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Review/Revue

Plant-parasitic nematodes associated with olive tree (*Olea europaea* L.) with a focus on the Mediterranean Basin: A review

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ABSTRACT

The olive tree (*Olea europaea* ssp. *europaea.*) is one of the most ancient cultivated trees. It is an emblematic species owing to its ecological, economic and cultural importance, especially in the Mediterranean Basin. Plant-parasitic nematodes are major damaging pests on olive trees, mainly in nurseries. They significantly contribute to economic losses in the top-ten olive-producing countries in the world. However, the damages they induce in orchards and nurseries are specifically documented only in a few countries. This review aims to update knowledge about the olive-nematode pathosystem by: (1) updating the list of plant-parasitic nematodes associated with olive trees; (2) analysing their diversity (taxonomic level, trophic groups, dominance of taxa), which allowed us (*i*) to assess the richness observed in each country, and (*ii*) to exhibit and describe the most important taxa able to induce damages on olive trees such as: *Meloidogyne*, *Pratylenchus*, *Helicotylenchus*, *Xiphinema*, *Tylenchulus*, *Rotylenchulus*, *Heterodera* (distribution especially in the Mediterranean Basin, pathogenicity and reactions of olive trees); (3) describing some management strategies focusing on alternative control methods; (4) suggesting new approaches for controlling plant-parasitic nematodes based on the management of the diversity of their communities, which are structured by several environmental factors such as olive diversity (due to domestication of wild olive in the past, and to breeding now), cropping systems (from traditional to high-density orchards), irrigation, and terroirs.

1. The olive tree: origins, dissemination and cultivation

Six *Olea europaea* subspecies with distinct geographic areas are distinguished [1,2] (Fig. 1):

- subsp. *europaea* present in the Mediterranean Basin, with two botanical varieties: *O. europaea* subsp. *europaea* var. *europaea* for the cultivated forms, and *O. e.* subsp. *e.* var. *sylvestris* for wild and spontaneous trees (usually named oleasters) [2];
- subsp. *laperrinei* in the Saharan mountains;
- subsp. *cuspidata* from southern Africa to southern Egypt and from Arabia to China;
- subsp. *guanchica* in the Canary Islands;
- subsp. *maroccana* in southern Morocco;
- subsp. *cerasiformis* in Madeira.

The Mediterranean olive (*Olea europaea* L. subsp. *europaea*; Oleaceae) is one of the first domesticated tree

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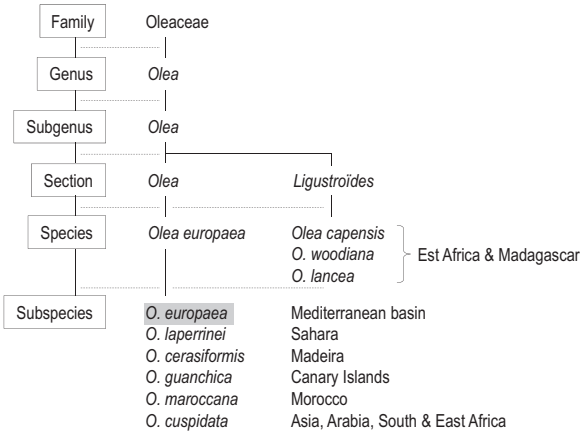

Fig. 1. Simplified diagram of the *Olea* genus (Oleaceae) and biogeography of taxa [11].

species [3,4]. Its origins and domestication history are still highly debated, but archaeological and molecular data sustain that the first cultivars originated from the Levant, very likely 6000 years ago, in a region presently located at the border between southwestern Turkey and northwestern Syria [5,6]. Genetic studies indicated also that olive domestication is a long and on-going process and cultivars have originated from multiple source populations, as for grape and figs [7–9]. It is currently established that western wild olives secondarily contributed to the cultivated gene pool, while most of present cultivars remain mainly related to eastern wild olives [10].

The genetic diversity of oleaster is somewhat greater than that of the cultivated olive [6,10,11]. This diversity is highly structured between the East and the West of the Mediterranean Basin [6,12,13]. The analysis of plastid DNA polymorphisms allowed the identification of 48 distinct profiles delineating three diverging lineages. Lineage E1 is currently distributed over the whole Basin, whereas lineages E2 and E3 exclusively occur in western and central Mediterranean areas [6,14].

The olive tree has long been considered as the most typical Mediterranean tree. It has been widely disseminated through conquests and exchanges that accompanied the expansion of the Mediterranean civilizations (Phoenicians, Greeks, Romans, and Arabs) [15]. Populations of wild olives are restricted to a few isolated areas of native Mediterranean forests, where pollen/stones may be spread by natural factors (wind and birds) [13]. Most other wild-looking forms of olive may include feral forms (either cultivated olive abandoned and becoming wild or olive from stones of cultivated olive spread by birds). The olive dissemination was accompanied by a secondary diversification that has led to a high genetic variability that reflects a wide range of morphological (tree vigour, fruit shape, yield, oil content, etc.) and physiological (adaptation traits to environmental stresses, particularly those related to climate and soil constraints) characteristics that can explain its large distribution in the Mediterranean Basin [16,17]. This diversity can also result from a series of events related to human practices made to meet microclimate and terroir requirements and to satisfy consumer taste [12].

More than 2000 Mediterranean varieties have been recognised based on fruit, pit, and leaf shapes and colours, tree architecture and phenology (i.e. flowering time) [18–21]. Olive cultivars are propagated vegetatively by cutting or grafting. Most of the modern varieties display a maternal lineage (E1) that is distributed all around the whole Mediterranean area [6,14,22]. However, the genetic diversity of cultivated populations exhibits a complex patchy pattern [23,24].

For cultural (traditions, landscapes) and economic (oil and olives) reasons, this tree is regarded as one of the most cultivated plant in the world, ranking the 24th among 35 species [25]. It is now distributed in the five continents. It grows extensively in Mediterranean climate regions in Australia, South Africa, North and South America and covers about 11 Mha, with 98% located in the Mediterranean Basin [26,27]. Eighty percent of the cultivated olive surface is located in northern Mediterranean countries (Spain, Italy, Greece, Turkey), 17% in the Middle East (Jordan, Syria, Iraq, Iran) and in North Africa (Morocco, Algeria, Tunisia, Egypt), and only 2% is located in North (USA) and South (Mexico, Argentina, Peru) America [28,29] (Fig. 2).

Olive diversity may also reflect a significant diversity of associated pests, some of them being specific. Major olive diseases are due to insects (e.g., the fruit fly *Bactrocera oleae*, the black scale *Saissetia oleae*, the moth *Prays oleae*, the borer *Palpita unionalis*), and to air-borne (e.g., the peacock spot *Spilocaea oleaginea*, the knot *Pseudomonas syringae*) or soil-borne (e.g., verticillium wilt *Verticillium dahliae* and plant-parasitic nematodes) parasites and pathogens.

2. Plant-parasitic nematodes associated with olive trees

2.1. General considerations

Nematodes are roundworms of the phylum Nematoda, Metazoa having unsegmented, cylindrical bodies with a non-ciliated tough outer cuticle. The group includes free-living forms and disease-causing parasites. Plant-parasitic nematodes (PPN) are soil-borne microscopic worms that mainly feed on plant-root cells using a spear-like structure, called a stylet. They introduce it in cells to inject digestion secretions and suck cell contents [30].

Thereby, these parasites cause significant economic damages to many types of crops as cereals, vegetables, tubers, fruit, and floral crops [31]. Annual losses caused by PPN are estimated from 8.8 to 14.6% of the world crop production (100–157 billion USD/year) [32,33]. In Europe, economic losses are estimated to 10% of the grain production and lead to reduce by 20 to 30% Mediterranean citrus production [34].

Olive trees are hosts of these parasites. But very few information is available about PPN communities associated with olive [27]. The first record was from the USA, where root-knot nematodes *Meloidogyne* spp. were detected [35]. Since then, some researches on olive PPN