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REVIEW

Phytopathogenic nematodes associated with olive trees (*Olea europaea* L.) in North Africa: current status and management prospects

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Abstract
The olive tree (*Olea europaea* L.) is a significantly important crop in an ecological, economic, and cultural manner, particularly in North Africa. Plant-parasitic nematodes (PPNs) are dangerous soilborne pathogens, particularly in olive nurseries, contributing to annual economic and yield losses. However, the impact of these nematodes on olive orchards and nurseries has been documented in only a few countries. This review aims to provide (1) an update on the current status of PPNs associated with olive trees in North African countries (Morocco, Algeria, Tunisia, Egypt, and Libya). (2) Reviewing their current diversity in different taxonomic levels and highlighting the frequencies of different taxa causing damage to olive trees, (3) describing their role as root and soil health bioindicators via potential affiliation with edaphic properties, and (4) listing current management strategies against PPNs in olives with a focus on integrated biocontrol methods. Dedicating more research topics to the nematode communities associated with olive trees is extremely important for assuring better management to reach cropping yield sustainability.

Keywords Olive · Plant-parasitic nematodes · North Africa · Management · Soil health

Importance of olive trees and current production trends

Olive trees (*Olea europaea* L.) are an important economic crop that has been cultivated for thousands of years in many parts of the world. The exact origins of olive trees are not well understood, but they are thought to have originated in the Mediterranean region and were likely domesticated by ancient civilizations in the region (El and Karakaya 2009). Olives and olive oil are highly valued for their culinary and medicinal properties, and olive trees are also an important source of wood, used for fuel and in the production of multiple products such as soap, furniture, and paper (Navas-Lopez et al. 2020).

Olive tree production is a significant global industry, with the world's leading producers being in Spain, Italy, Morocco, Greece, and Turkey (FAOSTAT 2022). However, olive trees are also grown in many other regions worldwide, including North Africa (NA). In the latter, Morocco, Egypt, Tunisia, and Algeria are among the largest producers of olives, with an estimated annual production of around 1.9, 1.08, 0.87, and 0.86 Mt, respectively (FAOSTAT 2022). Libya is also a significant producer of olives in the region, with an estimated annual production of around 140,175 metric tons (FAOSTAT 2022).

The Mediterranean olive is a widely cultivated tree that plays a significant role in the diet and economy of Mediterranean countries (Pérez-Jiménez et al. 2013). There are hundreds of olive varieties, each with unique characteristics,

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including fruit size, shape, and taste (Zbakh and El Abbassi 2012). In recent years, demand has been increasing for high-quality olive products, including olive oils (López-Miranda et al. 2010), which has led to the need for accurate and reliable methods for identifying and classifying olive varieties. However, this diversity has been threatened by a wide spectrum of pathogens including insects (e.g., *Saissetia oleae*, *Prays oleae*, *Palpita unionalis*, and *Bactrocera oleae*), airborne (e.g., *Pseudomonas syringae*, *Spilocaea oleaginea*), and soilborne (e.g., PPNs, bacteria, and fungi) pest and diseases (Ali et al. 2014).

Soilborne pathogens (SBPs) can have a significant impact on olive trees, causing a range of diseases that can affect tree growth and productivity (Table 1) (Cabrera and El-Borai 2018). In general, they can cause significant yield losses in olive production. For instance, Verticillium wilt can cause up to 100% yield loss in severely infected trees (Verhage et al. 2009), and Phytophthora root rot can cause severe yield losses, particularly in young trees or in areas with heavy, poorly drained soils (González et al. 2019). PPNs can also cause significant damage and yield losses by reducing the tree's ability to modulate water and nutrients (Cabrera and El-Borai 2018).

Given the importance and impact of these pathogens on olives production and the unfortunately limited information provided in NA, this review will cover (1) the current status of PPNs associated with olives trees in North African regions, (2) the interaction between these pests and edaphic patterns, (3) and the potential management strategies.

Incidence of phytopathogenic nematodes in North African olive tree orchards

General overview

PPNs are a diverse group of worms that feed on plants and can cause significant economic damage to agricultural systems (Keshari and Mallikarjun 2022). These pathogens are found in almost every corner of the world and can affect a wide range of crops, including cereals, vegetables, fruit trees, and ornamental plants (Bernard et al. 2017; Keshari and Mallikarjun 2022).

The economic impact of PPNs is significant, as they can reduce crop yields and quality, leading to financial losses for farmers and decreased food security for communities (Bernard et al. 2017). In addition, the management of these pathogens can be costly, as farmers may need to use specialized chemicals or adopt cultural practices to control nematode populations (Karuri 2022).

Olive trees (*O. europaea*) are known to be hosts for a variety of PPNs from over 30 genera (+100 species), such as *Pratylenchus* and *Meloidogyne* are found primarily on olive trees, while others as *Rotylenchulus* and *Helicotylenchus* are more commonly found as well (Castillo et al. 2010; Ali et al. 2016). Despite this, olive trees are generally able to thrive in dry, hilly areas where they are often grown, and in these conditions, nematodes generally do not cause significant economic damage to the trees (Castillo et al. 2010). Additionally, older olive orchards may have trees that are grafted onto wild olive rootstocks that have some level of tolerance to nematodes, while newer orchards may use cuttings from cultivars that are more resistant to nematode damage. However, it should be noted that olive trees can still be affected by nematodes, and in certain cases, these parasites can pose a threat to the health and productivity of the trees (Cabrera and El-Borai 2018). In NA, olive production is an important economic activity and a major source of income for many farmers. PPNs can have a significant impact, as they can reduce the vigor of olive trees and cause root decay, leading to reduced yields and lower-quality fruit (Castillo et al. 2010).

Diversity and distribution

Morocco

There are several genera of PPNs that are associated with olives in Morocco, including root-knot (RKNs), root-lesion (RLNs), spiral (SNs), and dagger (DNs) nematodes that can

Table 1 Major soilborne pathogens associated with olive trees (*Olea europea* L.)

Pathogen	Species	Symptoms	References
Verticillium wilt	*Verticillium dahliae*	Wilting, yellowing, premature leaf drop, cankers on trunk and branches	Verhage et al. (2009)
Phytophthora root rot	*Phytophthora cinnamomi*	Yellowing and wilting of leaves, tree death	González et al. (2019)
Olive knot	*Pseudomonas savastanoi*	Knots or galls on branches and trunk, deformity, reduced growth	Basim et al. (2019)
Root-knot nematodes	*Meloidogyne* spp.	Galls or knots on roots reduced growth and yield	Cabrera and El-Borai (2018)
Powdery mildew	*Oidium* sp.	White, powdery growth on leaves and branches	Bing et al. (2019)
Anthracnose	*Colletotrichum* sp.	Small, dark lesions on leaves, twigs, and fruit	Msairi et al. (2020)
Bacterial canker	*Pseudomonas syringae*	Cankers on branches and trunk, wilting of shoots	Kheira et al. (2019)

infect and damage roots and lower stems of olive trees (Ali et al. 2016). These nematodes feed on the roots and tissue of the tree, causing them to become stunted or even killed. Hamza et al. (2018) discussed the diversity of phytopathogenic nematode communities found in Moroccan olive nurseries and the potential impacts of these communities on the environment. They collected soil samples from several olive nurseries located in three agroecological regions (e.g., Souss Massa, Fes-Meknes, and Marrakech-Safi) and used molecular techniques to identify the distinct PPN species (Fig. 1). They found that the nematode communities in the olive nurseries were diverse, with a mix of native and introduced species. Thirteen nematode families were shown to be linked with olives including Telotylenchidae, Pratylenchidae, Longidoridae, and Hoplolaimidae (Fig. 2). The latter had the highest number of species identified (Fig. 2; Table 2). In terms of their occurrence, *Paratylenchus* spp., *Helicotylenchus* spp., and *Meloidogyne* spp. had the highest infestation frequencies (Table 2).

The RKNs are significant pathogens of olive trees, causing damage such as in many olive nurseries around the world (Hamza et al. 2017a). In Morocco, three species were encountered including *Meloidogyne incognita*, *M. javanica,* and *M. arenaria* (Table 2). Infestation with these nematodes can lead to significant reductions in plant growth, particularly in stem diameter. In addition, they can cause yellowing and defoliation of olive tree branches (Fig. 3). These symptoms have been observed in various locations around the world (Ali et al. 2014). This is due to their high adaptability to a wide range of temperatures. Controlled experiments have demonstrated the negative impact of *M. javanica* on various olive cultivars, which are commonly grown in the Mediterranean Basin. Interestingly, a new species of RKN, named *M. spartelensis* n. sp., was relatively identified in Northern Morocco based on molecular patterns (Ali et al. 2015). It has also morphological and morphometric features compared to the other RKNs.

The RLNs are migratory endoparasites that are widely distributed and capable of infecting a diverse range of plant species (Orlando et al. 2020). Among the nematodes that infect olive trees in Morocco, *Pratylenchus neglectus,* and *P. pinguicaudatus* were the most prevalent (Table 2). However, it is speculated that other species may be involved including *P. penetrans* and *P. thornei* (Hamza et al. 2018). Other

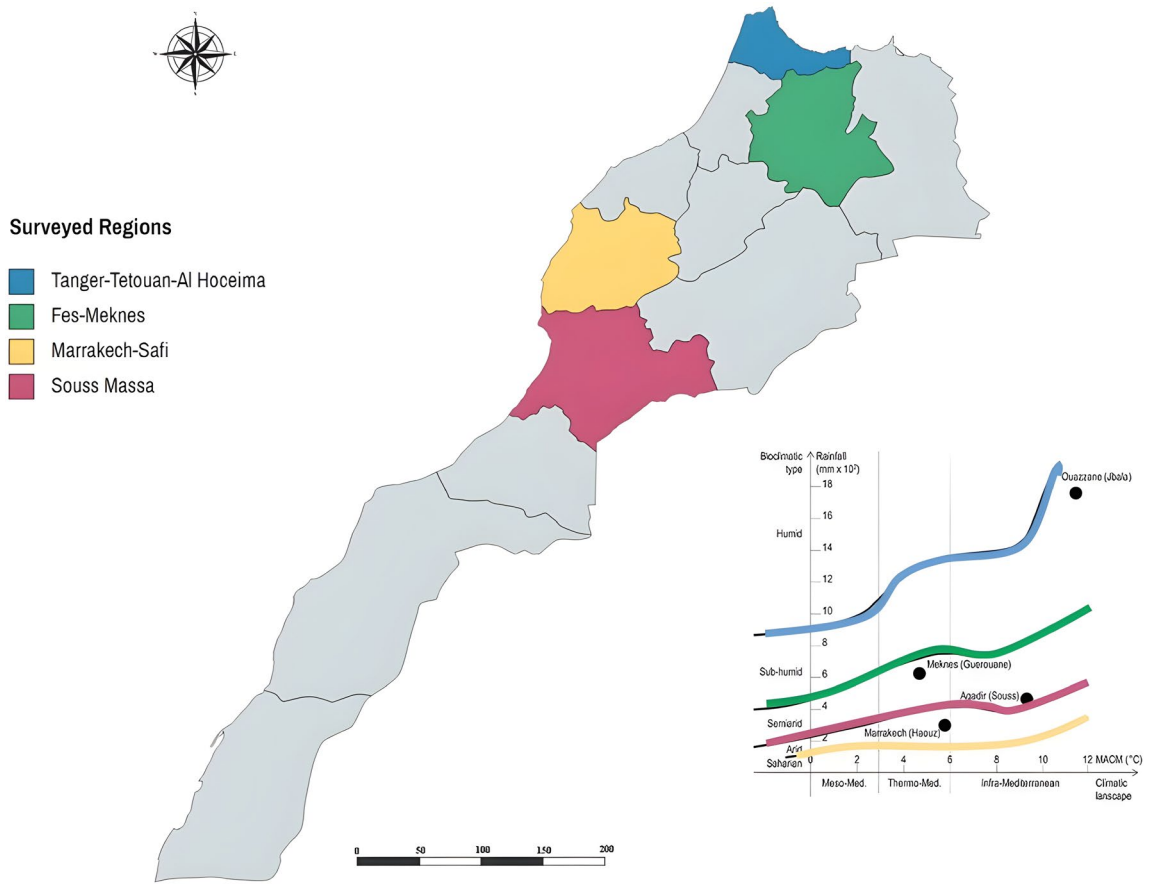


Fig. 1 Current agroecological regions surveyed for nematodes associated with Moroccan olive orchards and nurseries

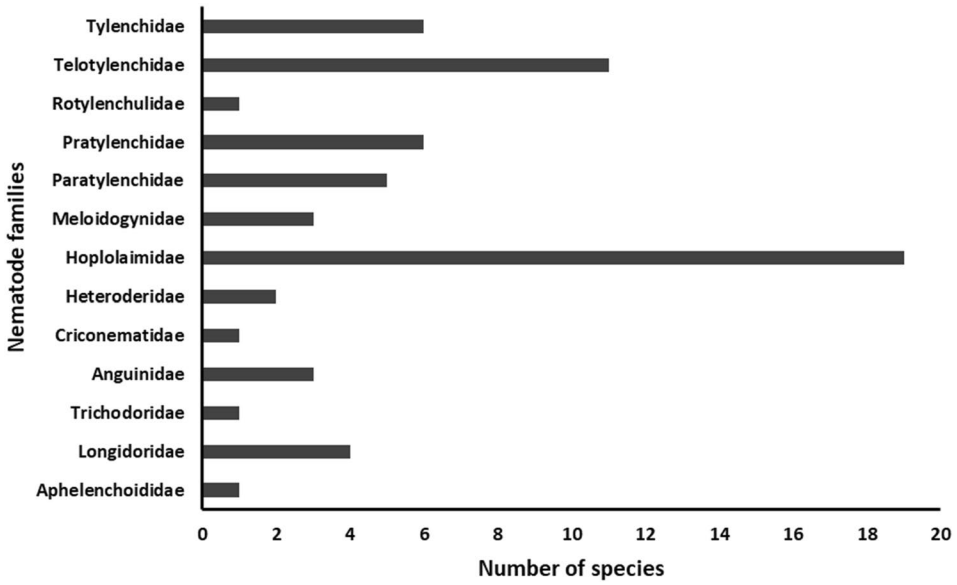


Fig. 2 Main PPN families obtained in Moroccan olives nurseries and orchards along with their respective number of species

studies have highlighted the diversity of these nematodes such as the presence of *P. zeae*, *P. mediterraneus*, *P. crenatus*, and *P. vulnus* (Nico et al. 2002; Cilbircioğlu 2007). Eventual infection can cause large necrotic areas on roots, and symptoms such as internode shortening, defoliation, and leaf chlorosis may also be observed (Orlando et al. 2020).

The occurrence of spiral nematodes (*Helicotylenchus* spp. and *Rotylenchus* spp.) has been well established in most Moroccan olive nurseries and orchards. A total of 11 species have been found belonging to the *Helicotylenchus* genus (Table 2) including *H. crassatus, H. digonicus, H. varicaudatus,* and *H. vulgaris* which were the most dominant (Hamza et al. 2018). *Helicotylenchus digonicus* is a dominant spiral nematode species in many olive orchards, with high prevalence in many regions (Palomares-Rius et al. 2012). However, other species (e.g., *H. oleae*) were found across Mediterranean countries (Inserra et al. 1979). On the other hand, four species of the *Rotylenchus* genus were found in Morocco (e.g., *R. goodeyi, R. buxophilus, R. robustus,* and *R. pumilus*) (Hamza et al. 2018) (Table 2). These nematodes can feed on the roots, leading to decreased water and nutrient uptake and ultimately reduced olive yield. They can be difficult to control due to their small size and ability to survive in a range of soil conditions (Sasanelli 2009).

Hamza et al. (2018) also analyzed the environmental factors that might be influencing the distribution and abundance of these nematodes, such as soil type and irrigation practices. They found that some of the introduced nematode species were more prevalent in nurseries with certain soil types and irrigation practices, suggesting that these factors may control the distribution patterns of these species.

Algeria

The olive crop has important trends in the economy of Algeria with an extensive value over the years. This value has been threatened by PPNs and caused significant damage to the most of national olive nurseries and orchards (Belahmar et al. 2015). Generally, there is limited information about the distribution and diversity of these pathogens in Algerian olive ecosystems which requires immediate research to be established. So far, the study conducted by Belahmar et al. (2015) provided novelties about the main PPNs presented in some Algerian olive-growing areas (Fig. 4). The bioclimatic conditions of the study sites varied considerably, suggesting diverse PPN patterns. A total of 16 nematode genera belonging to two main orders (Dorylaimida and Tylenchida) were identified including *Meloidogyne*, *Pratylenchus*, *Tylenchorynchus*, *Criconemoides*, *Boleodorus*, and *Xiphinema* (Table 3). Among these, *Pratylenchus* spp. was found to be the most dangerous and dominant, with high frequencies and population densities in both nurseries and orchards (Fig. 5; Table 3). These nematodes have the aptitude to cause significant damage to olive nurseries and orchards worldwide. Similarly, Chafaa et al. (2014) found that RLNs and RKNs are widely abundant in Northeast Algerian olive varieties. They assumed that this abundance is highly related to bioclimatic conditions, especially in the winter season.

Besides the RLNs, spiral nematodes (*Helicotylenchus* spp.) have been detected with high densities in the orchards (Fig. 5). The associated species feed on the olive rhizosphere in an ecto or endoparasitic manner, making them cosmopolitan pathogens (Cabrera and El-Borai 2018). On the other hand, the RKNs have only been recorded in two localities (Boumerdes and Mascara) and occurred in decent

Table 2 Phytopathogenic nematode communities associated with Moroccan olive trees

Family	Genus	Species	Infestation rate
Longidoridae	*Longidorus*	*Longidorus* sp.	+
	Xiphinema	*X. pachtaicum*	+
Trichodoridae	*Trichodorus*	*Trichodorus* sp.	+ + +
Anguinidae	*Ditylenchus*	*D. emus*; *D. equalis*	+ +
Criconematidae	*Criconema*	*Criconema* sp.	+ + +
Heteroderidae	*Heterodera*	*H. riparia*	+
Hoplolaimidae	*Aorolaimus*	*Aorolaimus* sp	+
	Helicotylenchus	*H. canadensis*	+ +
		H. crassatus	+ + + +
		H. crenacauda	+
		H. digonicus	+ +
		H. dihystera	+
		H. exallus	+
		H. minzi	+
		H. pseudorobustus	+
		H. tunisiensis	+
		H. varicaudatus	+ + +
		H. vulgaris	+ + +
	Hoplolaimus	*Hoplolaimus* sp.	+ +
	Rotylenchus	*R. buxophilus*	+ +
		R. goodeyi	+
		R. pumilus	+ +
		R. robustus	+ +
Meloidogynidae	*Meloidogyne*	*M. arenaria*	+
		M. incognita	+
		M. javanica	+ + + +
		M. spartelensis	+ +
Paratylenchidae	*Paratylenchus*	*Paratylenchus* sp.	+ + + +
		P. microdorus	+
		P. sheri	+
Pratylenchidae	*Pratylenchus*	*P. neglectus*	+ + +
		P. pinguicaudatus	+ +
	Pratylenchoides	*P. hispaniensis*	+ + +
	Zygotylenchus	*Z. guevarai*	+ +
Rotylenchulidae	*Rotylenchulus*	*Rotylenchulus* sp.	+ +
Telotylenchidae	*Merlinius*	*M. brevidens*	+ + + +
		M. microdorus	+
	Paratrophurus	*Paratrophurus* sp.	+ +
	Telotylenchus	*T. paaloofi*	+
		T. ventralis	+
	Trophurus	*T. sculptus*	+
	Trichotylenchus	*Trichotylenchus* sp.	+ + +
	Tylenchorhynchus	*T. clarus*	+ + +
		T. crassicaudatus	+
Tylenchidae	*Filenchus*	*F. filiformis*	+
		F. misellus	+
	Tylenchulus	*Tylenchulus* sp.	+ +
	Tylenchus	*Tylenchus elegans*	+ +

Infestation rates range from low (+) to high (+ + + +)



Fig. 3 Typical Root galling on olive trees caused by the root-knot nematodes (*Meloidogyne* spp.) (Photograph courtesy of Antonio via excelentesprecios 2019)

frequencies in both olive nurseries and orchards (Belahmar et al. 2015).

Rotylenchulus spp. (Reniform nematode) has been also detected by Lamberti et al. (1975). This nematode can cause yield loss affiliated with serious symptoms upon the occurrence in high densities. The most common symptom is the presence of galls, or swollen areas, on the plant's rhizosphere. The galls can be round, kidney-shaped (reniform), or elongated and can range in size from small to large (Castillo et al. 2003; 2010).

Tunisia

The olive industry is an important economic and agricultural sector in Tunisia. To increase olive production, many farmers are turning to intensive methods such as irrigation, new varieties, intercropping, and the use of integrated management approaches (Guesmi-Mzoughi et al. 2022). However, these methods may create a more favorable environment for pests and diseases including those of PPNs. In that manner, few research studies have been established to investigate the diversity and occurrence of PPNs infesting Tunisian olive orchards. For instance, Guesmi-Mzoughi et al. (2022) conducted for the first time a PPN screening in 10 olive-producing areas (Fig. 6). This study aimed specifically to determine which agronomic factors influence the reproduction and diversity of these nematodes. Eleven PPNs were identified, including *Helicotylenchus*, *Heterodera*, *Meloidogyne* (*M. incognita*, *M. arenaria,* and *M. javanica*), *Pratylenchus* (*P. neglectus*), *Rotylenchus*, *Tylenchorhynchus*, *Tylenchus*, and *Zygotylenchus* spp. (Table 4).

RLNs and RKNs have been shown to prevail in high densities (Fig. 7). This is due to the intensification through

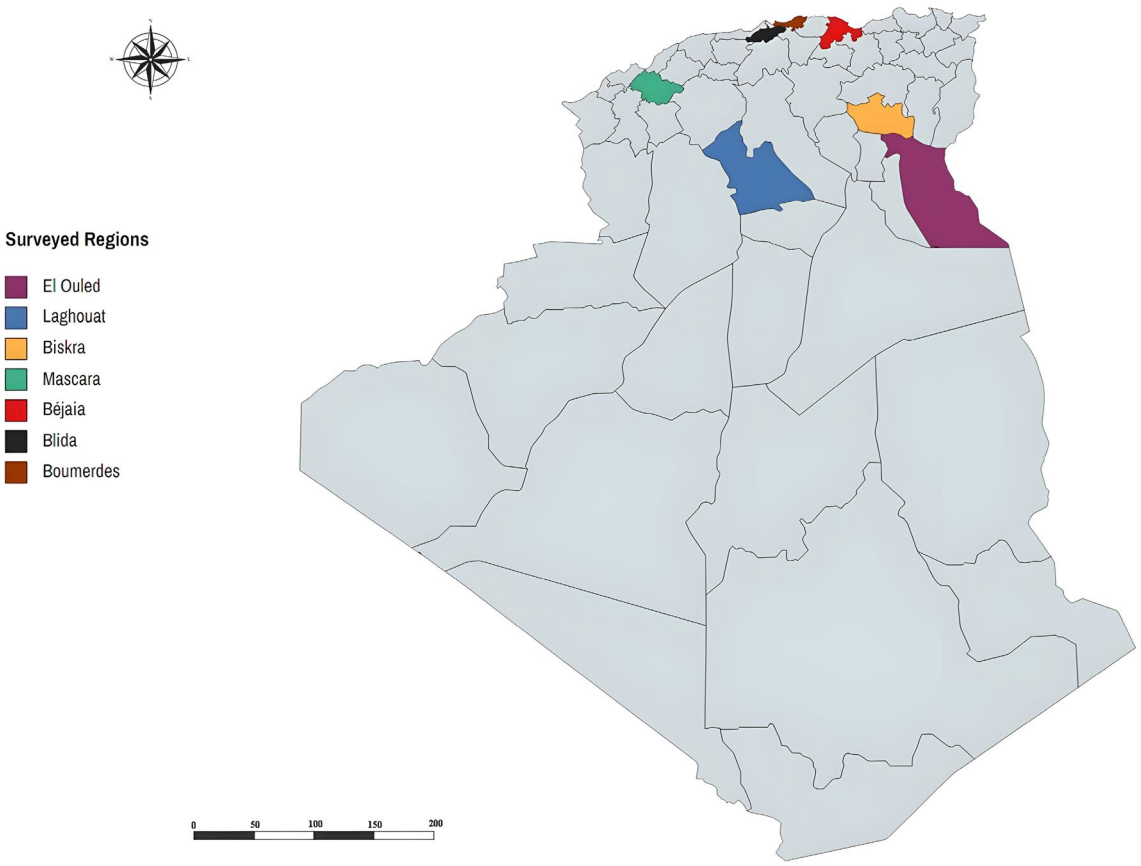


Fig. 4 Regions surveyed for PPNs of olive trees in Algeria

Table 3 Frequency of main nematode genera detected in Algerian olive nurseries and orchards

Family	Genus	Frequency (+)	
		Nurseries	Orchards
Longidoridae	*Xiphinema*	+ + +	+ +
Meloidogynidae	*Meloidogyne*	+ + + +	+ +
Pratylenchidae	*Pratylenchus*	+ + + +	+ + +
Hoplolaimidae	*Helicotylenchus*	+ + +	+ + + +
Tylenchulidae	*Paratylenchus*	+	+
	Tylenchulus	+ +	+
	Gracilacus	–	+
Telotylenchidae	*Tylenchorhynchus*	+	+ +
Criconematidae	*Criconema*	–	+
	Criconemoides	+	+
	Hemicriconemoides	–	+
Tylenchidae	*Boleodorus*	+	–
	Coslenchus	+	–
	Tylenchus	–	+
Belonolaimidae	*Telotylenchus*	–	+

Frequency rates range from high (+ + + +) to low (+); (-) no frequent

irrigation and intercropping as it could be a major factor in the reproduction and diversity of these nematodes (Guesmi-Mzoughi et al. 2022).

Other PPNs have been first time reported in Tunisian olive trees. In particular, a new species of cyst nematodes (*Heterodera mediterranea*) was diagnosed in diseased olive orchards (in the Monastir region) using molecular tools (e.g., ITS and D2–D3 regions) (Guesmi-Mzoughi et al. 2018) (Table 4). High infestation rates of this nematode species were observed in olive soil and root matrices. Another nematode species was the stunt nematode (*Tylenchorhynchus mediterraneus*) which was first reported in Center/Center East Tunisia and thus supposedly for the first time in NA (Guesmi-Mzoughi et al. 2016a). Furthermore, two new species of the spiral nematode (*Rotylenchus eximius* and *R. incultus*) were spotted in several localities (Guesmi-Mzoughi et al. 2016b).

Ectoparasitic nematodes were also widely explored across olive-growing areas in Tunisia. These nematodes have long life cycles and can cause damage to the foliage and fruit of the tree, leading to reduced crop yield. In addition, their special ability to transmit nepoviruses to different plants makes them even more dangerous (Decraemer and Robbins 2007).

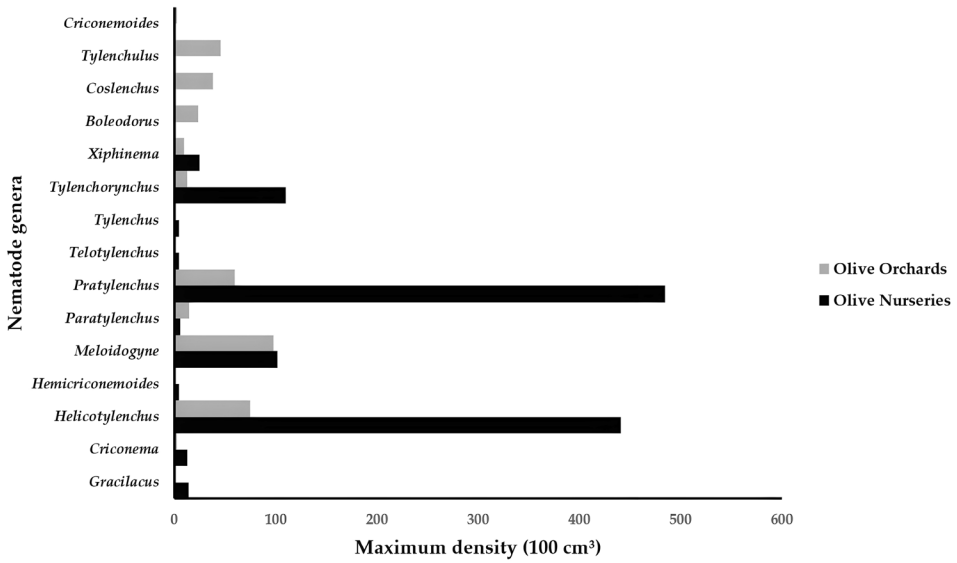


Fig. 5 Maximum density (per 100 cm^3 of soil) of phytopathogenic nematode genera associated with olive nurseries and orchards in Algeria

Dagger (*Xiphinema* spp.) and needle nematodes (*Longidorus* spp.) have been surveyed in several localities with cultivated olive (e.g., Chemlali and Chétoui) in Tunisia (Guesmi-Mzoughi et al. 2017). Five distinct species of *Xiphinema* were identified based on their molecular features including *X. italiae*, *X. meridianum*, *X. conurum*, *X. robbinsi*, and *X. pachtaicum*, while three species were reported from *Longidorus* including *L. glycines*, *L. euonymus*, and *L. africanus* (Table 4). Between the taxa, *Xiphinema* spp. exhibited the highest frequency.

Egypt

Phytopathogenic nematodes have been a tremendous threat to many crops in Egypt. In olive trees, most of the cultivars are particularly susceptible to nematode infestations, which can cause significant damage and yield loss (Ibrahim et al. 2010).

To date, four Egyptian governates (Ismailia, Alexandria, El-Behera, and Matrouh) were thoroughly surveyed for PPN presence in olive orchards (Fig. 8). A total of 12 nematode genera were detected, including *Meloidogyne*, *Pratylenchus*, *Helicotylenchus*, *Tylenchulus*, *Longidorus*, and *Xiphinema* (Ibrahim et al. 2010; Abdel-Baset et al. 2022). These nematodes have been infesting in different frequencies (Table 5), feeding on olive trees' rhizosphere, disrupting their physiological patterns, and ultimately weakening them (Cabrera and El-Borai 2018).

As anticipated, RKNs mainly represented by *M. javanica* and *M. incognita* were dominating all Egyptian olive fields with very high infestation rates of 90 and 96%, respectively (Abdel-Baset et al. 2022) (Table 5). This has serious implications for olive health attributes. For instance, it has been found that olive trees infected with *M. incognita* had significantly lower shoot and root growth compared to healthy trees. Moreover, they estimated that RKN infestations reduced olive tree growth and fruit production by up to 50% (Ibrahim and Mokbel 2009).

The occurrence of both genera (*Longidorus* and *Xiphinema*) has been well highlighted in Egyptian orchards. They were represented by three species *Longidorus africanus*, *L. elongatus*, and *Xiphinema elongatum*, respectively. At the species level, other PPNs were identified including *Helicotylenchus dihystera*, *Rotylenchulus reniformis*, and the citrus nematode *Tylenchulus semipenetrans* (Ibrahim et al. 2010).

Libya

General information on PPNs linked with olive orchards in Libya is extremely limited, despite the simultaneous importance of this crop and projections of new pests and diseases. A recent study conducted by Buarousha et al. (2020) investigated the incidence of PPNs in olive trees in the Eljabel Alakter region. Representative soil samples were taken from 17 different locations in the area and analyzed for the presence of nematodes. Results indicate that eight nematode genera are most common, including *Tylenchus*, *Helicotylenchus*, *Pratylenchus*, *Paratylenchus*, *Tylenchorhynchus*, and *Xiphinema*. *Tylenchus* spp. was the most frequent genus (55%), followed by *Aphelenchus* (48%). *Xiphinema pachtaicum* has also been identified based on morphological and morphometric features.

In addition to these nematodes, RKNs were reported to have occurred within Libyan olive orchards. Two main species, *M. incognita* and *M. javanica*, were detected with high prevalence rates (Edongali 1989).

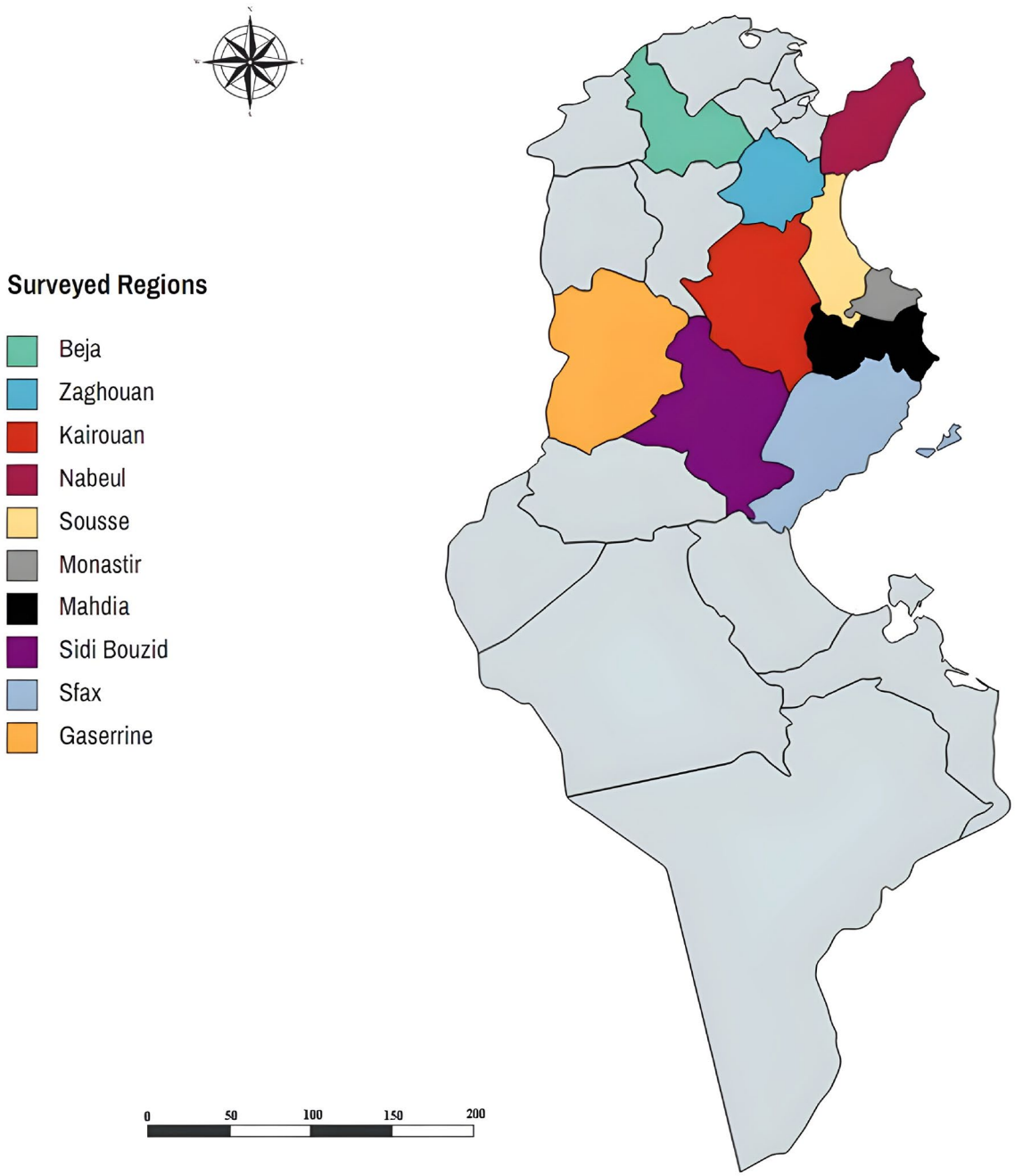


Fig. 6 Regions surveyed for phytopathogenic nematodes of Tunisian olive trees

Soil–nematode interaction patterns in olive trees

Relationship between phytopathogenic nematodes and edaphic factors

The study of nematode diversity and its correlation with edaphic proprieties in olive orchards revealed that different cultivars, orchards, and soil management practices, can impact these populations (Palomares-Rius et al. 2015). Additionally, the composition of PPNs was found to be closely tied to both the specific olive variety grown and the soil patterns. A correlation was observed between PPN community composition and various soil characteristics, such as pH, sand content, and exchangeable potassium, as well as climatic factors such as average maximum and minimum temperatures (Hamza et al. 2015). These findings indicate

Table 4 Nematode communities (to the species level) found in Tunisian olive orchards

Family	Genus	Species	Frequency (+)
Criconematidae	*Criconema*	*Criconema* sp.	+ +
Paratylenchidae	*Paratylenchus*	*Paratylenchus* sp.	+ +
Telotylenchidae	*Tylenchorhynchus*	*T. mediterraneus*	+
Tylenchidae	*Tylenchus*	*Tylenchus* sp.	+
Hoplolaimidae	*Helicotylenchus*	*Helicotylenchus* sp.	+ + + +
	Rotylenchus	*R. eximius*	+
		R. incultus	
Meloidogynidae	*Meloidogyne*	*M. arenaria*	+ + + +
		M. incognita	
		M. javanica	
Heteroderidae	*Heterodera*	*H. mediterranea*	+
Rotylenchulidae	*Rotylenchulus*	*Rotylenchulus* sp.	+
Pratylenchidae	*Pratylenchus*	*Pratylenchus* sp.	+ + + +
	Zygotylenchus	*Zygotylenchus sp.*	+
Longidoridae	*Longidorus*	*L. africanus*	+ +
		L. euonymus	
		L. glycines	
	Xiphinema	*X. conurum*	+ + +
		X. italiae	
		X. meridianum	
		X. pachtaicum	
		X. robbinsi	
		Xiphinema sp.	

Frequency rates range from high (+ + + +) to low (+)

that there is a wide range of PPNs found in association with olive cultivation and that the abundance and types of these nematodes can have differing effects on olive root health depending on the variety of olive being grown.

Another study established by Hamza et al. (2018) in Moroccan olive nurseries indicated that the soil's physicochemical factors had a relatively small impact on PPN diversity patterns. However, given that PPNs invest in their life cycle and that soil substrates often include mineral and organic amendments, they revealed that certain PPN species, such as *Meloidogyne* spp., *Telotylenchus* spp., and *Tricotylenchus* spp., were abundant in substrates that had intermediate particle sizes and high NPK amounts (nitrogen, phosphorus, and potassium). Conversely, other taxa, including *Helicotylenchus* spp., *Tylenchorhynchus* spp., and *Tylenchus* spp., were frequently found in organic soils.

Soil health bio-monitoring by terrestrial nematodes

The concept of "soil health" has recently emerged as a key area of study due to its importance in maintaining organic production, environmental quality, and plant health within a given ecosystem (Doran 2002). The structure of terrestrial nematode communities in the soil can provide valuable information on various processes occurring within the soil, food web, stability of agroecosystems, and soil biodiversity (Bongers 1990; Villenave et al. 2009). Nematode characteristics have been identified as useful bioindicators of agricultural soils, making them relevant for the study of environmental changes (Ferris et al. 2001). Studies have demonstrated that the nematode community can be used to evaluate soil quality in response to specific soil treatments (Bongers et al. 1997; Yeates et al. 1999; Laasli et al. 2022).

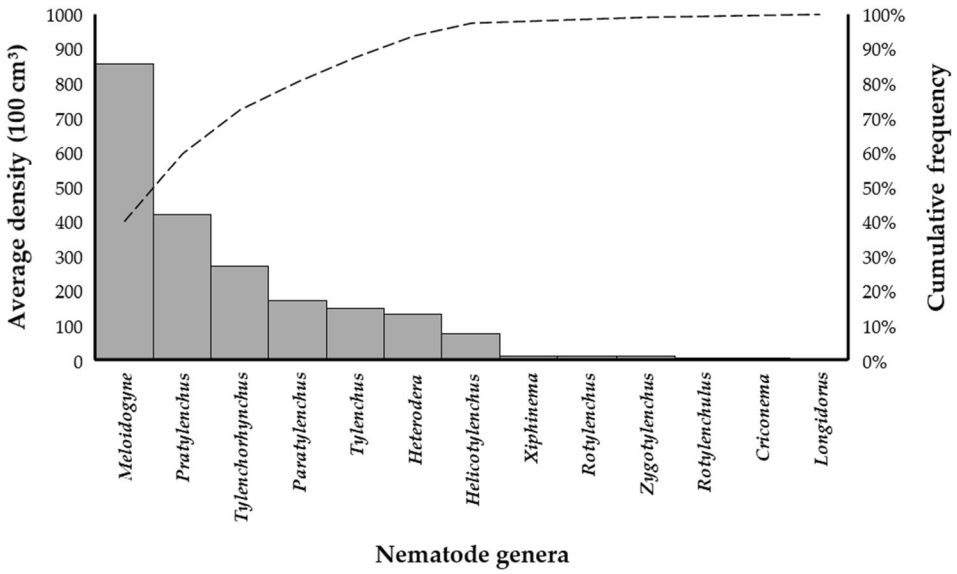


Fig. 7 Pareto chart plot displaying the main nematode taxa linked with olive trees in Tunisia

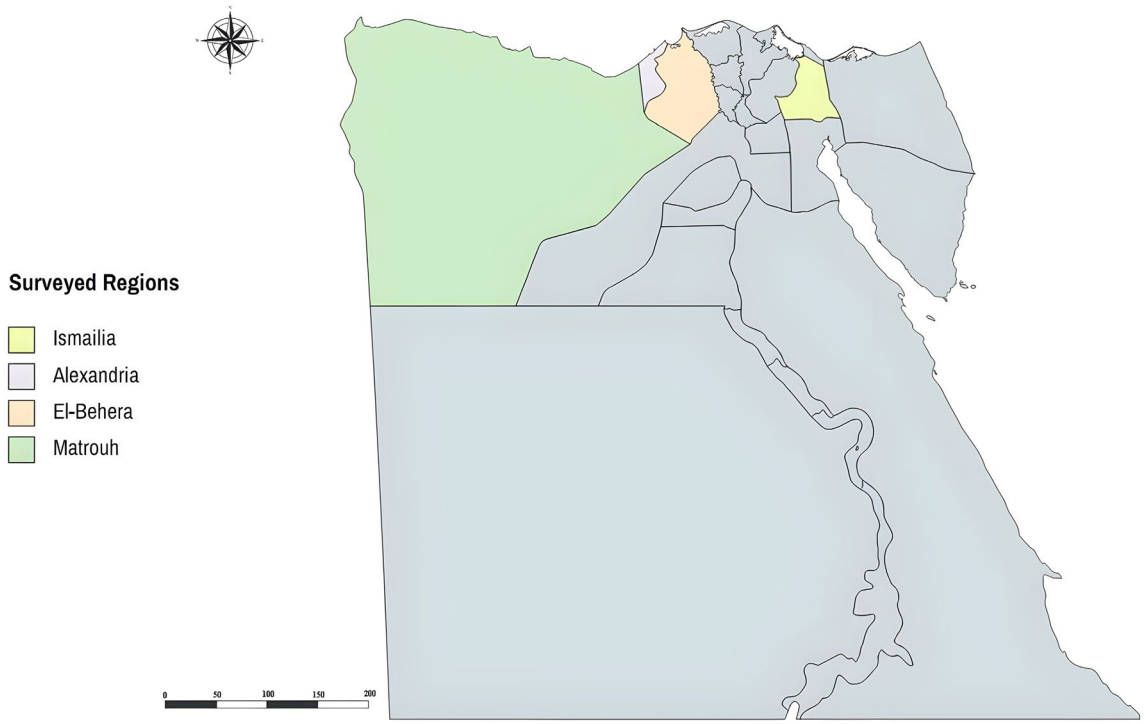


Fig. 8 Main governates surveyed for PPNs of olive trees in Egypt

Table 5 Nematode taxa associated with olive orchards in Egypt

Family	Genus	Species	Frequency (+)
Longidoridae	*Longidorus*	*L. africanus*	+ +
		L. elongatus	
		Longidorus sp.	
	Xiphinema	*X. elongatum*	+ +
		Xiphinema sp.	
Trichodoridae	*Trichodorus*	*Trichodorus* sp.	+
Criconematidae	*Criconemoides*	*Criconemoides* sp.	+
Hoplolaimidae	*Helicotylenchus*	*H. dihystera*	+ +
		Helicotylenchus sp.	
	Hoplolaimus	*Hoplolaimus* sp.	+
Meloidogynidae	*Meloidogyne*	*M. incognita*	+ + + +
		M. javanica	
Pratylenchidae	*Pratylenchus*	*Pratylenchus* sp.	+ +
Rotylenchulidae	*Rotylenchulus*	*R. reniformis*	+
Telotylenchidae	*Tylenchorhynchus*	*Tylenchorhynchus* sp.	+ +
Tylenchulidae	*Tylenchulus*	*T. semipenetrans*	+

Frequency rates range from high (+ + + +) to low (+)

In olive trees, there is a lack of information regarding the role of nematodes as soil and root health bioindicators. Recently, Guesmi-Mzoughi et al. (2022) discovered the effects of agronomic factors on nematode abundance. The study indicated that the use of irrigation in olive orchards and the cultivation of intercrops significantly impact the abundance and variety of PPNs that infect olive trees. Specifically, it has been observed that super-intensive olive orchards tend to have higher populations of RLNs, while the irrigated intercrops contribute to increasing RKN populations. These key nematode taxa could then provide an

early idea about the soil health attributes of different olive orchards.

Management prospects of phytopathogenic nematodes in olive ecosystems

Management of PPNs in olive nurseries and orchards can be practiced via many tactics. However, due to the threat imposed by adopting chemical control on health and the environment, alternative strategies that are both environmentally friendly and economically viable are extremely required (Westerdahl and McKenry 2016). In sustainable agriculture, effective management of nematodes can be achieved through the integration of various methods that fall under Integrated Pest Management (IPM).

Chemical management

Chemical control has been always one of the most effective strategies to eliminate pests and diseases. However, due to the eventual problems caused to the environment, the use of chemical nematicides can be merged with other approaches to reduce the amount applied. These products can be fumigant or non-fumigant. Fumigant nematicides (e.g., 1,3-dichloro propene, Dazomet, and Metam-sodium) should be applied in the pre-planting period (three weeks prior). These nematicides can be challenging to apply due to the required specialized equipment and their phytotoxicity. Research on PPN control has indicated the efficacy of fumigant nematicides on RKNs in some vegetable and tree crops (Qui et al. 2001; Ciccarese et al. 2007).

Non-fumigant nematicides (e.g., Oxamyl, Carbofuran, and Aldicarb) can be applied the day before or at the time of transplanting. Some of these nematicides are systemic and do not have phytotoxic effects, making them suitable for use in olive nurseries or with transplanted plants. Several PPNs were shown to be affected by the application of these products including *Meloidogyne javanica*, *Globodera rostochiensis*, and *G. pallida* (Woods and Haydock 2000).

Cultural management

Preventive measures for PPNs emergence

To protect olive trees from PPNs, it is important to use healthy plant material transplanted into soil that is free of these pathogens. This is specifically important in olive nurseries, where conditions are favorable for PPN multiplication and infestations that could be the key to further spreading to the orchards (Castillo et al. 1999). Many infestations of RKNs and RLNs in olive orchards are primarily caused by non-sanitized olive cultivars/rootstocks from uncertified nurseries (Lehman 1994). In that manner, it could be doable to perform nematode disinfection to produce healthy olive material. Cultural tactics including crop rotation, weed management (using herbicides), and fertilization can also contribute to reducing PPN populations and increasing the saprophytic attributes (Bridge 1996). Furthermore, mastering the cultural practices (e.g., cropping intensity, irrigation, and plantation planning) can create a better microbiome atmosphere in which PPN could be included (Castillo et al. 2010). However, these methods exhibit a limited factor via non-guaranteed total exclusion of damaging PPN species.

Soil practical measures

One of the cultural optimizations used to control PPNs is soil processing through solarization (Fig. 9). This strategy has been effectively established to control SBPs including bacteria (Bhai et al. 2019), fungi (Saremi et al. 2011), and PPNs (Butler et al. 2012). Optimally, this strategy requires high temperatures which are particularly fit for most of the North African regions. In olive nurseries, solarization can be used to control RKNs (e.g., *M. incognita*) (Melero-Vara et al. 2012), reducing their egg density by 95% to a particular soil depth (30–40 cm) 10 days post application. However, these nematodes could acquire resistance to this heat-based method due to the protective matrix surrounding the eggs which hardens their management (Nico et al. 2003a). Solarization may also be useful for controlling other PPNs such as RLNs (e.g., *P. vulnus,* and *P. penetrans*), as well as many SBPs (Castillo et al. 2004).

Genetic management

Implementing resistant/tolerant cultivars is an effective genetic strategy for managing PPNs in olive trees without chemical interference (Castillo et al. 2010). However, limitations occurred in their ability to yield properly. In that context, some olive lines are resistant/or tolerant to certain species of the RKNs, RLNs, and citrus nematodes (*Tylenchulus* spp.) (Nico et al. 2003b). For instance, Ascolano and Manzanillo olive lines are resistant to *Meloidogyne arenaria* and *M. hapla* but susceptible to *M. javanica*. In olive nurseries, it has been shown that some RKN species (e.g., *M. javanica* and *M. arenaria*) produced a high reproduction factor (RF) and galling index (GI) on Arbequina, Hojiblanca, and Manzanillo lines making them very susceptible (Palomares-Rius et al. 2019). On the other hand, Abbas and Mohammad (2005) have found three resistant lines to *M. javanica* including Leccino, Coratina, and Manzanillo while the majority of the others ranged from susceptible to highly susceptible reactions (Table 6).

Regarding resistance to RLNs, olive reactions varied depending on the genetic source. For instance, Arbequina

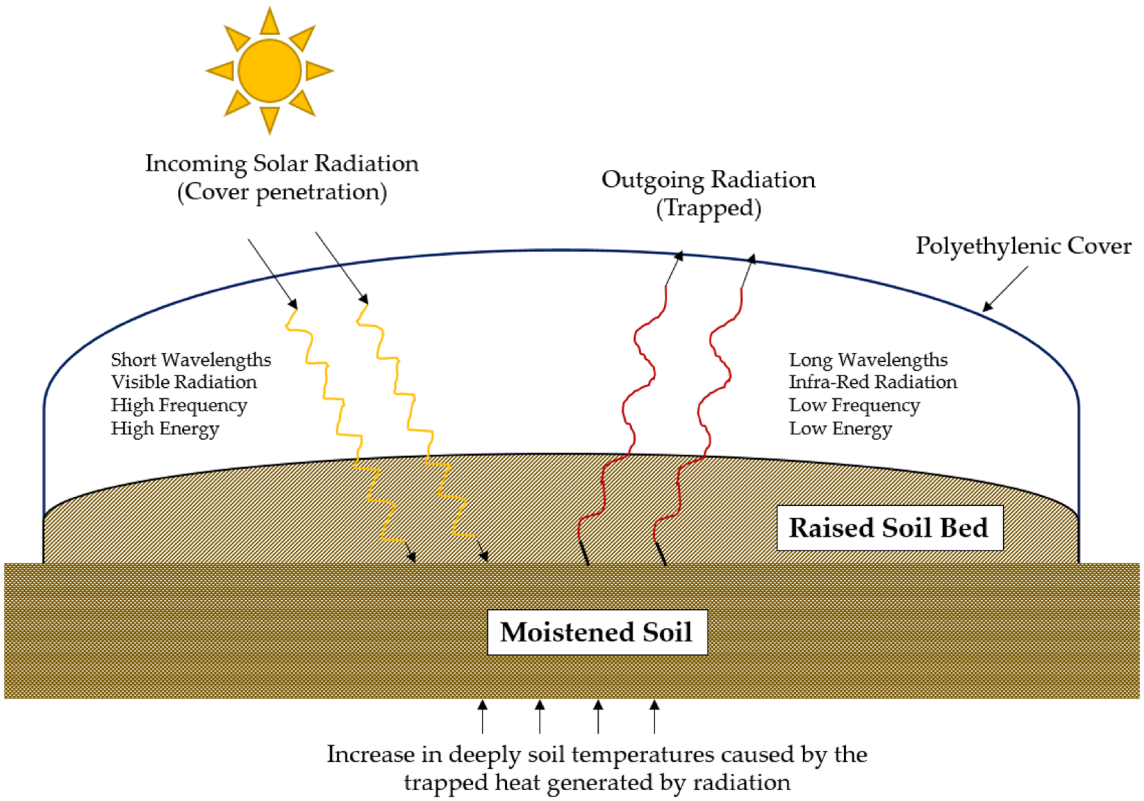


Fig. 9 Soil solarization basic principals in managing plant-parasitic nematodes on olive trees (adapted from Deepa et al. (2017))

and Picual genotypes did not allow *Pratylenchus thornei* and *P. fallax* to reproduce, confirming their resistance, while Picual cultivars were shown to be moderately susceptible to *P. vulnus* (Nico et al. 2003b) (Table 7). Even if susceptibility occurs, some lines may still able to be tolerant (e.g., Ascolana). Resistance screenings have been conducted for other PPNs (e.g., *Xiphinema* spp.) as some olive lines were susceptible to the *Xiphinema index* (excluding DA12I and FS17 genotypes) (Sasanelli et al. 1999). The same approach was followed with the cyst nematodes *Heterodera mediterranea* as they recorded a high level of genotype susceptibility (e.g., Arbequina) (Castillo et al. 2010). Overall, resistance attributes can be implemented for susceptible cultivars with high yield potential as stocks, thus creating optimal resistant and tolerant olive genotypes.

Biological management

Biological control of PPNs in olive trees through the use of naturally occurring antagonists, known as biocontrol agents (BCAs) such as nematophagous, endophytic, mycorrhizal fungi, and entomopathogenic nematodes (EPNs) (Sasanelli 2009). Additionally, strategies such as biofumigation and the incorporation of organic residues may enhance the biological management of these pathogens (Ali et al. 2014).

Nematophagous fungi

Nematophagous fungi (NFs) have been recognized as a potential tool for integrated pest management of PPNs (Liu et al. 2009). These fungi can inhibit the growth or development of PPNs through mechanisms such as antibiosis, parasitism, or predation (Lopez-Llorca et al. 2008). Some NFs use adhesive networks or buttons to trap nematodes, while others use constrictor rings or hyphae networks that produce sticky compounds to capture their prey. The specific enzymes produced by these fungi then affect the nematodes. The attachment of the fungi's mycelium to the nematode cuticle is often facilitated by compatible glycoproteins including lectins (Lopez-Llorca et al. 2008).

Hamza et al. (2017b) identified and evaluated the distribution and functional activity (in vitro) of native NFs. More than 300 soil samples were retained from representative Moroccan olive nurseries. Nineteen pure fungal species of NFs were isolated from nursery substrates contaminated with RKNs (Table 8). In in vitro predation tests, the fungus *Talaromyces assiutensis* killed all *M. javanica* J2s. *Monacrosporium* spp., and *Arthrobotrys* spp. trapped

Table 6 Host status of some olive lines to the root-knot nematode (*Meloidogyne javanica*)

Olive line	Origin	Host status*	References
Marri	Iran	S	Abbas and Mohammad (2005)
Fishemi	Iran	S	Abbas and Mohammad (2005)
Zard-e-Jonoub1	Iran	HS	Abbas and Mohammad (2005)
Zard-e-Jonoub2	Iran	HS	Abbas and Mohammad (2005)
Roghani	Iran	HS	Abbas and Mohammad (2005)
Shengeh	Iran	S	Abbas and Mohammad (2005)
Manzanilla	Spain	HS	Abbas and Mohammad (2005)
Amigdalifolia	Greece	MS	Abbas and Mohammad (2005)
Kalamata	Greece	S	Abbas and Mohammad (2005)
Amphisis	Greece	S	Abbas and Mohammad (2005)
Clonaris	Greece	S	Abbas and Mohammad (2005)
Coratina	Italy	R	Abbas and Mohammad (2005)
Beldy	Morocco	S	Abbas and Mohammad (2005)
Frangionato	Greece	MS	Abbas and Mohammad (2005)
Conservallia	Greece	S	Abbas and Mohammad (2005)
Mission	US	S	Abbas and Mohammad (2005)
Sevillana	Spain	S	Abbas and Mohammad (2005)
Leccino	Italy	R	Abbas and Mohammad (2005)
Arbequina	Spain	S	Abbas and Mohammad (2005)
Ayvalik	Turkey	MS	Palomares-Rius et al. (2019)
Hojiblanca	Spain	HS	Palomares-Rius et al. (2019)
Koroneiki	Greece	MS	Palomares-Rius et al. (2019)
Picual	Spain	MS	Palomares-Rius et al. (2019)
Sikitita	Spain	S	Palomares-Rius et al. (2019)
Lechin	Spain	S	Palomares-Rius et al. (2019)

*Host status classification according to the nematode reproduction factor (RF) = *Pf*/*Pi*

R resistant, *MS* moderately susceptible, *S* susceptible, *HS* highly susceptible

Table 7 List of Nematophagous fungi found in Moroccan olive nurseries according to Hamza et al. 2017b

Family	Genus	Species	Frequency (+)
Orbiliaceae	*Arthrobotrys*	*A. brochopaga*	+ + + +
		A. conoides	+ +
		A. oligospora	+
		A. thaumasia	+ + +
		A. scaphoides	+ +
	Dreschslerella	*D. brochopaga*	+
	Dactylaria	*Dactylaria* sp.	+ + + +
	Monacrosporium	*M. thaumasium*	+
		M. microscaphoides	+ + + +
Trichocomaceae	*Paecilomyces*	*P. lilacinus*	+
	Talaromyces	*T. assiutensis*	+
Pleurotaceae	*Nematoctunus*	*N. leiosporus*	+ +
Catenariaceae	*Catenaria*	*C. anguillulae*	+
Haptoglossaceae	*Haptoglossa*	*H. heterospora*	+ +
Clavicipitaceae	*Pochonia*	*P. chlamydosporia*	+ + + +
Hypocreaceae	*Trichoderma*	*T. asperellum*	+ + + +
		T. harzianum	+ + + +
		T. longibrachiatum	+ + + +
Nectriaceae	*Fusarium*	*F. oxysporum*	+ + + +

Frequency rates range from high (+ + + +) to low (+)

50–80% of the juveniles, while *Purpureocillium* and *Trichoderma* species killed around 30–50% of them (Fig. 10). The nematophagous species *T. assiutensis* has shown great efficacity against *M. javanica*. The use of NFs represents a promising alternative strategy for controlling nematodes in olive nurseries and preventing their spread into olive orchards.

Endophytic fungi

Endophytic microorganisms are defined as those that can be isolated from plant tissues, without causing visible harm to the plants. These microorganisms can belong to various taxonomic groups, including bacteria, archaea, fungi, and protists (Poveda et al. 2020). Among these, endophytic fungi (EFs) are particularly important in ecosystems, as they can protect plants from various stress factors (Yan et al. 2019). EFs are also known to have significant biotechnological potential due to their ability to produce enzymes and other molecules that can be used as BCAs, plant growth promoters, and in the bioremediation process (Zheng et al. 2016). In addition, endophytic fungi play a crucial role in nutrient cycling, as they can act as both saprophytes and decomposers (Saikkonen et al. 2015).

The mechanisms by which endophytic fungi can control PPNs are not well understood but are thought to be diverse. Nematodes can be directly attacked, killed, immobilized, or repelled by these fungi. The latter can interfere with the development of nurse cells; compete with nematodes for resources; or use a combination of these tactics (Yan et al. 2019; Poveda et al. 2020). For instance, *Fusarium oxysporum*, isolated from banana (*Musa* spp.), was shown to be capable of paralyzing and killing RLNs (*P. goodeyi*). In olive trees, several endophytic fungi species were found to antagonize *M. javanica*, including *T. assiutensis*, *A. brochopaga*, *M. thaumasium*, and *P. lilacinum* through active parasitism (Hamza et al. 2017b).

Mycorrhizal fungi

Mycorrhizal fungi (MF) are obligate symbionts found in almost all upper plants. They are classified into two types based on how they colonize plant roots: ectomycorrhizal fungi (EMF) and arbuscular mycorrhizal fungi (AMF) (Ferlian et al. 2018). EMF colonize the intercellular space, while AMF form arbuscles within plant cells. Mycorrhizal fungi have several mechanisms for interacting with plants, including competition for photosynthates, improving plant nutrition, altering root system morphology, changing the microbial populations in the mycorrhizosphere, and activating plant defense mechanisms (Berruti et al. 2016). These mechanisms allow mycorrhizal fungi to function as biological control agents against a variety of SBPs, including fungi, oomycetes, nematodes, and bacteria (Poveda et al. 2020).

Mycorrhizal fungi typically interact with PPNs indirectly through their effects on plants. They can enhance nutrient and water uptake, alter root morphology, increase plant competitiveness for resources, and modify rhizosphere interactions (Wani et al. 2017). Some studies have demonstrated that mycorrhizal fungi (*Glomus* spp.) can directly reduce root penetration PPNs, such as the false RKN *Nacobbus aberrans* (Marro et al. 2018), and *M. javanica* in peach trees (Calvet et al. 2001). The use of mycorrhizal fungi as BCAs against PPNs could be widely studied in olive crops.

Table 8 Moroccan EPNs isolated and used against *Meloidogyne* spp. according to El Aimani et al. (2022)

EPN species	Isolate name	Origin	Vegetation
Steinernema feltiae	SF-MOR9	El Jorf/Fezna	Date palms *(Phoenix dactylifera* L.)
	EL45	INRA-Rabat	Citrus trees
Heterorhabditis bacteriophora	EL27	Gharb	Olive trees (*Olea europaea* L.)
	HB-MOR7	El Fouarate	Plum trees (*Prunus* sp.)
Steinernema sp.	EL30	INRA-Rabat	Fig trees (*Ficus carica)*

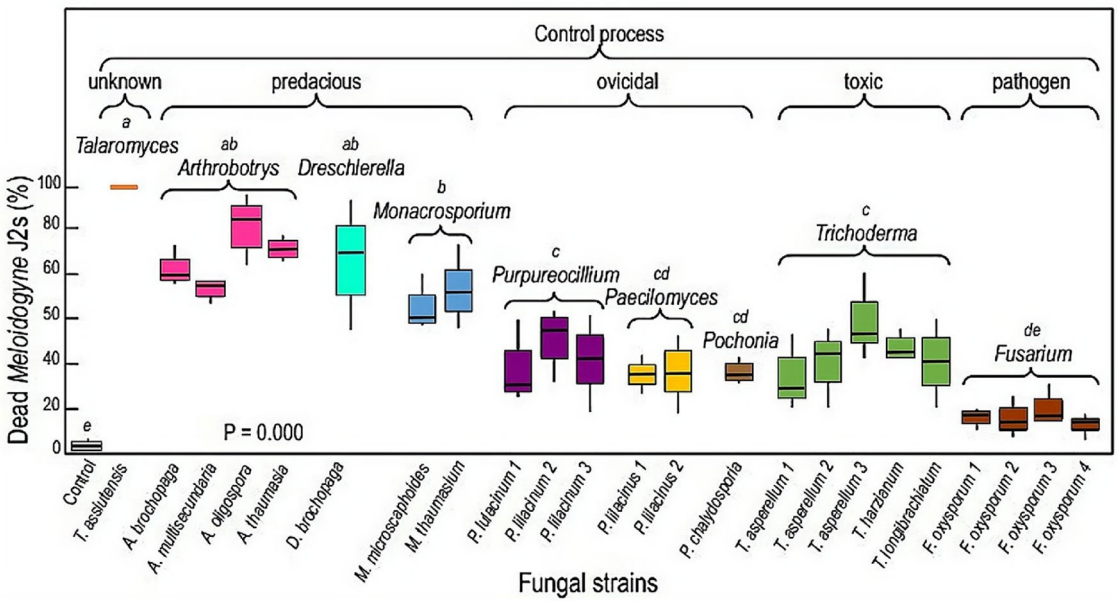


Fig. 10 Efficacy of Moroccan nematophagous fungal strains (in vitro) against *Meloidogyne javanica* infesting olive nurseries (adapted from Hamza et al. (2017b))

A study conducted by Castillo et al. (2006) aimed to investigate the effects of single and joint inoculation of olive planting stocks (cvs Arbequina and Picual) with AMF isolates and RKNs (*M. incognita* and *M. javanica*) under controlled conditions. The study evaluated the impact of these treatments on plant performance and nematode infection. The results showed that the establishment of fungal symbiosis significantly increased the growth of olive plants by 88.9%, regardless of olive cultivar, plant age, or nematode infection. Additionally, the infection of olive plants by RKNs significantly reduced the diameter of the plant's main stem by 22.8–38.6%. Furthermore, the establishment of AMF in olive plants showed a reduction in root galling severity by 6.3–36.8% and reproduction of both RKN species by 11.8–35.7%, indicating a protective effect against parasitism of these nematodes. However, the infection by nematodes influenced root colonization by AMF, and the net effect depended on the AMF isolate-olive cultivar combination. Overall, the prior inoculation of olive plants with AMF may contribute to improving the health status and vigor of the planting stocks during nursery propagation.

Entomopathogenic nematodes

Entomopathogenic nematodes (EPNs) from the genera *Steinernema* and *Heterorhabditis* are effective in controlling various insect pests (Morton and García-del-Pino 2009). These nematodes can quickly kill insects within 24–48 h by releasing toxins from their symbiotic bacteria, *Xenorhabdus* and *Photorhabdus*, into the insect's blood system. These toxins cause host cells to die through apoptosis or necrosis, resulting in the death of the insect (Dillman and Sternberg 2012).

The use of EPNs as BCAs for PPNs has been found to be effective (Sayedain et al. 2021; El Aimani et al. 2022). Research has shown that EPNs can effectively control PPN species such as *Meloidogyne*, *Rotylenchulus*, *Criconemoides*, *Rotylenchulus*, *Globodera*, and *Belonolaimus* spp. in both greenhouse and field conditions (Raza et al. 2015; Khan et al. 2016; Caccia et al. 2018). The highest level of control has been observed against RKNs when infective juveniles (IJs) are applied (Caccia et al. 2018). This results in a significant reduction of RKNs including the number of eggs and egg masses. Additionally, using symbiotic bacteria and/or their metabolites alone has been shown to significantly reduce RKN J2s in vitro and decrease host infectivity in greenhouse conditions (Caccia et al. 2018). This effect has similar attributes to chemical control (Vyas et al. 2008). Recently, several Moroccan strains of *Steinernema feltiae* and *Heterorhabditis bacteriophora* have been isolated, showing potential against RKNs (e.g., *M. javanica*) in vegetable crops (Caccia et al. 2018; El Aimani et al. 2022). However, their efficacy against PPN species in olives has not yet been evaluated.

Biofumigation

Soil biofumigation is a sustainable method for controlling PPNs and soilborne pathogens that utilize plant biomasses rich in glucosinolates. When these biomasses are incorporated into the soil and damaged, they are released and hydrolyzed by the enzyme myrosinase into various products, including isothiocyanates (Kruger et al. 2013). The latter has demonstrated toxicity to a range of soilborne bacteria, nematodes, and fungi (Ntalli and Caboni 2017). Using this strategy via cruciferous plant amendments has been shown to effectively suppress root-knot nematodes (D'Addabbo et al. 2004). However, there is a lack of research on the effectiveness of biofumigation in controlling nematodes in olive trees.

Organic amendments

The application of organic amendments to the soil, including various types of waste materials such as oilseed cakes, composts, agro-industrial waste, and animal manure, has been demonstrated to be an efficient technique for managing soilborne pathogens (SBPs) (Oka 2010). These amendments not only possess potential nematicidal properties but also enhance soil health and promote plant growth (Wachira et al. 2009).

The addition of forest residues to soil can provide organic matter that can stimulate the growth of soil microflora, potentially leading to the suppression of PPNs such as RKNs (*M. javanica* and *M. incognita*) (Oka 2010). Composted dry cork, particularly when used in olive nursery settings, has been shown to be an effective method for controlling RKNs (Nico et al. 2004). This may be due to toxic compounds released, including ammonia and phenolic compounds, which can be detrimental to the nematodes (Oka 2010). In addition to its potential nematicidal properties, the use of composted materials can also have beneficial effects on soil health and olive growth (Ali et al. 2014).

Conclusion and future perspectives

This review indicates that there is a significant diversity of PPN communities associated with olive trees across different countries in NA. Some nematode taxa, including *Meloidogyne* spp., *Pratylenchus* spp., and *Helicotylenchus* spp., were dominating in terms of abundance and frequency, which could be dangerous for olive nurseries and orchards upon their direct/indirect transmission unless urgent management is acquired.

Generally, most of the research studies conducted in olive trees focused on PPNs not mentioning the other communities (e.g., saprophytic nematodes). These communities

are extremely important in the sense that they can play a crucial role in soil health and food web dynamics. In that manner, focusing on these aspects could provide novelties and helpful insights for sustainable crop protection and management. However, implementing distinct control strategies (especially the biocontrol approaches) may alter nematode communities but may not necessarily decrease their overall damage. Therefore, from an ecological perspective, following a realistic workflow merging IPM tactics could help the growers to increase olive yield sustainably.

Future directions for research in this area could include (1) developing better methods for detecting and monitoring PPNs in olive tree nurseries and orchards, (2) exploring the dynamics of other nematode communities for better soil and root health understanding, (3) identifying new resistance sources from cultivated and wild olive tree relatives, (4) determining the effect of cultivation practices and soil characteristics on nematode populations, and (5) studying the efficacy of biocontrol agents (e.g., entomopathogenic nematodes and endophytic fungi) as potential alternatives to chemical control.

Declarations

Conflict of interest The authors declared no conflict of interest.

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