO) A2 Alert list (EPPO, 2010), which means that EPPO recommends its member countries to regulate this nematode as a quarantine pest.

In order to achieve successful regulation practices, accurate identification is an essential prerequisite. As mentioned above, morphological identification of *M. enterolobii* is not a simple task, even for a well qualified taxonomist. By contrast, esterase patterns have been shown to be a valuable tool for the specific identification of this pest (Esbenshade & Triantaphyllou, 1985; Carneiro *et al.*, 2000). However, the limitation of this technique is that second-stage juveniles (J2) cannot be reliably diagnosed, hindering its use in routine examination of soil samples. More recently, a number of molecular tools have been developed and demonstrated as efficient in differentiating *M. enterolobii* from the most common species of *Meloidogyne*, based on the presence/absence and/or size of the amplicons in PCR reactions. The molecular targets chosen in the various protocols available mainly include mitochondrial DNA (Blok *et al.*, 2002; Brito *et al.*, 2004; Xu *et al.*, 2004), ribosomal DNA (Adam *et al.*, 2007), satel-

lite DNA (Randig *et al.*, 2009) and an anonymous SCAR marker (Tigano *et al.*, 2010).

The need for efficient control strategies

Many excellent general reviews describing the several management practices that may be used to reduce populations of root-knot nematodes to below economically damaging threshold levels are available in recent literature (e.g., Coyne *et al.*, 2009; Nyczepir & Thomas, 2009). Below, the results of experimental studies focusing on the specific control of *M. enterolobii* are summarised. Basically, taking into account the banning of most chemical nematicides, current research focuses mainly on the hunt for new natural resistance sources and specific biological control agents.

As indicated above, *M. enterolobii* is not controlled by known resistance genes active against the major tropical species of root-knot nematodes, i.e., *Mi-1* in tomato or *N* in pepper. However, plant resistance is currently considered as a method of choice for management of root-knot nematodes, and some efforts have been devoted to the identification of new sources of resistance to *M. enterolobii*. A decade ago, a screening experiment using high and durable inoculum pressure indicated that *Ma* genes in *Myrobalan* plum, known to control the main tropical species of root-knot nematode, also control resistance to *M. enterolobii* (Rubio-Cabetas *et al.*, 1999). In peach, commercial rootstocks carrying the *R Mia* resistance gene (Claverie *et al.*, 2004) were shown to be resistant to the nematode in glasshouse evaluation tests (Nyczepir *et al.*, 2008; Daniel Esmenjaud, pers. commun.). In the cultivation of guava trees, which can suffer severe damage in cases of heavy infestation, resistance has recently been identified in *Psidium* sp. accessions originating from native forests in Brazil (Carneiro *et al.*, 2007; de Almeida *et al.*, 2009). In all such cases involving perennial crops, the strategy of control is based on the development of resistant rootstocks, which further implies that grafting compatibility should be associated with resistance in the genotypes of interest. In the case of annual plants fewer data are available in the literature. However, two carrot cultivars and collard were reported to exhibit very little or no nematode reproduction in host range studies of cultivated plants, including vegetable crops of importance in Florida (Brito *et al.*, 2007b). Clearly, searching for new sources of resistance to *M. enterolobii*, especially in vegetables and annual crops, and their introgression into cultivars of agro-

nomic interest, currently represents a major challenge to plant breeders worldwide.

Another alternative to chemical nematicides is based on the use of biocontrol agents, and several organisms have been investigated for their antagonistic effects against *M. enterolobii*. The nematode-trapping fungus, *Arthrobotrys oligospora*, proved to be efficient at reducing nematode populations either *in vitro*, in pot experiments or in field trials (Duponnois *et al.*, 1995, 1996). In addition, the beneficial effects of the fungus were strengthened by some rhizosphere bacteria (Duponnois *et al.*, 1998), and when organic amendment was used concomitantly (Duponnois *et al.*, 2001). Recently, potential egg-parasitic fungi associated with *M. enterolobii* eggs have been isolated and characterised, i.e., *Pochonia chlamydosporia* and *Lecanicillium psalliotae*, but further studies are required to clarify the potential of these fungi as biocontrol agents (Arevalo *et al.*, 2009). In laboratory assays and microplot trials, spores of bacterial isolates of *Pasteuria penetrans* generally exhibited poor pathogenicity and levels of infection on *M. enterolobii* that were rarely suppressive (Trudgill *et al.*, 2000; Carneiro *et al.*, 2004). Conversely, bioassays showed that the entomopathogenic nematodes *Heterorhabditis baujardi* and *Steinernema feltiae* could affect nematode populations by inhibiting hatching and J2 infection (Molina *et al.*, 2007). Although somewhat promising, the results of all these studies require validation in various field conditions before a biological agent active against *M. enterolobii* may be commercially released. However, the urgent need to reduce the dependence on chemical nematicides should provide the necessary impetus for the huge amount of research and development still required to ensure the successful use of such biocontrol agents.

Meloidogyne enterolobii as a model plant-parasitic nematode?

Considering its wide host range, aggressiveness and ability to develop on crop genotypes carrying resistance to the major species of root-knot nematodes, *M. enterolobii* should be considered as a useful model to decipher the intimate mechanisms of pathogenicity of plant-parasitic nematodes. However, to our knowledge, this species has not (yet?) been included in research programmes focusing on nematode genomics and/or the molecular determinants of the plant-nematode interactions. The recent completion of two *Meloidogyne* genomes has opened the way for genomic approaches to elucidate the biology of these para-

sites (Bird *et al.*, 2009), and the sequencing of other *Meloidogyne* genomes (*e.g.*, *M. arenaria* and *M. javanica*) is currently underway, but so far *M. enterolobii* has not been chosen as a species of interest for such a purpose. Indeed, it is symptomatic to note that, although more than 70 000 ESTs from species of root-knot nematodes have been released in public databases (see <http://www.nematode.net>), no single EST is currently available for *M. enterolobii*. Nevertheless, with the ongoing development of next-generation sequencing technologies, it is expected that comparative genomics of root-knot nematodes should expand in the near future, and the pathogenic peculiarities of *M. enterolobii* will certainly constitute a strong argument for its inclusion in such studies. From the plant side, the recent cloning of the resistance gene *Mal* in *Prunus*, and the discovery of its very unusual molecular structure (Claverie *et al.*, 2011), provides an opportunity to characterise the determinants of the specificity of the plant-*Meloidogyne* interaction, and/or the molecular basis of the polyphagy of these parasites. Considering the extreme pathogenicity of *M. enterolobii*, and the current lack of appropriate control methods against it, a better understanding of the nematode biology will surely shed light on the origins of its parasitic success, and lead to the development of new and efficient control strategies.

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