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REVIEW

Diversity, distribution, and biological control strategies of plant parasitic nematodes: insights from Morocco within a global context—a comprehensive review and future research perspectives

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Abstract

Background The privileged geographical position of Morocco as a Mediterranean country confers upon it a pivotal role in both regional and global food security. Leveraging its diverse geography and varying climate, the country contributes significantly to the worldwide supply chain by cultivating a wide array of crops. However, the extensive use of chemicals in the production process, particularly for pest management, has led to substantial degradation of environmental resources. Plant parasitic nematodes (PPNs) pose a significant threat to agricultural productivity, causing considerable crop yield losses. With growing concerns about the environmental and human health impacts of nematicides, restrictions on their usage have prompted the exploration of alternative control strategies for effective safe PPNs management.

Main body The present review provides a comprehensive overview of research on plant parasitic nematodes (PPNs) in Morocco. It covers PPN taxa inventory, diversity, prevalence on different crops, and responses to environmental factors. The review also maps the distribution of the most dangerous genera, analyzes biological control methods for root knot nematodes *Meloidogyne* particularly, and identifies gaps and future research needs for sustainable PPN management. A total of 61 genera of PPNs were identified in Morocco, with *Meloidogyne* spp. being the most prevalent and dangerous genus, posing a serious threat to crop production in the country. The extensive distribution of PPNs, notably root knot, may be attributed to factors such as contaminated plant material and a lack of farmer awareness. Biological agents from Morocco's ecosystems, including plant extracts, nematophagous fungi, and entomopathogenic nematodes, showed great potential as control agents for root knot nematodes. This review significantly contributes to Mediterranean and global nematological knowledge by providing insights into the diversity and sustainable management of plant parasitic nematodes.

Conclusion The biological richness of Moroccan ecosystems can provide valuable resources for researchers in developing commercial effective bionematicides for plant pests.

Keywords Soil · Biological control · Sustainable management · Agrosystem · Nematicide

Introduction

Agriculture plays a crucial role in global food security and human development. In Morocco, the agri food sector is a significant driver of economic and social progress, contributing 21% to the gross domestic product and employing nearly 39% of the workforce, with 73.7% of jobs located in rural areas (Elboukhary et al. 2020). Encompassing an extensive land area of almost 8.7 million hectares, the utilized agricultural area (UAA) encompasses diverse agroclimatic systems, enabling the production of a wide range of agricultural products. In 2017, agricultural exports accounted for more than 22% of total exports, totaling around $5.57 billion. Moroccan agricultural exports have experienced substantial growth (59%) since 2010, with the European Union being the primary market for Moroccan products (Lahlali et al. 2022).

Nevertheless, various biotic and abiotic factors contribute significantly to yield losses in agriculture. Abiotic factors such as climate change, drought, desertification, pollution, and soil degradation are primary concerns affecting agriculture in Morocco due to the unsustainable utilization of

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natural resources (Salhi et al. 2020). Among the biotic factors, plant parasitic nematodes (PPNs) play a crucial role in causing root damage, leading to significant reductions in crop yields. PPNs affect nearly all crops (Sasser 1980), and their influence on global agricultural production losses has been quantified to be greater than 25% (Nicol et al. 2011), translating to an economic range of 100–157 billion USD per year (Sasser and Freckman, 1987; Koenning et al. 1999). It is worth noting that this estimate may be conservative, especially in developing countries where many farmers lack awareness of PPNs. These pathogens are often inconspicuous in the soil, and the symptoms they induce are often nonspecific (Jones et al. 2013). Approximately 4.000 known species of PPNs exist across all major biomes (Press and Phoenix 2005). A list of the top 10 nematodes was constructed based on their scientific and economic importance and broad host range (Jones et al. 2013).

The greatest challenge facing agricultural production systems is the simultaneous achievement of productivity and less environmental damage (Garrett et al. 2017). While crop losses can be mitigated through the application of highly toxic soil fumigants or non-fumigant nematicides, the economic burden of these chemicals poses a significant obstacle for many farmers (Elling 2013). Moroccan agriculture has undergone intensification since the twentieth century, marked by the introduction of chemical fertilizers, mechanization, and new irrigation techniques (Schilling et al. 2012). Despite potential dangers, 95% of farmers utilize chemicals in the production process, highlighting a concerning lack of awareness (Rhioui et al. 2023). The "Green Morocco Plan" (2008–2018) has successfully led to a remarkable increase in crop yields. However, this policy has also contributed to environmental resource degradation (Croitoru and Sarraf 2017). The use of chemicals for plant protection has been linked to biodiversity loss and human health issues, especially with uncontrolled use by farmers (Farahy et al. 2021). These substances face current restrictions under more stringent European legislation, given that the European Union is a key partner for Morocco (Marchand 2017).

Morocco recently launched the "Green Generation 2020–2030" agricultural strategy to enhance the profitability and sustainability of farming through the adoption of production systems that preserve soil health, ecosystems, and public health (El Bilali et al. 2021). Consequently, the search for alternative pest management methods, particularly for PPNs, has become imperative. Biopesticides have emerged as crucial components of environmentally friendly pest control strategies today (Glare et al. 2012).

Within this context, this review aims to (i) compile an inventory of all reported plant parasitic nematodes (PPNs) in Morocco, discussing their biodiversity, distribution, response to environmental factors, prevalence, and economic importance; (ii) create a distribution-prevalence map specifically focusing on the most dangerous PPNs; and (iii) establish a comprehensive database encompassing all biocontrol tests conducted for PPN management in Morocco to date.

The surveyed crops and their importance

Based on the bibliography, studies on PPNs in Morocco have primarily focused on nine crops of great local and global importance, which can be classified into three types: tree crops (olive, citrus, and argan trees), perennial crops (grapevines and saffron), and annual crops (organic vegetables, watermelon, strawberry, and wheat). The olive tree (*Olea europaea* ssp. *europaea* L.) covers approximately 57% of the total wooded area, making it a major fruit crop. In 2019, olive crops occupied 1.020.569 hectares, with a total production of 1.039.117 tons (Tabet 2020). Three types of olive-growing systems can be distinguished in Morocco: traditional orchards (80–400 trees/ha), high-density orchards (up to 1800 trees/ha), and wild olives in the High Atlas Mountains (Ali et al. 2017). *Citrus* fruits play a significant role in Morocco's agricultural landscape. In 2016, the total citrus-growing surface was more than 126.600 hectares, with 32% located in Souss Massa, 20% in Gharb, 16% in Moulouya, and 13% in Tadla, yielding an annual production of 2.6 million tons, positioning Morocco as the second largest supplier after Spain (Jaouad et al. 2020; Lahlali et al. 2021). *Argania spinosa* L. Skeels, an endemic non-cultivated tree found in the vast fragmented forest of approximately 800.000 hectares in west-central Morocco (Msanda et al. 2021), holds significant economic value for the local population due to its production of argan oil, known for its high quality in both culinary and cosmetic applications (Koufan et al. 2020). Viticulture has grown considerably under the Green Morocco Plan (2008–2018), with 38.200 hectares and 172.000 tons allocated for table grapes, and 10.800 hectares and 58.000 tons allocated for wine grapes (Mokrini 2019). Although Morocco is renowned for producing high-quality saffron, increased attention and intensification of saffron cultivation have been observed in the Taliouine and Taznakht regions due to initiatives like the Green Generation 2020–2030 ministerial strategy (Benjlil et al. 2020). Organic farming has also attracted significant attention and benefited from the allocation of additional land to encourage more sustainable crops, with 11,000 hectares of organic land area in 2019 (EL Bilali et al. 2021). Watermelon has been an important crop for many years, with noticeable increases in both area and production over the past five decades. In 2018, the total cultivated area reached 17.600 hectares, with an average plant density of 3.000 plants/ha (Laasli et al. 2021). Cultivation of red fruits, including strawberry, raspberry, and blueberry fruits, has proved to be a lucrative venture, with production concentrated in the Loukkos basin and Souss Massa region, contributing to sales exceeding three billion DH in 2016/2017 (Harbouze et al. 2019). As of 2017, the total area dedicated to raspberry cultivation reached 2,040 hectares, yielding an estimated 24.580 tons primarily designated for export. Cereals constitute a substantial portion, accounting for 59% of the overall agricultural area in Morocco. During the 2019–2020 campaign, approximately 80 million tons of wheat (*Triticum* spp.) were produced (MAPMEFDR, 2019).

Diversity of phytoparasitc nematodes in Morocco

Surveys play a crucial role in disclosing the biodiversity, prevalence, and significance of PPNs. They provide valuable insights into PPN communities, host areas of prevalent species, and the pathological problems they cause (Abebe et al. 2015). Accurate information about targeted specimens is essential for any nematode management or control plan. In Morocco, the first recorded instance of PPNs dates back to 1982 when four *Meloidogyne* species *M. hapla, M. javanica, M. incognita* and *M. arenaria* were reported in various agricultural areas (Janati et al. 1982). Since then, numerous studies on PPNs have been conducted across different regions and crops (Fig. 1), with 14 focusing on PPN biodiversity (Table 1) and others on molecular and morphological characterization of specific species, including *Meloidogyne morocciensis* (Rammah and Hirschmann 1990), the cereal cyst nematode *Heterodera latipons* (Mokrini et al. 2012), dagger nematode *Xiphinema diversicaudatum* (Mokrini et al. 2014; Mokrini et al. 2019a, b), *Pratylenchus* and *Heterodera* (Meskine et al. 1993; Mokrini 2016). The studies on PPN diversity spanned a wide range of crops (Table 1), including olive trees (4 surveys), citrus trees (1 survey), argan trees (1 survey), saffron (2 surveys), grapevines (1 survey), organic

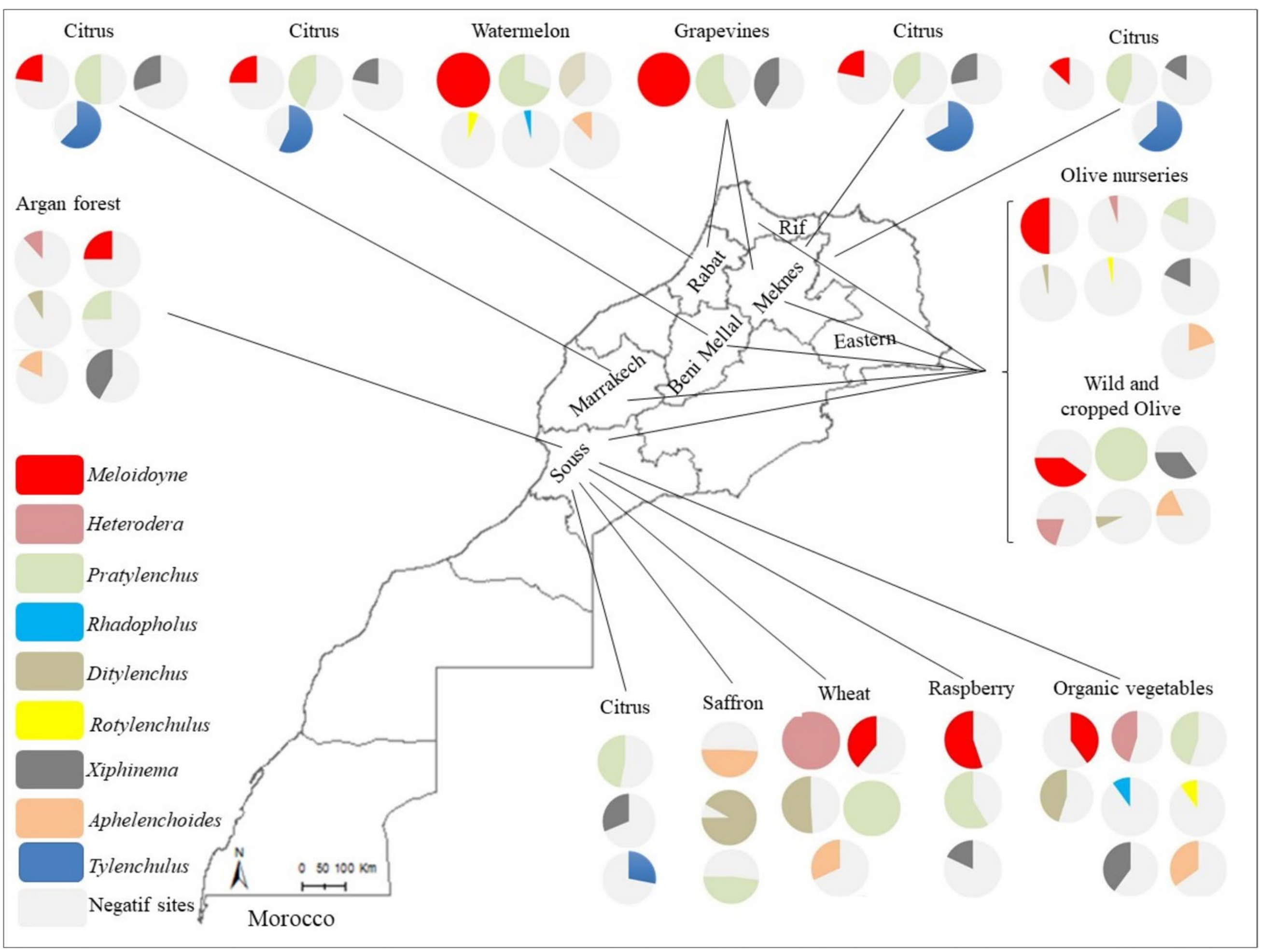

Fig. 1 Geographic distribution and prevalence of the most dangerous PPNs associated with economically important crops in different regions of Morocco. Each pie chart illustrates the frequency of a nematode genus at the surveyed sites, indicating the percentage of sites where this genus was identified

Table 1 Summary of Plant Parasitic Nematode Surveys in Morocco: Crops and Associated Genera

Location	crops	Reported taxa	FR/Dom genera	references
Sous Massa Haouz	Wild and cropped olive	**14 genera**: *Ditylenchus, Tylenchorynchus Aphelenchoides, Pratylenchus, Helicotylenchus, Rotylenchus, Criconema, Paratylenchus, Heterodera, Longidorus, Xiphinema, Hoplolaimus, Gracilacus,* and *Meloidogyne*	*Helicotylenchus, Rotylenchus, Pratylenchus, Meloidogyne*	Ait Hamza et al. (2015)
Souss, Haouz, Tadla, Zaïane, Guerouane, Kandar, and Rif	Wild, feral and cultivated olives	**47 genera**: *Helicotylenchus, Meloidogyne, Merlinius, Paratylenchus, Tylenchorhynchus, Tylenchus, Ditylenchus, Filenchus, Telotylenchus, Rotylenchulus, Zygotylenchus, Pratylenchus,, Criconema, Heterodera, Longidorus, Xiphinema, Aphelenchoides, Trichodorus, Paratrichodorus, Nothotylenchus, Psilenchus, Amplimerlinius, Bitylenchus, Scutylenchus, Basiria, Malenchus, Miculenchus, Ottolenchus, Boleodorus*, ***Coslenchus Aorolaimus, Cacoporus, Trichotylenchus, Trophurus, Paratrophurus, Discotylenchus, Irantylenchus, Aprutides, Cacopaurus, Aglenchus, Nagelus, Ogma, Criconemella, Neodolichorhynchus, Pratylenchoides, Rotylecnhus*** and ***Gracilacus***	*Filenchus, Xiphinema, Merlinius, Helicotylenchus, Rotylecnhus, Paratylenchus, Pratylenchus*	Ali et al. (2017)
Sous Massa Guerouane Jbala Haouz	Olive nurseries	**26 genera**: *Gracilacus, Helicotylenchus, Meloidogyne, Merlinius, Paratylenchus, Tylenchorhynchus, Tylenchus, Aorolaimus, Cacoporus, Ditylenchus, Filenchus, Telotylenchus, Trichotylenchus, Trophurus, Paratrophurus, Rotylenchulus, Zygotylenchus, Pratylenchus, Aorolaimus, Rotylecnhus, Criconema, Heterodera, Longidorus, Xiphinema, Aphelenchoides* and *Trichodorus*	*Helicotylenchus, Rotylenchus, Tylenchorhynchus, Tylenchus, Meloidogyne*	Aït Hamza et al.(2017b)
Sous Massa, Guerouane, Rif**,** Haouz Tadla	Olive trees	Study of specific diversity of *Meloidogyne* genus: **5 species** were detected *M. javanica* *M. arenaria, M. hapla, M. spartelensis* and an undescribed species *Meloidogyne* n.sp.	*Meloidogyne javanica*	Ali et al. (2016)

Table 1 (continued)

Location	crops	Reported taxa	FR/Dom genera	references
Souss, Haouz, Tadla, Zaïane, Guerouane, Kandar, Rif,	Olive nurseries and orchards	**25 genera**: *Ditylenchus,Tylenchorynchus Aphelenchoides, Pratylenchus, Helicotylenchus, Rotylenchus, Criconema, Paratylenchus, Heterodera, Longidorus, Xiphinema, Hoplolaimus, Meloidogyne, Filenchus, Telotylenchus, Rotylenchulus, Zygotylenchus, Trichodorus,Coslenchus*, *Trophurus,, Merlinius, Pratylenchoides*, *Criconematoides, Tylenchus* and *Aphelenchus*	*Meloidogyne, Pratylenchus, Helicotylenchus*	Laasli et al.(2023)
Marrakech Tadla Berkan Souss Massa Gharb	Citrus	**15 genera**: *Tylenchulus, Pratylenchus*, *Helicotylenchus*, *Xiphinema, Tylenchus, Paratylenchus, Tylenchorhynchus, Longidorus, Hemicycliophora, Criconemoides, Hoplolaimus, Scutellonema, Rotylenchus, Meloidogyne* and *Trichodorus*	*Tylenchulus* *Helicotylenchus Pratylenchus*, *Xiphinema*	Zoubi et al. (2022)
Souss Massa	Argan forest	**34 genera**: *Amplimerlinius, Merlinius, Aphelenchoides, Nagelus, Aphelenchus, Basiria, Neodolichorhynchus, Boleodorus,Neopsilenchus, Bitylenchus, Nothotylenchus, Cactodera, Ottolenchus, Coslenchus, Paratylenchus, Ditylenchus, Pratylenchoides, Filenchus, Pratylenchus, Helicotylenchus, Quinisculcius, Heterodera, Rotylenchus, Hoplolaimus, Sauertylenchus, Longidorus, Scutylenchus, Macroposthonia, Telotylenchus, Malenchus, Tylenchorhynchus, Meloidogyne, Xiphinema* and *Zygotylenchus*	*Telotylenchus, Paratylenchus, Xiphinema Helicotylenchus*	Mateille et al (2016)
Taliouine and Taznakht	Saffron (Crocus sativus)	**14 genera:** *Pratylenchus, Helicotylenchus, Tylenchorhynchus, Ditylenchus, Rotylenchus, Longidorus*, *Tylenchus, Hoplolaimus, Criconema, Aphelenchoides, Trichodorus, Xiphinema, Paratylenchus* and *Hemicriconemoides*	*Pratylenchus, Helicotylenchus, Tylenchorhynchus, Ditylenchus*	Mokrini et al. (2019a, b)
Taliouine and Taznakht	Saffron (*Crocus sativus*)	**15 genera**: *Aphelenchus, Ditylenchus, Tylenchus, Tylenchorynchus Aphelenchoides, Pratylenchus, Helicotylenchus, Rotylenchus, Dorylaimus, Anguina, Criconema, Paratylenchus, Heterodera, Zygotylenchus* and *Trichodorus*	*Aphelenchus, Ditylenchus, Tylenchus, Tylenchorynchus*	Benjlil et al. (2020)

Table 1 (continued)

Location	crops	Reported taxa	FR/Dom genera	references
Ben Slimane Meknes Marrakech Khemisset Bouznika	Grapevines	**6 genera**: *Xiphinema, Meloidogyne, Pratylenchus, Helicotylenchus, Paratylenchus* and *Tylenchus*	*Meloidogyne*, *Xiphinema*	Mokrini (2019)
Sous Massa	Organic vegetables	**24 genera**: *Axonchium,Tylenchorhynchus, Anguina, Tylenchulus, Aphelenchoides, Tylenchus, Aphelenchus, Xiphinema, Ditylenchus, Dolichodorus, Helicotylenchus, Heterodera, Hoplolaimus Longidorus, Meloidogyne, Pararotylenchus, Paratrichodorus, Paratylenchus, Pratylenchus, Radopholus, Anguina, Rotylenchulus, Rotylenchus* and *Trichodorus*	*Aphelenchus, Longidorus, Meloidogyne, Pratylenchus, Tylenchorhynchus, Tylenchus, Telotylenchus*	Alaoui et al.(2021)
Sous Massa	Organic vegetables	**12 genera**: *Helicotylenchus*, *Xiphinema, Pratylenchus, Paratylenchus, Tylenchorhynchus, Meloidogyne, Rotylenchus, Longidorus, Tylenchus, Hoplolaimus, Criconemoides* and *Trichodiorus*	*Meloidogyne Pratylenchus*	Krif et al.(2020)
Moulay Bousselham	Watermelon	**18 genera:** *Meloidogyne*, *Pratylenchus*, *Tylenchus*, *Helicotylenchus*, *Xiphinema*, *Ditylenchus, Hoplolaimus*, *Mesocriconema, Criconema, Aphelenchoides, Belonolaimu, Rhadopholus, Rotylenchulus, Scutellonema, Trichodorus, Longidorus, Tylenchorhynchus,* and *Paratylenchus*	*Meloidogyne*, *Pratylenchus*, *Tylenchus*, *Helicotylenchus*	Laasli et al. (2021)
Souss Massa	Raspberry	**12 genera:** *Helicotylenchus*, *Xiphinema, Tylenchus, Pratylenchus, Paratylenchus, Tylenchorhynchus, Meloidogyne, Rotylenchus, Longidorus, Tylenchus, Hoplolaimus* and *Criconemoides*	*Pratylenchus* *Meloidogyne Helicotylenchus Tylenchus*	Mokrini et al (2019)
Souss Massa	Wheat	**11 genera**: *Helicotylenchus*, *Tylenchus, Pratylenchus, Paratylenchus, Tylenchorhynchus, Meloidogyne, Heterodera, Longidorus, Hoplolaimus, Psilenchus* and *Merlinius*	*Pratylenchus* *Helicotylenchus* *Paratylenchus*	Laasli et al. (2022)
Gharb, Sais, Zaers,Tadla Doukkala, Chaouia,	Wheat and barely	**5 species**: *Pratylenchus neglectus, P.penetrans, P.thornei, Heterodera avenae* and *Merlinius brevidens*	*Pratylenchus penetrans*	Meskine et al., 1993)

Table 1 (continued)

Location	crops	Reported taxa	FR/Dom genera	references
Gharb, Saiss, Zaeir, Dokkala, Chaouia	Wheat, barely,	**6 species:** *Pratylenchus penetrans, P. thornei, P. pseudocoffeae and P. pinguicaudatus* *Heterodera avenae* and *H. latipons*	*Pratylenchus penetrans, Heterodera avenae*	Mokrini et al. (2009)

vegetables (2 surveys), watermelon (1 survey), cereals (3 surveys), and raspberry (2 surveys). Across all surveyed sites, a total of 61 genera of PPNs from 19 families were identified (Table 2). The most common genera across various crops were *Pratylenchus*, *Meloidogyne*, *Tylenchorenchus*, *Helicotylenchus*, *Tylenchus*, *Ditylechus* and *Xiphinema* (Table 1). Moroccan crops exhibit the prevalence of 9 out of the top ten most dangerous PPNs (Fig. 1) (Jones et al. 2013), showcasing their high adaptability to diverse climates and their polyphagous strategy. Among them, *Pratylenchus* was detected in all regions and crops, followed by *Meloidogyne*, which was absent only in saffron and citrus of the Souss Massa region. *Meloidogyne* and *Pratylenchus* were prevalent in major agricultural regions in Morocco (Rabat, Meknes, Marrakech, and Souss Massa) (Fig. 1), emerging as the most polyphagous and damaging PPN genera in Morocco, with *M. javanica* identified as the predominant species within *Meloidogyne* (Ali et al. 2016; Aït Hamza et al. 2017b; Janati et al. 2018). Conversely, *Pratylenchus penetrans* and *Heterodera avenae* were the most detected species in Moroccan cereals (wheat and barley) (Table 1).

Phytoparasitic nematodes associated with olive trees

A study was conducted at twenty-three olive-growing sites in Souss Massa and Marrakech regions, Morocco, to investigate nematode communities associated with olive trees, revealing 14 genera of PPNs (Ait Hamza et al. 2015) (Table 1), while this study focused only on the southern regions of Morocco (Souss and Marrakech). A complimentary investigation was carried out by Ali et al. (2017) to cover the main olive-growing regions in Morocco. Analysis of 213 samples from 94 sites spanning seven regions detected 117 species belonging to 47 genera of PPNs. Compared to Mediterranean countries, such as Spain (38 genera), Jordan (28), Italy (24), Greece (20), and Turkey (16) (Ali et al. 2014), the diversity of PPNs in Moroccan olives stands out as the highest. However, this number falls short of the global count of 56 (Ali et al. 2014). 11 genera being *Nothotylenchus Malenchus, Miculenchus Ottolenchus Cacoporus, Trichotylenchus, Paratrophurus, Cacopaurus, Nagelus, Neodolichorhynchus*, and *Aorolaimus* were exclusively associated with Moroccan olive trees (Table 1). On the other hand, 15 genera reported in global olive tree ecosystems, such as *Trophotylenchulus, Tylenchulus, Neopsilenchus, Quinisulcius, Radopholus, Hemicycliophora, Criconemoides, Crossonema, Hemicriconemoides, Mesocriconema, Neolobocriconema, Nothocriconema, Dolichodorus, Paralongidorus* and *Paraphelenchus,* were not observed in Morocco (Table 1) (Ali et al. 2014; 2017). This indicates significant variations and diversity within global olive tree ecosystems.

Table 2 Plant Parasitic Nematode genera reported in Morocco with their feeding types

Order	Family	Genus	Feeding types
Aphelenchida	Aphelenchidae	*Aphelenchus*	Fungivores
	Aphelenchoididae	*Aphelenchoides*	Fungivores
		Aprutides	Fungivores
Dorylaimida	Longidoridae	*Longidorus*	Herbivores—ectoparasites
		Xiphinema	Herbivores—ectoparasites
Triplonchida	Trichodoridae	*Paratrichodorus*	Herbivores—ectoparasites
		Trichodorus	Herbivores—ectoparasites
Tylenchida	Anguinidae	*Ditylenchus*	Fungivores
		Nothotylenchus	Fungivores
	Criconematidae	*Criconema*	Herbivores—ectoparasites
		Criconemoides	Herbivores—ectoparasites
		Criconemella	Herbivores—ectoparasites
		Hemicycliophora	Herbivores—ectoparasites
		Macroposthonia	Herbivores—ectoparasites
		Ogma	Herbivores—ectoparasites
		Mesocriconema,	Herbivores—ectoparasites
	Belonolaimidae	*Belonolaimus*	Herbivores—ectoparasites
		Neodolichorhynchus	Herbivores—ectoparasites
		Trichotylenchus	Herbivores—ectoparasites
		Tylenchorenchus	Herbivores—ectoparasites
		Quinisulcius	Herbivores—ectoparasites
	Heteroderidae	*Heterodera*	Herbivores—sedentary parasites
		Cactodera	Herbivores—sedentary parasites
	Hoplolaimidae	*Aorolaimus*	Herbivores—semiendoparasites
		Helicotylenchus	Herbivores—semiendoparasites
		Hoplolaimus	Herbivores—semiendoparasites
		Scutellonema	Herbivores—semiendoparasites
		Rotylenchus	Herbivores—semiendoparasites
	Meloidogynidae	*Meloidogyne*	Herbivores—sedentary parasites
	Merliniidae	*Pratylenchoides*	Herbivores—semiendoparasites
	Neotylenchidae	*Neotylenchus*	Fungivores
	Paratylenchidae	*Cacopaurus*	Herbivores—ectoparasites
		Gracilacus	Herbivores—ectoparasites
		Paratylenchus	Herbivores—ectoparasites
	Pratylenchidae	*Pratylenchus*	Herbivores—migratory endoparasites
		Radopholus	Herbivores- migratory endoparasite
		Zygotylenchus	Herbivores—migratory endoparasites
	Psilenchidae	*Psilenchus*	Herbivores—epidermal/root hair feeders
	Rotylenchulidae	*Rotylenchulus*	Herbivores—sedentary parasites

Table 2 (continued)

Order	Family	Genus	Feeding types
	Telotylenchidae	*Amplimerlinius*	Herbivores—ectoparasites
		Bitylenchus	Herbivores—ectoparasites
		Merlinius	Herbivores—ectoparasites
		Nagelus	Herbivores—ectoparasites
		Paratrophurus	Herbivores—ectoparasites
		Scutylenchus	Herbivores—ectoparasites
		Telotylenchus	Herbivores—ectoparasites
		Trophurus	Herbivores—ectoparasites
		Sauertylenchus	Herbivores—ectoparasites
	Tylenchidae	*Aglenchus*	Herbivores—epidermal/root hair feeders
		Basiria	Herbivores—epidermal/root hair feeders
		Boleodorus	Herbivores—epidermal/root hair feeders
		Coslenchus	Herbivores—epidermal/root hair feeders
		Discotylenchus	Herbivores—epidermal/root hair feeders
		Filenchus	Fungivores
		Irantylenchus	Herbivores—epidermal/root hair feeders
		Malenchus	Herbivores—epidermal/root hair feeders
		Miculenchus	Herbivores—epidermal/root hair feeders
		Neopsilenchus	Herbivores—epidermal/root hair feeders
		Ottolenchus	Herbivores—epidermal/root hair feeders
		Tylenchus	Herbivores—epidermal/root hair feeders
	Tylenchulidae	*Tylenchulus*	Herbivores—semiendoparasites

In the two regions (Souss and Marrakech) where Ait Hamza et al (2015) reported 14 genera, Ali et al. (2017) documented a total of 29 PPNs genera, which is double the former(Table 1). This observation revealed issues with morphological identification, which is not always precise due to confusion between certain taxa, especially within the Tylenchidae family.

A recent study conducted in the same region previously surveyed by Ali et al. (2015) found only 25 genera of PPNs under Moroccan olive trees (Laasli et al. 2023), significantly fewer than the 47 reported by Ali et al. (2015). The differences in taxa richness between the tree studies can be attributed to three main factors. Firstly, there are morphologic identification issues. Secondly, variations in the number of samples and their distribution across distances play a role. Finally, differences in the sampling period are significant, given the sensitivity of PPNs to climatic variations such as temperature and moisture. Ali et al. (2017) addressed these issues by increasing the number of samples across varied regions and utilizing molecular techniques for identification. Therefore, the study of Ali et al. (2017) is an essential contribution carried out in Morocco with global significance. Despite these variations, all studies agree that *Helicotylenchus, Pratylenchus,* and *Meloidogyne* are the most prevalent genera under Moroccan olive trees (Table 1; Fig. 1).

Furthermore, the impact of anthropogenic practices on PPN abundance and richness is evident. Non-cultivated olives (wild and feral) exhibit higher generic richness, while cultivated orchards show elevated abundance. Moreover, genera such as *Xiphinema*, *Longidorus*, and *Heterodera* were observed to be associated with natural ecosystems (wild olive), whereas *Meloidogyne*, *Pratylenchus*, and *Tylenchorhynchus* are favored under cultivated and high-density olives (Ali et al. 2017). This suggests the role of agricultural practices in fostering certain genera of PPNs, especially those with economic significance.

The abundance of PPNs in olive trees in the Souss region was significantly greater than that in the Haouz region, despite the latter having greater diversity. The Haouz region exhibited a prevalence of *Meloidogyne* syndrome (Fig. 1), which is potentially linked to the prevalent irrigation systems in this area (Ait Hamza et al. 2015). Nematodes of the genera *Helicotylenchus* and *Rotylenchus* are better adapted to rainfed conditions on cultivated or wild olive trees in the Souss region, consistent with findings by Castillo et al. (2010) across the entire Mediterranean Basin. Additionally, Landi et al. (2022) reported that the Telotylenchidae, Paratylenchidae, and Meloidogynidae families were more prominent in high-density olive orchard systems, potentially explaining the prevalence of genera from these families in the Haouz region. 19 genera were reported exclusively in the northern olive-growing regions (The genera written in bold in Table 1) (Ali et al. 2017). This can be explained by the high sampling effort (213 soil samples) covering a wide range of climates. It has been reported that climate, particularly rainfall and temperature, emerged as key factors influencing PPNs distribution from northern to southern Morocco (Mateille et al. 2016). The climate in northern Moroccan regions is humid and become more arid toward the south. Additionally, large proportion of samples collected in wild and feral olive areas (163 samples) may increase high PPNs diversity. As a second complementary study to cover all olive-growing types in Morocco, to understand why *Meloidogyne* is associated with high-density orchards in the most regions and to elucidate the community structure and taxonomical diversity of the PPNs associated with this crop, a survey conducted by Aït Hamza et al. (2017c) focused on twenty-five olive (*Olea. europaea. subsp. europaea*) nurseries and 49 orchards. Sixty-three species belonging to twenty-six genera were detected (Table 1). The prevalent genera included *Helicotylenchus*, *Rotylenchus*, *Tylenchorhynchus*, *Tylenchus* and *Meloidogyne*. *Meloidogyne* was found in more than 50% of surveyed sites (Fig. 1). *Meloidogyne* spp. was detected in nineteen Mediterranean Basin countries, indicating its economic significance and potential threat to olive trees (Koenning et al. 1999; Ali et al. 2014). A study by Ali et al. (2016) in the main olive-growing areas and wild olive trees in Morocco revealed the distribution of four species of *Meloidogyne* spp. (*M. javanica, M. arenaria, M. hapla*, and *M. spartelensis*) in addition to an undescribed species (*Meloidogyne* n.sp). The predominant species was *M. javanica,* which was found abundantly in all cultivated areas, especially in high-density olive trees. The distribution of *M. javanica* was attributed to dissemination from nurseries and specific cultural practices such as irrigation and tree density (Connor et al. 2014; Ali et al. 2016; Ait Hamza et al. 2017b) (Table 1). As a conclusion, Moroccan olives trees are menaced by the 7 most dangerous plant parasitic nematodes (Fig. 1) including *Pratylenchus* and *Meloidogyne*.

Phytoparasitic nematodes associated with *citrus* trees

Zoubi et al. (2022) conducted a study in the key citrus-growing regions in Morocco assessed the diversity of plant parasitic nematodes and factors affecting their community structure. The study identified fifteen genera of PPNs, with the most predominant genera being *Tylenchulus* (88% of the total samples), *Helicotylenchus* (75%), *Tylenchus* (51%), *Pratylenchus* (47%) and *Xiphinema* (31%). A species of dagger nematode, *Xiphinema diversicaudatum*, was reported in the Gharb citrus-growing areas (Mokrini et al. 2014). This species is known as a virus vector, responsible for transmitting viruses such as Arabis mosaic and ringspot viruses. Although this species is not known to cause direct damage to citrus trees, attention should be given to this nematode, especially concerning the risk of its spread through soil. This is particularly relevant as vineyards are often planted amid citrus orchards in several regions (Mokrini et al. 2014; Zoubi et al. 2022). The citrus nematode, *Tylenchulus semipenetrans*, a globally recognized threat to citrus plants, was the most common species and exhibited varying frequency and abundances across regions. It was highly prevalent in Meknes (67% of sampled sites) and less prevalent in Souss Massa (28%) (Fig. 1). *T. semipenetrans* is known for causing a slow decline, resulting in substantial yield losses ranging from 10–30% (Abd-Elgawad 2020). The widespread distribution of *T. semipenetrans* worldwide underscores its adaptability to diverse environmental conditions, with factors such as contaminated planting material, infected seedlings, organic amendments, irrigation, and machinery contributing to its prevalence (Abd-Elgawad and McSorley 2009; Kumar and Das 2019; Abd-Elgawad 2020). Zoubi et al. (2022) highlighted soil physicochemical parameters, including mineral nutrients (K, Ca, Na, and C) and organic matter content, as crucial factors influencing PPN communities in citrus orchards. Understanding these influences is vital for designing effective integrated pest management strategies (Bello et al. 2022).

Phytoparasitic nematodes associated with argan trees

A pioneering study by Mateille et al. (2016) in the Argan Biosphere Reserve aimed to assess the diversity of PPNs associated with argan trees. The study identified 34 genera, with *Telotylenchus, Paratylenchus, Xiphinema*, and *Helicotylenchus* being the most dominant (Table 1). Although root knot nematodes (*Meloidogyne*) and lesion nematodes (*Pratylenchus*) were present, their frequency and abundance were relatively low (Fig. 1) (appearing in 25% of the samples or less). Climate, particularly rainfall and temperature, emerged as key factors influencing nematode distribution in argan forests. The study pointed at the sensitivity of nematodes to soil moisture and aeration conditions, aligning with findings from other studies linking climate to PPN community distribution (Hunt et al. 2001). These results are consistent with those of other studies showing the influence of climate on the distribution of PPN communities (Neilson and Boag 1996; Aït Hamza et al. 2017b, a; Benjlil et al. 2020). The diversity of PPNs in the argan forest decreased with increasing aridity toward the southern region of the reserve. Surprisingly, PPNs were more abundant at sites with minimum mean temperatures in the coldest month (3–6 °C), contrary to the findings of several studies suggesting that higher temperatures can enhance nematode reproduction (Tzortzakakis and Trudgill 2005; Evans and Perry 2009). Mateille et al. (2016) did not report an influence of climatic factors on individual nematode taxa. Considering that the geographic range of each nematode species is determined by the optimal temperature for its life processes (Luc et al. 2005), this information is crucial. For instance, the reproductive and developmental rates of *Pratylenchus* are known to increase with increasing temperature (Duyck et al. 2012). To enhance the study of Mateille et al. (2016), future research should incorporate various biotic and abiotic factors, such as vegetation and soil parameters, recognized as significant drivers structuring soil nematode communities (Neher 2010). Integrating these factors into subsequent projects could provide a more comprehensive understanding of PPNs dynamics in relation to the unique argan tree ecosystem.

Phytoparasitic nematodes associated with saffron crop

The first study on PPNs diversity on saffron in Morocco was conducted by Mokrini et al. (2019a, b) in the primary region of saffron cultivation in Souss Massa region, particularly in the provinces of Taznakht and Taliwin (Fig. 1). The study reported the presence of 14 genera of PPNs. The most common PPNs in the Taliouine region were *Pratylenchus*, *Helicotylenchus*, *Tylenchorhynchus*, and *Ditylenchus* (Table 1). A second study by Benjlil et al. (2020) in the same region identified 15 genera of PPNs, with *Aphelenchus*, *Ditylenchus*, *Tylenchus*, and *Tylenchorhynchus* being the predominant genera observed in 90% of the sampled sites (Fig. 1). Both studies reported *Ditylenchus*, *Pratylenchus* and *Helicotylenchus* as the most prevalent genera in saffron crops (Table 1). However, although both studies were conducted in the same region, there were differences in certain reported genera such as *Xiphinema*, *Longidorus*, and *Criconematoides* (reported only by Mokrini et al. (2019a, b)) and *Aphelenchus*, *Anguina*, *Paratylenchus*, *Zygotylenchus* (reported by Benjlil et al. (2020)). This discrepancy is normal as the authors did not sample the same localities in the region; for example, the localities Siroua, Ouisselsate, and Taouyalt were not surveyed by Mokrini et al. (2019a, b). On the other hand, *Aphelenchus* was not reported by Mokrini et al. (2019a, b), possibly because some authors classify it as a fungal feeder nematode rather than a plant feeder. In both surveys, soil properties were revealed as the main abiotic factors impacting PPN communities. Moreover, Benjlil et al. (2020) noted the role of humidity, rainfall, and minimum temperature in shifting PPN assemblages.

PPNs diversity in Moroccan saffron differs from that reported other counties worldwide, such as Italy (Sheikh 2014), Spain (Cirujeda et al. 2016), India (Thakur et al. 2021), and the valley of Kashmir (Torrini et al. 2020). However, the genera *Ditylenchus, Aphelenchoides, Pratylenchus,* and *Helicotylenchus* were consistently identified as enemies of saffron worldwide. *Ditylenchus*, in particular, is known to cause a general yield losses of up to 62% (Jones et al. 2013). The critical question that future research on phytonematodes associated with saffron should address is the extent to which phytoparasitic nematodes impact saffron production. Understanding the impact of these nematodes is crucial for developing effective strategies to mitigate their effects on saffron cultivation.

Phytoparasitic nematodes associated with grapevines

Moroccan vineyards face various biotic constraints, including viral and cryptogamic diseases, insects, mites, weeds, and PPNs, all of which can limit productivity (Habbadi et al. 2021). A survey was conducted across different regions of Morocco to investigate the diversity of PPNs associated with grapevines, revealing a total of 6 genera of PPNs (Table 1). Globally, the main nematode parasites affecting grapevines include *Meloidogyne, Pratylenchus, Criconemella, Tylenchulus, Tylenchus, Helicotylenchus, Heterodera, Xiphinema, Paralongidorus*, and *Longidorus*, the last three genera, known to transmit viral diseases, such as grapevine fanleaf virus, to grapevines (Malik et al. 2022). The *Xiphinema index*, a species that serves as the vector for grapevine fanleaf virus (GFLV), was identified in several sampled vineyards in Morocco (Fig. 1), although the infestation levels remained below the threshold considered problematic according to Wilson and Barnes. (1992) (i.e., 3 nematodes per 100 cm^3). In terms of yield losses, the most damaging PPNs to grapevines are *Meloidogyne*, *Xiphinema*, *Criconemoides, Paratrichodorus*, and *Namidorus* (Addison and Fourie 2008; Walker and Stirling 2008).

Phytoparasitic nematodes associated with organic vegetables

Organic growers often encounter more frequent nematode problems than conventional farmers due to restrictions on synthetic chemical inputs, presenting limited options for pest management in organic fields (Briar et al. 2016). A survey conducted across various organic vegetable soil sites in the Souss Massa region by Alaoui et al.(2021) identified 24 genera of

PPNs, marking the highest number compared to that reported in a similar previous study in the same region (Souss Massa) by (Krif et al. 2020) (12 genera) (Table 1). The significant difference between these studies is possibly due to variations in sample size (59 for the first and 53 for the second), sampling season (March for the first and January for the second survey), sampled vegetable species (host or non-host for certain PPNs), or morphological identification issues. The prevalent genera included *Aphelenchus*, *Longidorus*, *Meloidogyne*, *Pratylenchus*, *Tylenchorhynchus*, and *Tylenchus* (Table 1). Globally recognized as the three most dangerous nematodes, *Meloidogyne*, *Heterodera* and *Pratylenchus* (Jones et al. 2013) were found in different percentages in the organic soils of Morocco: *Pratylenchus* in 56% of the samples, *Meloidogyne* in 51%, and *Heterodera* in 15% of the samples (Fig. 1). The prevalence of these genera differs according to vegetable species; for example, they were detected in 82% and 73% of sampled soils under tomato and onion, respectively, and were less prevalent under thyme plants (Krif et al. 2020). In a study under intensive vegetable cultivation, two species of root knot nematodes, namely *Meloidogyne javanica* (in 86.4% of samples) and *M. Incognita* (in 13.5%), were identified (Janati et al. 2018). Unfortunately, the first two studies didn't identify PPNs to species level in organic vegetables to make a comparison with intensive vegetables in order to develop appropriate strategies for their sustainable management, such as using resistant crops. An additional study is further recommended to assess and compare PPN species occurring in both organic and intensive vegetable cropping in a wide range of Moroccan regions, given that vegetables are one of the main crops in the country and are sensitive to PPNs.

Soil parameters such as texture, organic matter, pH, nitrogen, zinc, magnesium, copper, and moisture were identified as key drivers of the abundance, distribution, and community structures of PPNs (Alaoui et al. 2021). Despite the potential for severe damage by PPNs in organic farming, little is known about their densities and resulting damage on a global scale (Briar et al. 2016). In Germany, PPN can cause severe damage in organic farming, leading to complete crop loss, with yield losses exceeding 50% for crops such as carrots, onions, and cereals (Hallmann et al. 2007). In Morocco, both Alaoui et al. (2021) and Krif et al. (2020) lacked information on the potential damage caused by nematodes in organic farming systems and did not assess organic producers regarding nematode problems and associated crop losses. Such insights are needed for developing a sustainable management strategy for these crops.

Phytoparasitic nematodes associated with watermelon

Watermelon production faces substantial challenges, particularly from various pests, including aphids, viruses, and nematodes, with a notable impact from the root knot nematode (RKN) *Meloidogyne* spp. (Liu et al. 2015). A recent survey conducted by Laasli et al. (2021) in watermelon fields in northwestern Morocco aimed to assess the occurrence of PPNs, revealing the presence of 18 PPN taxa. The most common genera were *Meloidogyne, Pratylenchus, Tylenchus*, and *Helicotylenchus.* Similar findings have been reported globally (Luc et al. 2005; Abd-Elgawad et al. 2007; Marais et al. 2017; Bello et al. 2020). 11 PPN genera were detected in association with watermelon in Nigeria, with *Meloidogyne* being the most common, followed by *Helicotylenchus*, *Pratylenchus*, and *Scutellonema* (Bello et al. 2020). Numerous studies, including those mentioned above, have consistently highlighted watermelon susceptibility to *Meloidogyne* infestations. Infections by these nematodes have been shown to significantly reduce the biomass of watermelon plants, ultimately leading to yield loss (Dhankhar & Sharma 1986; Xing et al. 2006). These findings underscore the importance of ongoing research and management strategies to mitigate the impact of nematodes on watermelon cultivation.

Phytoparasitic nematodes associated with Raspberry

Despite its profitability, raspberry cultivation faces significant challenges posed by plant parasitic nematodes, which are prominent pests that cause yield reduction and economic losses in various regions of global production (Bélair 1991; Poiras et al. 2014; Mohamedova and Samaliev 2018). A study conducted by Mokrini et al. (2019a, b) in the Souss Massa region identified 12 genera of PPNs in 41 raspberry polytunnels. The most prevalent genera at the surveyed sites were *Pratylenchus*, *Meloidogyne* and *Helicotylenchus* (Table 1). In comparison, studies in Moldova reported 21 genera associated with raspberry (Poiras et al. 2014), while 60 genera were documented in the USA (McElroy 1977). Among the identified PPNs, the root lesion nematode *Pratylenchus* has emerged as the most common and damaging genus affecting raspberries (McElroy 1977; Zasada et al. 2015; Troccoli et al. 2021). This underscores the importance of addressing nematode-related challenges for sustainable and profitable raspberry cultivation.

Phytoparasitic nematodes associated with wheat crops

Notably, PPNs represent a significant biotic challenge, leading to a global reduction in production. The management of these pests presents formidable challenges (Smiley and Nicol 2009). A study conducted by Laasli et al. (2022) aimed to assess the diversity of nematodes associated with wheat in southern Morocco. The survey identified 11 PPN genera, with *Pratylenchus, Helicotylenchus,* and *Paratylenchus* being the most dominant. In contrast, *Heterodera, Pratylenchus, Meloidogyne, Anguina,* and *Paratrichodorus* are considered the most economically important genera, causing a notable reduction in wheat yield worldwide (Smiley and Nicol 2009; Jones et al. 2013) (Fig. 1). *Anguina* and *Paratrichodorus* were found in this survey. PPNs belonging to the genus *Pratylenchus* hold particular economic significance in wheat production systems (Castillo and Vovlas 2007). Several studies have highlighted that specific species within this genus can lead to a global reduction in spring wheat yields ranging from 20 to 69% (McDonald and Nicol 2005; Smiley et al. 2005; Toktay 2008). In Morocco, actual yield losses may be substantial, given the limited availability of nematological expertise and research. The absence of comprehensive data underscores the urgency of further research and efforts to address the impact of nematodes on wheat production in the region. Molecular and morphological techniques revealed the occurrence of four species of root lesion nematode (RLN) under Moroccan wheat, being *Pratylenchus penetrans, P. thornei, P. pseudocoffeae*, and *P. pinguicaudatus*, along with two species of cereal cyst nematode (CCN), *Heterodera avenae* and *H. latipons* (Meskine et al. 1993; Mokrini et al. 2009; Mokrini et al. 2012; 2016). *Pratylenchus penetrans* and *Heterodera avenae* were the most prevalent (Table 1). The infestation rate with *P. penetrans* reached 70% in soil and 60% at roots in the main wheat-growing regions (Gharb and Tadla). The CCN, *Heterodera avenae*, was prevalent in the Gharb and Dokkala regions (Mokrini et al. 2009; Meskine et al. 1993). Among RLN species, *P. penetrans* and *P. neglectus* are less widespread and damaging on cereals compared to *P. thornei* (Nicol et al. 2011). On the other hand, Smiley and Nicol. (2009) reported that *H. avenae* is the most widely distributed and damaging CCN species on cereals under a wide range of climates worldwide.

Management of phytoparasitic nematodes in Morocco

Nematode management transcends the simplistic approach of identifying a specific nematode pest and resorting to chemical nematicides for eradication. Relying solely on this approach is often impractical, as effective and environmentally safe chemical nematicides may not always be available or suitable for certain situations or for all nematode groups (endoparasitic, semiendoparasitic, and ectoparasitic nematodes). For example, endoparasitic nematodes reside within the roots, beyond the reach of nematicides. In addition, coexist in communities comprising a mixture of genera and species, each with varying sensitivities to specific nematicides. Moreover, the majority of chemical nematicides present environmental hazards, posing risks to non-target organisms, including humans, animals, and beneficial microorganisms (Xiang et al. 2018; Kim et al. 2018). Therefore, it is imperative to explore alternative nematode management methods that employ novel control methods, excluding synthetic chemicals to enhance sustainable agriculture. A comprehensive review of the literature reveals thirteen studies conducted in Morocco to investigate alternative methods to chemical nematicides. These studies can be broadly categorized into three types: those examining the nematocidal properties of plant products (10 papers), those exploring biogenic control through nematophagous fungi (2 papers), and those assessing the effectiveness of entomopathogenic nematodes against nematodes (1 paper) (Table 3).

Management of root knot nematodes (RKN) by plant extracts

The most research projects in Morocco have evaluated the potential of plant extracts and essential oils (EOs) as biopesticides against RKN (Table 3). Several extracts (dried powder, aqueous extract, hexane extract, emulsified oil, methanolic extract, and essential oils) from different plants collected in different regions of Morocco were tested, including *Senecio glaucus* subsp. *Coronopifolius, Asteriscus imbricatus, Pulicaria mauritanica, Artemisia herba-alba* and *Origanum compactum* (Asteraceae), *Ridolfia segetum* (Apiaceae), *Azadirachta indica* (Meliaceae),, *Lavendula dentate, Rosmarinus officinalis* and *Thymus satureioides* (Lamiaceae) (Lamiaceae), *Globularia alypum* (Plantaginaceae), *Hesperolaburnum platycarpum* (Fabaceae), *Argania spinaosa* (Sapotaceae) and *Ricinus communis* (Euphorbiaceae), *Citrus sinensis* (Rutaceae). The methanolic and aqueous seed extracts of *Piganom*

Table 3 Summary of biocontrol methods tested in Morocco for the control of root knot (*Meloidogyne* spp.) and of other nematodes

Biocontrol agent (BCA)	Original region	Phytochemical composition	Tested extract	Targeted nematode	Test conditions	Result: the most active product	Effective doses	Effect on yield	Authors
Argania spinosa Ricinus communis	S.M	Not mentioned	Amendment: Oil cake, argan dry shoots and neem cake	*M.* spp.	In vivo: Melon and cucumber	Reduce extremely the population of *Meloidegyne* (100%) and limit galling	5 T/ha	Improve plant growth	Azim et al. (2011)
Piganum Harmala	S.M	Alkaloids	Methanolic extract Aqueous extract Hexane extract Emulsified oil	*M. j*	In vitro	94.33% to 97% reversible nematostatic effect	368 ppm	–	Mayad et al. (2019)
Piganum Harmala	S.M	Alkaloids	Dryed powder Aquous extract Hexane extract Emulsified oil Methanolic extract	*M. j*	In vivo: Melon	Powder, aqueous extracts and oil seeds limit population growth and galling	2%	Seed oil is phytotoxic	Mayad et al. (2013)
Artemisia herba-alba, Origanum compactum Hesperolaburnum platycarpum Ricinus communis	S.M	Not detected	Methanolic extract	*M.j*	In vitro	Mortality: *R. communis* extract 29.67% *A. herba-alba* 26%	100 µg/ml	–	Mayad et al. (2006)
Biocontrol agent (BCA)	Original region	Phytochemical composition	Tested extract	Targeted nematode	Test conditions	Result: the most active product	Effective doses	Effect on yield	Authors
Senecio glaucus subsp.	S.M	Terpenic compound	Essential oil	*M. j*	In vitro	95% immobility 92% inhibition of hatch Nematostatic effect	16,000 ppm	–	Basaid et al. (2020)
Ridolfia segetum	S.M	Not detected	essential oil	*M. j*	In vitro	75.35% of hatch inhibition 71% immobility of J2	16 µL/mL	–	Basaid et al. (2021)

Table 3 (continued)

Biocontrol agent (BCA)	Original region	Phytochemical composition	Tested extract	Targeted nematode	Test conditions	Result: the most active product	Effective doses	Effect on yield	Authors
Biocompost: *Ricinus communis*	S.M	Not detected	Amendment: *Ricinus communis* powder	*M. j*	In vivo: Banana	*Ricinus communis* powder Reduced meloidogyne population with 65,77% and reduce gall index	100 g/plant	Improve plant growth	Ferji et al. (2006)
Azadirachta indica *Ricinus communis*	S.M	Not detected	Oil cake Dried and grounded aerial plant parts	*M. j*	In vivo: Tomato	Dried and grounded aerial plant parts of *Ricinus communis* reduce *Meloidogyne* population with 82,1% and reduce gall index	Not mentioned	Improve plant growth	Ferji et al. (2013)
Entomopathogenic nematodes (EPNs) of the genera: *Steinernema* and *Heterorhabditis*	–	Not detected	Entomopathogenic nematodes effectiveness root knot against nematode	*M. j*	In vivo: Tomato	Reduced J2s densities in the soil by 95% and in the root by 90% Reduced gall index and number of egg masses	25, 50 and 75 IJs cm^{-2} of soil	Increases in plant height and enhance root fresh weight	El Aimani et al. (2022)
Biocontrol agent (BCA)	Original region	Phytochemical composition	Tested extract	Targeted nematode	Test conditions	Result: the most active product	Effective doses	Effect on yield	Authors

Table 3 (continued)

Biocontrol agent (BCA)	Original region	Phytochemical composition	Tested extract	Targeted nematode	Test conditions	Result: the most active product	Effective doses	Effect on yield	Authors
Asteriscus imbricatus *Pulicaria mauritanica* *Lavendula dentate Globularia alypum*	S.M	Flavonoids Terpenes Alkaloids	Petroleum ether extract Chloroform extracts Aqueous extract	*M.*spp *M.*spp	In vitro In vivo*:* Tomato	Mortality: extract of *A. imbricatus* Chloroform extract: 92, 71% Petroleum ether extract: 89, 31% Chloroform and petroleum ether extract of *A. imbricatus* reduced the gall index	2000 ppm 6000 ppm	– Not signaled	Senhaji et al. (2018)
Artemisia herba-alba, Citrus sinensis, Rosmarinus officinalis and *Thymus satureioides*	M.Saf, M. At, B.M	Borneol, thymol, cis- and trans-thujone, camphor, 1,8-cineole and limonene	essential oils	*M. incognita* *P. vulnus* *X. index*	In vitro In vivo*:* Tomato	*A. herba-alba*: 94% mortality of *M. incognita* J2 and 100% mortality of X. index *R. officinalis* and *T. saturejoides:* 75% mortality of *P. vulnus* Soil fumigation or a water solution of EOs: reduction in gall index and J2 numbers	15 µg/ ml^{-1} 100 µg/kg^{-1} of soil	increase in plant biomass	Avato et al. (2017)
nematophagous fungi: *Paecilomyces, Purpureocillium, Trichoderma, Fusarium, Talaromyces, Arthrobotrys, Dreschslerella, and Monacrosporium*	S.M	–	Nematicidal effect of nematophagous fungi against						

Table 3 (continued)

Biocontrol agent (BCA)	Original region	Phytochemical composition	Tested extract	Targeted nematode	Test conditions	Result: the most active product	Effective doses	Effect on yield	Authors
Meloidogyne spp	*M.*spp	In vitro In vivo: Tomato	Maximal mortality of juveniles range from 64 to 73% using *Purpureocillium lilacinum* and *Arthrobotrys oligospora* None of the treatments showed significant effects	10^6 spores/ml	– Not signaled	Tazi et al. (2021)			
nematophagous fungi genera: The Orbiliaceae species *Talaromyces assiutensis* *Fusarium oxysporum* *Paecilomyces Trichoderma* *P. lilacinus* *P. chlamydosporia*	Cultured on Potato Dextrose Agar (PDA)	–	Nematicidal effect of nematophagous fungi against *Meloidogyne javanica*	*M.j*	In vitro	*Talaromyces* assiutensis killed all juveniles The Orbiliaceae species trap 50 to 80% of the J2s *Paecilomyces* and *Trichoderma* strains killed 30 to 50% of the J2s *Fusarium oxysporum* killed less than 20% of J2s *P. lilacinus and P. chlamydosporia* strains infected all the *M. javanica* eggs	Fungal strains were subcultured in Petri dishes with 100 J2 of *M. j*	–	Ait Hamza et al. (2017a)

Harmala were the most nematotoxic in vitro when applied at 2%, with toxicity levels ranging from 94.33 to 97% against immobile J2. Methanol and hexane extracts were found to be toxic at concentrations as low as 0.02%, resulting in immobile J2 percentages between 38.33 and 40% after 72 h. In vivo tests against *M. javanica* associated with *Cucumis melo* L. (melon) crops showed that the aqueous extract and powder applied at 2% and oil used at 0.2% and 2%, respectively, reduced *M. javanica* densities in the soil. These treatments minimized damage to melon crops and significantly improved various plant growth parameters. However, emulsified harmala oil exhibited a phytotoxic effect despite complete suppression of *M. javanica* (Mayad et al. 2013; 2019). Notably, variations between in vivo and in vitro tests may occur due to factors in the soil, such as the degradation of nematicide active ingredients, pH, organic compounds, and the chemical and biological characteristics of the soil. Temperature and other elements can also contribute to these variations (Forghani & Hajihassani 2020). In another study, the methanolic extract of *Ricinus communis* demonstrated the highest nematicidal activity on J2 larvae at a concentration of 100 µg/ml (29.67%), followed by *A. herba-alba* (26%) and *O. compactum* (18.03%) (Mayad et al. 2006). Additionally, the addition of dried and ground aerial parts of *Ricinus communis* to tomato and banana plants as amendments resulted in a substantial reduction in *Meloidogyne* populations in the soil, with an 82.1% decrease under tomato treatment and a 62.1% decrease under banana treatment (Ferji et al. 2006; 2013). Avato et al. (2017) reported that *A. herba-alba* essential oil (EO) induced 94% mortality of *M. incognita* juveniles after 24 h exposure to a 15 µg/ml and 100% mortality of *Xiphinema index* females in vitro (Table 3). This indicates that *A. herba-alba* EO is more effective against RKN compared to its methanol extract tested by Mayad et al.(2006). In the same study by Avato et al. (2017), essential oils from Moroccan ecotypes of *Citrus sinensis*, *Rosmarinus officinalis,* and *Thymus satureioides* were comparatively evaluated for their in vitro activity against *M. incognita*, *Pratylenchus vulnus*, and *Xiphinema index*. Mortality of *P. vulnus* reached 75% after a 96 h exposure to 15 µg/ml of *R. officinalis* EO. On the other hand, EO of *Citrus sinensis* showed weak activity against *M. incognita* and *X. index,* but was significantly active against *P. vulnus* (Table 3). The four EOs significantly reduced *M. incognita* infestation on tomato roots in vivo assays, with *A. herba-alba* EO being more active than the others. The application in aqueous solutions was less effective than fumigation treatments (Avato et al. 2017). In addition, all EOs increased tomato plants biomass (Table 3).

Senecio glaucus subsp. *coronopifolius* EO, at a concentration of 16,000 ppm, exhibited nematostatic effects, with 95% immobility of *M. javanica* J2 and 92% inhibition of egg hatching (Basaid et al. 2020). *Ridolfia segetum* EO, at a concentration of 16 µL/mL, inhibited *M. javanica* egg hatching by 75.35% after 10 days of incubation and resulted in 71% immobility rate of J2 after 72 h (Basaid et al. 2021). The study of Senhaji et al. (2018) revealed that petroleum ether and chloroform extracts of *Asteriscus imbricatus* induced significant mortality in *Meloidogyne* spp. in vitro at a concentration of 2000 ppm, reaching 89.31% and 92.71%, respectively. However, the aqueous extract had a mortality rate of 78.76% at a concentration of 20,000 ppm. In vivo tests on *Meloidogyne* spp. associated with tomatoes revealed that the petroleum ether and chloroform extracts of *A. imbricatus* exhibited significant nematicidal activity at 6000 ppm, while the aqueous extract was ineffective. Azim et al. (2011) studied the efficacy of oilcake-based amendments (Argan, neem, oilcake, and crushed castor leaves) to control the *Meloidogyne* spp. and on the agronomic parameters of cucumber and melon plants in greenhouses. In the melon pot experiment, argan and castor oil cakes were found to be the most effective than other treatments, resulting in the total suppression (100%) of nematodes present in roots and in soil larvae population. These oil cakes also led to 112% improvement in yield compared to that of the control. In cucumber cultivation, argan and castor oil cakes showed a reduction in gall formation, nematode density in the soil, and root infestation, as well as an improvement in plant height and yield compared to those of the control, while neem cake was less effective.

Nematophagous *fungi* from Morocco potentially biocontroling *Meloidogyne* spp

Over the past three decades, there has been an increasing focus on potential nematophagous fungi (NFs) for the management of phytonematodes. The use of local strains of these fungi has shown promising results in combating phytoparasitic nematodes, garnering interest in both developed and developing countries (Askary 2015). NFs can be classified into toxin-producing fungi, endoparasites, egg and female parasites, and nematode-trapping fungi (Jansson et al. 1997). Among the most important species are *Actylellina, Arthrobotrys, Aspergillus, Catenaria, Dactylellina, Hirsutella, Pochonia, Purpureocillium,* and *Trichoderma* (Abd Elgawad and Askary 2018). However, research in Morocco concerning the use of biocontrol agents for fungal species targeting nematodes is limited and still at an early stage. According to the literature, two studies have been carried out in this field to date (Table 3). The first study, led by Ait Hamza et al. (2017a), aimed to identify the occurrence and diversity of NFs isolated from olive tree nurseries and assess the in vitro their predatory potential against *M. javanica* juveniles (J2) and eggs. Morphological and molecular analyses revealed 19 NF species, from eight families and six orders. *Arthrobotrys* (from Orbiliaceae family) was the most diverse genus, with five species, followed by *Trichoderma,* with three species. While the abundance of fungal species was generally low (fewer than five strains per species), *Paecilomyces lilacinus* was found among 36 strains. In vitro tests demonstrated promising results, with *Talaromyces assiutensis* killing all the juveniles, *Arthrobotrys* trapping 50 to 80% of the J2s, and *Paecilomyces* and *Trichoderma* strains killing 30 to 50% of the J2s. *Fusarium oxysporum* was less effective than the other fungus and killed less than 20% of the J2s. Another noteworthy finding was that the *Purpureocillium lilacinus* and *P. chlamydosporia* strains infected all *M. javanica* eggs.

The second study, conducted by Tazi et al.(2021), aimed to evaluate the nematocidal activity of several previously isolated nematophagous fungi from olive tree nurseries (Ait Hamza et al. 2017a) both in vitro and in vivo. In vitro tests of *Purpureocillium lilacinum* and *Arthrobotrys oligospora* revealed maximal mortality of J2 ranging from 64 to 73%. However, *Talaromyces assiutensis* displayed low effectiveness against *M. javanica*, contrary to the findings of Ait Hamza et al. (2017a). Several studies have shown that *Arthrobotrys oligospora*, *Paecilomyces lilacinus*, and *Trichoderma harzianum* can be used as effective bioagents against *M. javanica*, *M. graminicola* and *M. incognita* (Spiegel and Chet 1998; Kiewnick and Sikora 2006; Singh et al. 2012; Jamshidnejad et al. 2013).

However, in vivo assays revealed that none of the treatments significantly affected the gall index or nematode population density compared to that of untreated tomato roots. According to Tazi et al. (2021), these results can be attributed to the experimental conditions favoring the development of *M. javanica* in the greenhouse during the summer, limiting the effectiveness of the NFs used. Soil parameters such as neutral pH, low nitrogen content, and low organic matter content also influence the performance of antagonistic fungi. Additionally, the NFs tested were isolated from an olive soil ecosystem and were used to control root knot nematodes in the presence of tomatoes, the preferred host of *M. javanica.* Similar interpretations have been reported in previous studies (Stirling et al. 1979; Duffy et al. 1997; Widmer et al. 2002). Using fungi as biological control agents (BAs) against plant parasitic nematodes requires a profound understanding of various factors affecting nematode efficacy, particularly soil physicochemical properties (pH, moisture, structure, temperature, etc.), the biocontrol agent's niche, root adhesion capacity, and the nature of host–parasite interactions (Spiegel and Chet 1998; Elshafie et al. 2006).

Biocontrol potential of entomopathogenic nematodes from Morocco against *Meloidogyne javanica*

Several studies have highlighted the antagonistic activity of entomopathogenic nematodes (EPNs) against plant parasitic nematodes (PPNs), particularly *Meloidogyne* spp. (Ishibashi et al. 1986; Grewal et al. 1997; Sayedain et al. 2021). In Morocco, the first and only study on this antagonistic effect was conducted by El Aimani et al. (2022), who aimed to evaluate the biocontrol activity of five local strains (SF-MOR9, EL45, EL27, HB-MOR7 and EL30) of EPNs (*Steinernema* sp., *Heterorhabditis bacteriophora*, and *Steinernema feltiae*) against *M. javanica* under greenhouse conditions.

The results indicated that all treatments significantly reduced the final nematode population density in both soil and roots compared to that in the positive controls. Notably, the *S. feltiae* strain (EL45), at doses of 50 and 75 infective juveniles (IJs) per cm^2, achieved a 95% reduction in J2 density in the soil and a 90% reduction in J2 in the plant's roots. The authors suggest that specific strains of *Steinernema feltiae*, particularly EL45 and MOR9, hold promise for effectively controlling harmful nematode populations in both soil and roots.

However, the tested EPNs also had a significant impact on plant growth parameters. An increase in plant height was observed when the *S. feltiae* strain (EL45) was applied at 50 IJ cm^2, while the *H. bacteriophora* strains (EL27 and HB-MOR7) produced the lowest plant heights. Additionally, compared with the positive control strain, the *Steinernema* strain (EL30) was the most effective at stimulating root growth.

These findings differ from those of Sayedain et al. (2021), who reported in a study of the antagonistic effect of three EPNs against *M. javanica* infecting cucumbers that *S. feltiae* produced no significant differences in pathogenicity indices or plant growth parameters compared to those of the control. These contrasting results might be attributed to the limited penetration capacity of *S. feltiae* into plant roots (Fallon et al. 2002) and the importance of the inoculation method. Previous studies have suggested that colonized cadavers exhibit more effective biocontrol activity than aqueous suspensions of IJs (del Valle et al. 2013; Kepenekci et al. 2016; Sayedain et al. 2021).

Overall, the successful eradication of root knot nematodes by EPNs is influenced by factors such as the inoculum dose, application time, species of both the PPNs and EPNs, and host plant species (Pérez and Lewis. 2002; 2004). While this study in Morocco provides valuable insights into the use of EPNs for the biological control of *M. javanica* on tomato plants, further research is recommended to explore all potential factors affecting the outcomes of using EPNs as biocontrol agents against root knot nematodes. The selection of local EPN species is encouraged, as they may be better adapted to local environmental conditions.

Conclusions and prospects

This review provides an updated inventory of PPNs in Morocco, highlighting progress in the search for biocontrol methods against crop pest nematodes, especially *Meloidogyne* spp. 61 genera of PPNs have been documented to pose a threat to various crops. The extensive distribution of PPNs, notably root knot and lesion nematodes, may be attributed to factors such as contaminated plant material and a lack of farmer awareness. Due to the decrease in chemical nematicide availability, the exploration of eco-friendly alternatives is urgently needed. While biocontrol studies using plant extracts and essential oils show promise, further optimization is needed. Moreover, Morocco's diverse plant species offer potential for discovering bioactive compounds for nematode control, necessitating in-depth investigations. Future research should encompass broader dimensions of PPN control, including host plant resistance, farming practices, environmental factors, and damage assessment. Addressing the gaps in understanding nematode ecology in both natural ecosystems and agrosystems is crucial for sustainable pest management. The integration of new technologies can sustain crop growth and address plant parasitic nematodes; collaborative efforts among researchers, policymakers, and farmers are needed to implement innovative, eco-friendly approaches for a resilient agricultural sector in Morocco.

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