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Nematodes Affecting Potato and Sustainable Practices for Their Management

Fábia S.O. Lima, Vanessa S. Mattos, Edvar S. Silva,
Maria A.S. Carvalho, Renato A. Teixeira,
Janaína C. Silva and Valdir R. Correa

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Abstract

Plant-parasitic nematodes are a significant factor limiting potato production and tuber quality in several regions where potato is produced. Overall, parasitic nematodes alone cause an estimated annual crop loss of \$ 78 billion worldwide and an average crop yield loss of 10–15%. As a result, sustainable food production and food security are directly impacted by pests and diseases. Degrading land use with monocultures and unsustainable cropping practices have intensified problems associated with plant pathogens. Proper identification of nematode species and isolates is crucial to choose effective and sustainable management strategies for nematode infection. Several nematode species have been reported associated with potato. Among those, the potato cyst nematodes *Globodera rostochiensis* and *G. pallida*, the root-knot nematode *Meloidogyne* spp., the root lesion nematode *Pratylenchus* spp., the potato rot nematode *Ditylenchus destructor* and the false root-knot nematode *Nacobbus aberrans* are major species limiting potato yield and leading to poor tuber quality. Here, we report a literature review on the biology, symptoms, damage and control methods used for these nematode species.

Keywords: control, disease, lesion nematodes, pest, potato cyst nematodes, root-knot nematodes, *Solanum tuberosum*, yield loss

1. Introduction

Potato (*Solanum tuberosum* L.) is the fourth most important staple food worldwide after maize, rice and wheat and the first vegetable and non-grain economically important food crop. It is cultivated in several regions worldwide, especially in Europe, America and Asia. Europe and Asia are major

producers and account for about 80% of world potato's production, and the main consumers are Europe, North America and Asia. Potato is cultivated in an area of 20 million hectares and produces close to 400 million tons annually that are consumed freshly or processed [1–3].

There has been increasing demand for food supply and food security. Unsustainable cropping production systems with monocultures, intensive planting and expansion of crops to newly opened areas have increased problems associated with new pests and diseases [4].

Nematodes are diverse, microscopic multicellular animals comprising free living to plant parasitic species. They parasitize a wide range of plant species, including monocots and dicots, and are one of the most limiting factors for major crops, causing substantial annual crop loss worldwide. Plant parasitic nematodes are a limiting factor for potato production and lead to decreased yield, physical and chemical changes in potato tubers, poor tuber quality and malformations, which overall make them unmarketable [3, 5–6]. Nematodes alone can cause average yield losses in potato up to 12% [7]. Nonetheless, potato yield losses due to nematode parasitism also depend on a combination of factors, including cultivar, favorable environment, soil structure, population density and time of planting, and could lead to a more severe decline in yield at particular cropping systems [3, 5, 8–10].

Several nematode species are found associated with potato; some of which cause significant yield losses, while others may cause minor injuries and are of local importance. The main nematode species associated with potato includes the yellow potato cyst nematode *Globodera rostochiensis* (Woll.) and the white potato cyst nematode *G. pallida* (Stone), the two worldwide most significant nematode species found in temperate regions where potato is cultivated. The false root-knot nematode *Nacobbus aberrans* (Thorne), the potato rot nematode *Ditylenchus destructor* (Thorne), the root lesion nematode *Pratylenchus* spp. and the root-knot nematode *Meloidogyne* spp. can also cause significant yield losses in potato [3, 5]. Other minor nematode species can be a problem to potato field depending on conditions that favor nematode growth, including the stubby-root nematodes *Trichodorus* spp. and *Paratrichodorus* spp., the lance nematode *Hoplolaimus galeatus* (Cobb) and the dagger nematode *Xiphinema* spp., among others.

Since pathogens such as plant parasitic nematodes represent major losses in agricultural systems, especially when the crops are not managed sustainably, the searches for information on the occurrence of nematodes in the production system, population density, species, level of damage and monitoring and management of these populations are essential in regions where crops will be set [3–4]. In addition, reliable, fast and proper nematode diagnosis and specimen identification are mandatory for choosing adequate management control strategies and for avoiding spreading of exotic nematodes in quarantine materials.

The objective of this chapter is to report a literature review on major nematode species that affect potato growth, yield and quality worldwide and to point out methods normally used for their sustainable management in the field. We will focus on the main nematode species that cause mostly damage to potato, including (i) the potato cyst nematodes *G. rostochiensis* and *G. pallida*; (ii) the root-knot nematode *Meloidogyne* spp.; (iii) the false root-knot nematode *Nacobbus aberrans*; (iv) the root lesion nematode *Pratylenchus* spp.; (v) the potato root rot nematode *Ditylenchus destructor* and (vi) the stubby-root nematodes *Trichodorus* and *Paratrichodorus* spp. A list of most common nematode species associated with potato is summarized in **Table 1**.

Common name	Species name
Potato cyst nematodes	<i>Globodera pallida</i> <i>G. rostochiensis</i>
Root-knot nematodes	<i>Meloidogyne acrona</i> <i>M. arenaria</i> <i>M. chitwoodi</i> <i>M. incognita</i> <i>M. fallax</i> <i>M. hapla</i> <i>M. javanica</i>
Root lesion nematodes	<i>Pratylenchus andinus</i> <i>P. brachyurus</i> <i>P. coffeae</i> <i>P. crenatus</i> <i>P. mediterraneus</i> <i>P. minyus</i> <i>P. neglectus</i> <i>P. penetrans</i> <i>P. scribneri</i> <i>P. thornei</i> <i>P. vulnus</i> <i>P. zae</i>
Potato rot nematode	<i>Ditylenchus destructor</i>
The false root-knot nematode	<i>Nacobbus aberrans</i> <i>N. dorsalis</i>
Bulb & stem nematode	<i>D. dipsaci</i>
Stubby root nematode	<i>Paratrichodorus</i> spp. <i>Trichodorus</i> spp.
Sting nematode	<i>Belonolaimus longicaudatus</i>
Spiral nematode	<i>Helicotylenchus pseudorobustus</i>
Lance nematode	<i>Hoplolaimus galeatus</i>
Stunt nematode	<i>Tylenchorhynchus claytoni</i>
Dagger nematode	<i>Xiphinema</i> spp
The reniform nematode	<i>Rotylenchulus reniform</i>
Burrowing nematode	<i>Radopholus similis</i>

Table 1. List of some nematode species associated with potato.

2. Major nematode species affecting potato

2.1. Potato cyst nematodes (*Globodera* spp.)

Potato cyst nematodes (PCN)—the golden nematode *G. rostochiensis* and the pale nematode *G. pallida*, are the two major yield-limiting nematode species that affect potato in several subtropical regions where this crop is cultivated. Within the genera *Globodera*, there are about 15 minor species [11] and are taxonomically positioned alongside the genus *Heterodera*. They belong to the Order Rhabditida, Suborder Tylenchina and Family Heteroderidae, and due to their similar morphological characteristics, *Globodera* spp. was initially classified within the genus *Heterodera* [12].

Mature females of PCN, *Globodera* spp., form cysts, which are dead females that become darker in color and store their eggs inside their body when conditions are not proper for their survival [11]. In the species *G. rostochiensis*, the cysts turn from white to yellow and then become brownish, whereas in *G. pallida*, the cysts do not become yellow, it turns from white to brownish directly [11]. This dormant stage of the eggs inside the cysts can last for up to 20 years, even in the absence of host or other adverse environmental conditions [12]. Due to these non-ideal conditions, the death of eggs that are internally within the cysts occurs gradually. Annual mortality varies from 50% for temperate regions and over 75% in warmer climates [13]. This higher egg mortality in warmer climates occurs due to *Globodera* spp. is better adapted to subtropical regions and its cycle is interrupted at temperatures above 28°C [12]. The species *G. pallida* develops best between 10 and 18°C, while *G. rostochiensis* is better adapted to a warmer temperatures, between 15 and 25°C [14].

The nematodes, *Globodera* spp., have a worldwide distribution and are present in every continent. In the Oceania, the species occur in countries such as Australia and New Zealand. In Asia, this species can be found in the Philippines, India, Israel, Japan, Lebanon, Malaysia, Oman, Pakistan, Sri Lanka and Turkey. The species is more widespread in Europe, occurring in most countries, such as Austria, Belgium, Croatia, Denmark, Finland, France, Germany, Greece, Ireland, Italy, Netherlands, Norway, Poland, Portugal, Sweden, Switzerland and United Kingdom. They are present in Algeria, Egypt, Libya, Morocco and South Africa, as well as in North America—e.g. Canada, USA and Mexico (*G. rostochiensis*). In Central America, they have been detected in El Salvador (*G. rostochiensis*), Costa Rica, Guatemala and Panama (*G. pallida*), while in South America, they have been detected in Argentina (*G. pallida*), Bolivia, Chile, Colombia (*G. pallida*) and Ecuador (*G. pallida*) [15]. In Brazil, the potato cyst nematodes have not been detected and are considered an A1 quarantine pest [16].

Field dissemination of PCN occurs through several ways, including irrigation water, rainfall runoff, infested soil particles, infested commercial seed potato tubers, contaminated packing of seed potato tubers, footwear, animal hooves, as well as with infested implements and machineries, among others [17, 18].

The host range of PCN includes potato, tomato (*S. lycopersicum*), African eggplant (*S. aethiopicum*), eggplant (*S. melongena*) and other solanaceous plants, including *Physalis* spp., *Datura* spp., *Hyoscyamus* spp., *Physoclaina* spp., *Salpiglossis* spp. and *Saracha* spp. [15]. Species

such as *D. ferox*, *Nicotiana acuminata*, *S. ligustrinum* and *S. pinnatum* are also reported as hosts of *G. rostochiensis* patotype Ro1 in Chile [19].

PCN are considered major pest to potato production in which yield losses can vary from slight losses, reach up to 70% or to a complete loss [20]. The level of damages and losses, however, depend on a combination of factors, including nematode population buildup, number of generations per year, length of potato growing season, soil temperature and host factors [20, 21]. In addition, due to non-specific symptoms in potato, especially above ground, losses are often not taken into account or attributed to adverse factors, such as other pathogens, inadequate plant nutrition and lack of soil moisture [18]. Typical symptoms of nematode infestations occur in patches of poor growth in the field, modifying the genetic characteristics of the crop, causing smaller, curled and abnormally colored leaves, tending to show brown spots on the margins and reduction of the numbers and sizes of leaflets, which overall affect the photosynthesis [6].

Potato plants infected with *Globodera* spp. show yellowish symptoms similar to water and nutrients deficiency, reduced size and number of tubers, with small lesions, making them unmarketable. Plants with damaged roots become wilted, especially during warmer temperatures within the day and may remain wilted even with irrigation. The root system becomes less developed and plants produce a greater amount of lateral roots, leading to overall decreased plant growth, premature death and do not respond properly to fertilization input [14, 22].

Globodera spp. are quarantine A1 pests in Brazil and some other countries. Due to the difficulties in eradicating this nematode once they have been introduced into potato fields, preventive containment measures to avoid their introduction, including non-importation of potato from countries where the nematodes are reported, regardless whether potato is for consumption or for planting, are some of the regulations to avoid spread of the nematode [23].

Once the nematodes are reported into potato fields, other management measures should be used in order to avoid their dissemination or to decrease their population level and thus improve yield. The success in decreasing their population level is variable and depends on the initial population density, soil type and plant genotype, among others. Generally, long-cycle potatoes planted in the fall and harvested in spring have more pronounced yield losses than short-cycle cultivars [21].

Control methods for PCN include the use of quarantine regulations, crop rotation and crop succession [15, 21] and the use of resistant varieties and nematicides. For instance, crop rotation with barley has showed reduction in *G. rostochiensis* up to 87% [15]. Crop rotation with the nematode main hosts, e.g. potato, tomato and egg plants or other solanaceous species, should be avoided as well.

The use of resistant varieties against nematode infection is one of the most effective and environmentally safe methods to control their infection. Resistant varieties against *Globodera* spp. have been successfully used with control rate up to 95% [19]. In addition, there are several breeding programs worldwide aiming to find resistance genes to these nematodes [19].

Trap plants can also be used to control these nematodes. These plants will trigger hatching of nematode eggs with posterior prevention from completing their cycle by destroying the host. The length of time is critical and plants should be destroyed at a proper time after planting in

order to stop the nematode cycle [24]. If plants are not destroyed or occur too late, the nematode population will build up. Some examples of the use of trap plants include the plant species *S. sisymbriifolium* (Lam.), which have been shown significant reduction of PCN population density in the field up to 80% [25]. Other includes *S. tuberosum*, *S. nigrum*, *S. dulcamara* and *D. stramonium*, which have been shown promising results as well [20].

Alternatively, the use of antagonist plants can be used to control these nematodes. Antagonistic plants will initially stand nematode infection; however, later in their cycle, plant factors will stop their further development. The following plant species *Crotalaria spectabilis*, *C. juncea*, *Tagetes patula*, *T. minuta*, *T. erecta* and *Estizolobium* spp. are being used to manage root-knot nematode problems in potato fields in Brazil [23] and could be used to control *Globodera* spp. as well.

Other control methods include soil solarization, especially in regions with warmer temperatures. Chemical control with nematicides has also being used in several regions with satisfactory rate of control. Products, such as carbamates, aldicarb and carbofuran, have been used successfully. However, soil solarization and the use of nematicides are costly, and nematicides may cause side effects to human and to the environment [21].

2.2. Root-knot nematodes (*Meloidogyne* spp.)

Root-knot nematodes (RKNs), *Meloidogyne* spp., are the most aggressive, damaging and economically important group of plant parasitic nematodes significantly impacting major crops worldwide [9, 26]. Currently, there are more than 90 described species [26], of which *M. javanica*, *M. incognita*, *M. arenaria* and *M. hapla* represent up to 95% of RKN in cultivated soils, some of them having several races which parasitize more than 2000 susceptible plant species [27], and overall represent a real threat to the agriculture worldwide [26, 28].

This group of nematodes is highly diverse, mainly due to their variations in cytogenetics (aneuploidy and polyploidy states), types of reproduction (amphimixis to parthenogenesis), complex mode of parasitism (advanced interactions with their hosts), interspecific hybridization, cryptic species and wide host ranges [27, 29–32].

Root-knot nematodes are endo-sedentary parasitic nematodes. The second-stage juvenile (J2) is the infective stage. After RKN hatch from eggs, the J2 migrates through the soil towards suitable root and uses special enzymes and the stylets to force penetration into the vascular cylinder where RKN establishes their feeding site by inducing hypertrophy and hyperplasia of a group of cells leading to swelling and formation of giant cells. On this site, nematode goes through three more ecdysis (molting) to become a swollen young female. Mature females begin laying eggs in the root, forming mass eggs wrapped in a gelatinous matrix. Each egg mass contains 400–500 eggs on average, and it is formed in the midst of cortical parenchyma or on the surface of the roots. The embryonic development of the nematode results in the first stage (J1), passing through an ecdysis (molting) in the egg, followed by the second stage (J2). Adult males do not feed on infected plants; they leave the roots and move freely in the soil until they die [4, 27].

Symptoms in the field include yellowing, stunting, wilting, brown spots and rotting of tubers. RKNs induce hypertrophy and hyperplasia of infected cells leading to swelling of tissues commonly known as galls. Affected tubers also develop galls, known as ‘popcorn’, which overall leads to low quality of tubers (Figure 1) [5, 33]. The number and sizes of galls vary depending on

the susceptibility of the cultivars, population density and favorable temperatures [26]. RKN-infected roots change their nutrient and water uptake, leading to pronounced poor growth and tuber quality and decreased yield. Commonly, there are high levels of intraspecific variation within *Meloidogyne* genome, and this variability may play an important role in changes in morphology and cytogenetics and ultimately their ability to reproduce in certain hosts [27].

Often, the invasion of potato root system is non-damaging, but as soon as tubers begin to initiate, tubers are invaded by the infective second-stage juvenile (J2) and a rapid development and spread occur. Thus, if potato roots and tubers become infected early, several generations of the pathogen will occur before harvest, which typically is about 110 days after planting [34]. However, this depends on each cultivar and the management systems. Potato production in warmer regions or in sandy soils with irrigation system will result in a mix of favorable temperatures, soil structure and moisture status, which may lead to a significant increase in the severity of RKN infections [34].

Losses caused by RKN infection may in extreme cases reach up to 100% in potato fields. Also, variable losses occur as a result of the planting season and the level of soil infestation [33].

RKN species have been increasingly found in association with potato crops in the tropics and subtropics, causing substantial economic impact due to crop losses depending mainly on the cultivars, favorable climate and nematode density present during planting [5, 8–9, 27, 35, 36]. A few RKN species have been reported as increasing problems for potato cultivation in several

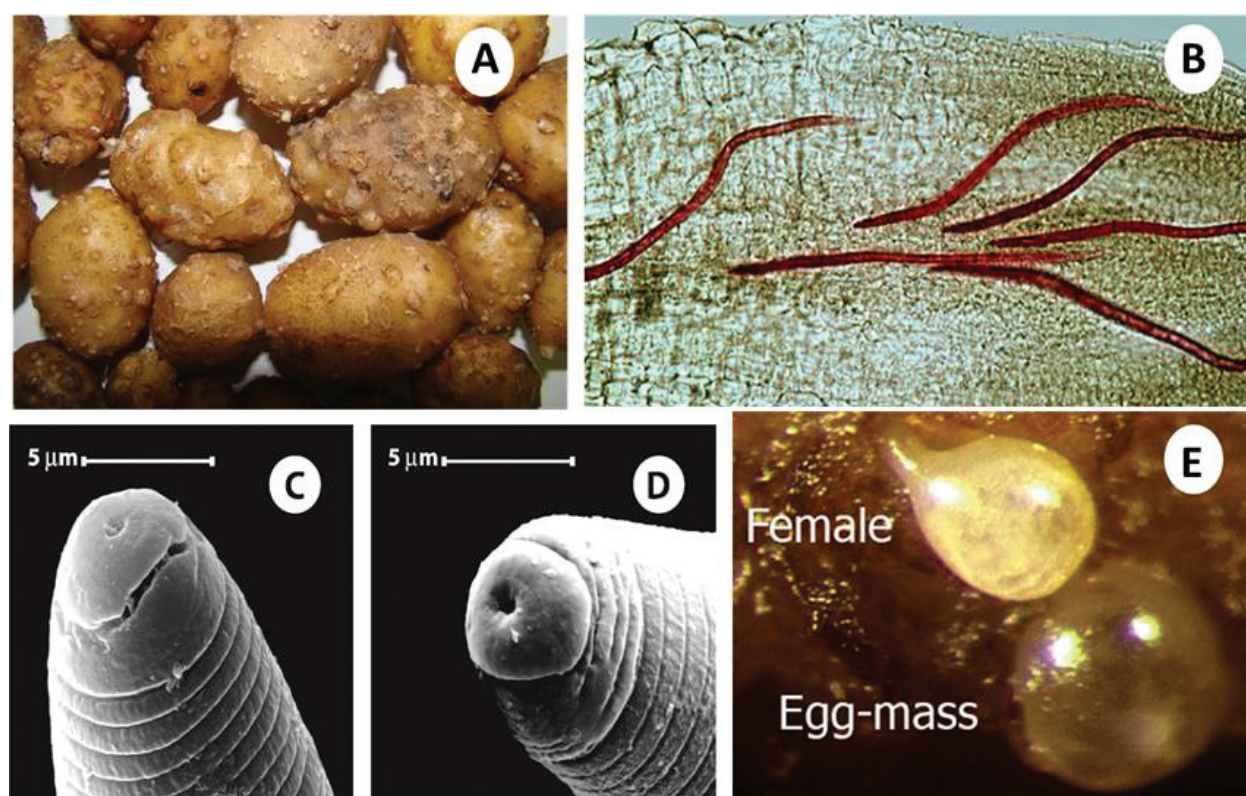


Figure 1. Nematode induced symptoms and nematode characteristics. (A) Potato tuber showing RKN galling (swellings) symptoms, (B) RKN second-stage juveniles (J2) inside root tissues, (C, D) scanning electron micrographs showing an overview of the RKN labial region and (E) RKN female and their egg-mass protruding from plant tissue. Courtesy of (A) Israel Medina (Univ. Nac. Del Altiplano Puno, Peru), (B, E) Jonathan Isenback (Viginia Tech, USA) and (C, D) Regina Carneiro (Embrapa Recursos Genéticos e Biotecnologia, Brazil).

regions worldwide, and the most important ones are *M. chitwoodi* (Golden), *M. fallax* (Karssen), *M. incognita* (Kofoed and White), *M. javanica* (Treub), *M. arenaria* (Neal) and *M. hapla* (Chitwood) [5, 35–37].

In temperate regions, i.e. North America, Europe and Australia, *M. chitwoodi* is a widespread and the most important RKN species affecting potato, in which severe damage, poor tuber quality and economic losses have been reported [34]. This RKN species tolerates much lower temperatures than *M. incognita* and *M. javanica* and is reported to cause damage to tubers at temperatures below 6°C [34]. In addition, the approved rates of some nematicides in the USA for controlling *M. chitwoodi* are higher than for other *Meloidogyne* spp. Thus, any spread of this nematode will further complicate its control. *Meloidogyne fallax* is also recognized as a serious pest of potato in Europe, New Zealand and Australia, where it is also a cold-tolerant species [34]. *Meloidogyne acronea* (Coetzee) has also been reported as infecting potato but are rare in commercial plantings and little is known about its distribution [34].

In a survey for RKN species in potato fields in southern Brazil [3], it was found that *M. javanica* was the most prevalent species (90%), followed by *M. incognita* (6.4%), *M. arenaria* (4.3%) and *M. ethiopica* (2.1%). The authors also found that *M. javanica* isolates showed differences in aggressiveness towards two susceptible potato cultivars tested, an information important for screening promising progenies to develop resistant materials.

In a similar survey, [36], using multiple loci sequencing approaches such as the intergenic region (IGS), D2-D3 expansion segments within 28S rDNA and *cytochrome oxidase subunit II* gene (COII) of mitochondrial DNA, it was reported several *Meloidogyne* species parasitizing potatoes in South Africa, including *M. javanica* (23%), *M. incognita* (23%), *M. arenaria* (17%), *M. enterolobii* (14%), *M. chitwoodi* (3%), *M. hapla* (1%) and unidentified *Meloidogyne* spp. (19%). Thus, these surveys show a trend of increased problems associated with RKN infection to potato fields related to climate change and to the breeding of potato cultivars suitable for planting in warmer regions worldwide. The extent of yield losses in potato field associated with RKN is to be better quantified.

The most effective, low cost, environmentally and healthy sound way to control RKN is to use resistant cultivars that stand good yield performance and have been tested for a particular region where potato is produced. However, currently there is no potato cultivar resistant to *Meloidogyne* spp., even though there are studies reporting the identification of resistant genes in wild potato genotypes and posterior introgression into breeding lines [38, 39].

The best characterized resistant gene against RKN in wild potato (*Solanum* sect. *Petota*, solanaceae) is *RMc1(blb)* from *S. bulbocastanum*, a gene that is effective against some races of *M. chitwoodi* [38]. The resistance mechanism of *RMc1(blb)* is based on a hypersensitive response and involves calcium signaling [40]. Recent studies suggested that *M. chitwoodi* resistance in different species of *Solanum* is based on the same gene, thereby limiting the diversity of available resistant genes [41]. Resistance to *M. incognita*, *M. javanica* and *M. arenaria* have also been reported in the wild potato species *S. sparsipilum* and are being used as breeding lines to develop resistant potato cultivars (International Center for Potato—CIP).

Alternatively, chemical nematicides have been used for the control of RKN in potato, especially in large cropping areas [6]. Other control methods, include crop rotation or succession with non-host and poor hosts, even though they should be used carefully since RKN have a

very wide host range and it could host other non RKN species, i.e. *Pratylenchus* spp. and be a further problem [42]. To be effective, rotation should last for at least 4 years, together with effective weed control. Due to this requirement, crop rotation may not be economically the best way to manage these nematodes for certain cropping system and regions. Some oat cultivars (*Avena sativa*), cotton (*Gossypium hirsutum*) and grasses that exhibit resistance to RKN may be used in rotation with potato in order to minimize the damage. Other crop rotation schemes that have been employed for *M. javanica* include the use of sorghum, maize and castor bean resistant to this species. Overall, brassica crops, including cabbage, cauliflower, mustard and Chinese cabbage, are used to rotate with RKN nematodes [42]. Other recommended management practices are the regular and timely cultivation and drying of soil, immediate destruction of volunteer potato plants and tubers, planting certified potato tuber, selecting planting dates to avoid high RKN population during tuber growth, shortening of potato cycle by using early maturing cultivars and, finally, just before planting, at planting and post-planting, the rational use of registered nematicides [34].

2.3. The false root-knot nematode (*Nacobbus aberrans*)

The false root-knot nematode *Nacobbus aberrans* (Thorne & Allen) (Nematoda, Pratylenchidae) is a plant parasitic nematode found mainly in some regions of North (Mexico and the USA) and South America (Argentina, Peru, Ecuador, Chile and Bolivia) [43–45]. In the USA, *N. aberrans* parasitizes sugar beet and other vegetable crops, but do not infect potato, while in Mexico and some South America countries, this nematode species is a serious problem on potato fields [43, 45].

This species is a quarantine regulated pest to several regions and it is considered a serious pest to potato in which yield losses up to 55–90% have been reported [43–45]. This nematode species has been detected in greenhouses in England, Netherlands, Finland, Russia, India and China [43, 45]; however, it has not been found in the field of any other region outside North and South America [43] and may have been eradicated following its detection in Europe and Asia countries. In the Andean region of Peru and Bolivia, for instance, *N. aberrans*, along with the potato cyst nematodes, *G. rostochiensis* and *G. pallida* and the RKN *Meloidogyne* spp. are considered major nematode species significantly affecting potato production when heavily infested soils are commonly reported [43, 44].

Potato is the most significant host of *N. aberrans*; however, it has a broad host range and parasitizes several other economically important plant species. Among these species includes solanaceous plants, i.e. *Solanum* and *Capsicum*; carrots, lettuce, cabbage, pea, sugar beets, cucumbers, *Opuntia* spp., Cactaceae, Poaceae and some weeds as well [43, 44].

Symptoms of *N. aberrans* infection in potato are similar to those caused by *Meloidogyne* spp., including the formation of galls, which are more discrete and rounded, whereas galls from RKN are elongated forming swellings along the roots. Affected potato roots also negatively impact tuber formation [43–45].

The life cycle of *N. aberrans* is similar to those of RKN species. The second-stage juveniles (J2) hatch from eggs, migrate through the soil towards suitable roots and use its stylet and enzymes to force entry. They penetrate the vascular system and modify a group of cells that lead to the development in galls. Different from RKN species, the third, fourth stage and immature females of *N. aberrans* are migratory. Eggs are produced in a gelatinous matrix that

protrudes from cortical tissue. The nematode can complete 2–3 generations during the crop season depending on ideal temperature which range from 14 to 25°C [43, 44].

Control methods for *N. aberrans* include the use of nematicides, crop rotations (4–6 years), biological control with antagonist fungi and bacteria, the use of resistant or tolerant potato cultivars and quarantine regulations for regions free from this nematode species [43, 44].

2.4. Root lesion nematodes (*Pratylenchus* spp.)

Root lesion nematodes *Pratylenchus* spp. are important plant parasites in the tropics and subtropics [46]. They have a broad host range and are widely distributed in tropical and subtropical regions, especially in Brazil, Southern United States and Africa [46, 47]. At least 15 species have been reported parasitizing potato worldwide, including *P. andinus*, *P. brachyurus*, *P. coffeae*, *P. crenatus*, *P. minyus*, *P. penetrans*, *P. scribneri*, *P. thornei*, *P. vulnus*, *P. neglectus* and *P. zae* [35, 48]. In Brazil, at least 10 species have been reported in several crops, in which *P. brachyurus*, *P. coffeae*, *P. zae* and *P. penetrans* are reported as the most frequent in potato [46], with the predominance of *P. brachyurus* in most potato fields throughout the country [6, 46]. *Pratylenchus penetrans* is considered the most important species of *Pratylenchus* spp. for potato fields, especially in Canada and other countries in North America, where substantial yield losses have been reported [49].

Pratylenchus species is commonly referred to as the root lesion nematodes due to the typical symptoms of necrosis they cause in the roots. The species is considered a migratory endoparasitic nematode, normally found within the roots and between the roots and soil particles [46]. *Pratylenchus* species are smaller than 1 mm in length. Males and females are wormlike, differing only in the sexual characters. Females have one ovary (monovarial) and reproduce by sexual reproduction called amphimixis or by mitotic and meiotic parthenogenesis. They are easily recognized by the sclerotized labial region and ventral overlapping esophageal glands and usually by dark intestinal contents. The stylet is well developed with broad basal bulbs. Most species are polyphagous, showing the ability to parasitize cultivated plants-perennials, semi-perennials, annuals as well as weeds [46].

Pratylenchus spp. of varying life stages penetrate the sub epidermal layers of potato tubers and move through the cortex where they feed on parenchyma cells and cause lesions that become dark spots on the tubers. They migrate continuously in the tissues, intra and inter cells causing such lesions. Depending on favorable temperature and soil conditions, they may have up to 3 generations during the potato cycle and may reach up to 10,000 individuals per 10 g of potato samples [46]. Besides that, these lesions in the root and tubers facilitate invasion of secondary infection by bacterial and fungal pathogens, which results in further necrosis of tubers [46, 50]. Infected tubers may rot and have a shorter shelf life as compared to healthy tubers. On the field, infected potato plants have poor growth as evidenced by scattered patches of stunted plants and show late flowering and intense necrosis in the roots [46]. Overall, infection of *Pratylenchus* spp. to potato may reduce yield by up to 50% in some reported cases, depending on several factors such as population level, temperature, soil conditions and potato cultivars [46, 50].

Management practices for *Pratylenchus* spp. include a successful integration of rotation and succession of crops, the use of resistant cultivars and genotypes, proper physical and chemical management of soil and elimination of weeds in the harvest and off season. Potato planting should be avoided during high temperatures and excessive rainfall [42].

All *Pratylenchus* spp. have a wide host range, which include several cultivated crops and weed species as well. Successive planting of soybean, potato, pasture and corn favors the buildup of nematode population [6]. The authors [51] evaluated the effects of crop rotation and soil management practices such as reduced planting, cover crops and organic fertilizer applications on *P. neglectus* population densities in potato in a sandy soil in the south of Alberta, Canada. Rotated crops from 3 to 6 years included potato, dry beans, wheat, sugar beet and oats. Conservation practices included autumn cover crops and incorporation of compost as a substitute for inorganic fertilizer. *Pratylenchus neglectus* populations were affected by rotation length, but not by soil management practices. Population densities at 3-year rotation were higher as well as potato yields in the conventional 3-year rotation was consistently lower than at longer rotation periods.

Some other plant species such as *Crotalaria* and *Tagetes* are excellent options for rotation/succession with potato. The authors [52] carried out a study to monitor root lesion nematodes, mainly *P. penetrans* on two marigolds (*Tagetes tenuifolia* cv. NemaKill and cv. NemaNon), annual ryegrass (*Lolium multiflorum* cv. Lemtal), red clover (*Trifolium pratense* cv. Florex) and soybean (*Glycine max* cv. Proteus) and potato (cv. Superior) for three subsequent plantings. The population levels of the nematode were consistently lower with *Tagetes* spp. compared to other cover crops tested. As a result, the mean yield of potato was significantly higher (8–14%) when planting potato after *Tagetes* spp. Red clover and soybean allowed the highest nematode build up with mean potato yield lower than other cover crops tested.

The lack of crop rotation or succession with crops that are good hosts, such as soybeans, beans, corn, sorghum and several forage grasses, no-tillage system; the use of sandy to medium texture soils and poor nutrition of plants are some of the facts that may increase root lesion nematode-associated problems in potato. Favorable temperatures and humidity (ca. 20–25°C and 60–80% humidity) and excess of nitrogen fertilization also intensify problems associated with these nematodes [42].

2.5. The root rot nematode (*Ditylenchus destructor*)

The genera *Ditylenchus* (Nematoda, Tylenchida) has a complex systematic position and has been renamed several times, with several synonyms [53]. Currently, there are 81 described species within the genera, and *D. angustus*, *D. dipsaci* and *D. destructor* are plant parasitic nematodes of economic importance, with the last two species being important pathogens of potato, especially when associated with fungal pathogens. In addition, these nematodes are listed as quarantine pests to several countries.

Ditylenchus spp. have been reported in several regions worldwide causing direct and indirect damage to cultivated crops and overall have a wide host range [48]. The species *D. destructor* and *D. dipsaci* are important pathogens of potato, especially in temperate climates. *Ditylenchus destructor* is a major pathogen of potatoes in regions such as Europe, specially Russia, Asia, North America, Oceania and some isolated regions of South America and South Africa [48].

The symptoms caused by *D. destructor* are not commonly seen in the above ground of the affected plant. The heavily infected tubers give rise to a compromised plant due to physiological and morphological disorders caused by the nematode infection which may eventually lead to plant death. Early infections can be detected by peeling off the tuber and may reveal small and whitish spots [48].

Ditylenchus dipsaci, also known as the stem and bulb nematode, is more common in garlic, but it also damages other plant species as well, including potato, and affects stalks, stolons and tubers. Affected potato tubers show gray to brownish lesions with an overall poor plant growth. Diseased stems become swollen and curved. Galls may also form on the leaves, which cause significant leaf distortion [54].

The use of crop rotation for controlling *D. destructor* and *D. dipsaci* is not feasible due to their wide host ranges. The use of resistant genotypes is the most effective, economically and environmentally safe control method for nematode infection. Currently, there is limited information on the availability of resistant and tolerant potato cultivars against these nematodes. The authors [55] evaluated 25 potato varieties for resistance and tolerance against infection of *D. destructor* and *D. dipsaci*, and based on the nematode reproduction factor (RF), 16 varieties were rated as susceptible (S), while 5 other as resistant (R) to *D. destructor*; potato varieties 'Innovator', 'Aveka' and 'Spunta' were rated as resistant to *D. dipsaci* as well. In their study, the potato cultivar 'Désirée' was rated as highly susceptible to both *D. destructor* and *D. dipsaci*.

Other control measures for these nematodes include the use of nematode free field, nematode free seed potato tuber, and ultimately the use of chemical nematicides may be recommended.

2.6. The stubby-root nematodes (*Trichodorus* and *Paratrichodorus* spp.)

The stubby-root nematodes, *Trichodorus* and *Paratrichodorus* spp. (Trichodorids), belong to the family Trichodoridae (Thorne). Nematodes of this family are a group of important plant parasitic pathogens and include nearly 100 described species within five genera [56]. The stubby-root nematodes are ectoparasites that usually aggregate at the root tips and have a long, solid and curved stylet called onchiostyle that they use to pierce plant cells during feeding, preferably meristem cells of root tips. The damage caused by their direct feeding may be considerable, with thickened root and atrophy, early senescence and interruption of plant growth (stunting), a condition known as 'stubby root' [56].

Trichodorids have a wide distribution around the world, although some species are restricted to a particular region. Studies on the distribution and ecology of trichodorids, as well as the mechanisms involved in the transmission of certain viruses, may eventually result in new strategies for their control [56]. *Trichodorus* spp. are found in sandy soils in several regions worldwide. Although they are more specialized to monocots, they parasitize dicots as well and are considered an important nematode to potato in the tropics and subtropics. However, the level of damage in the field, their overall distribution and economic losses associated with their infection are not well studied [57].

Even though there is a considerable amount of data reporting the impact of these nematodes as a plant parasite, their ability to vector certain viruses has increased their importance to the agriculture, when several species of Trichodoridae were identified as a viral vector [56]. Thus, they are considered economically important for potato production, both because of their direct damage and due to the viruses they transmit. For instance, *Trichodorus* spp. have the ability to disseminate viruses to potato varieties, especially the Tobacco Rattle Virus—TRV, a virus of the genus Tobravirus, which cause the potato disease known as corky-ring spot [6, 57]. The juvenile and adult stages of *Trichodorus* spp. can vector these viruses after feeding on diseased plants. The viruses are stuck in the stylet region and do not circulate inside the nematode

body; however, the nematodes may remain with the virus for up to 4 months or until ecdysis occur, in which the nematode loses its viral load [56].

TRV-infected potato plants exhibit systemic and local symptoms, such as necrosis, chlorosis and overall stunting. Affected potato tubers may exhibit necrotic lesions with brittle tissues and low quality commercial potato tubers may occur even when mild symptoms are seen [58].

Other symptoms associated with TRV infection include delayed emergence of plant and subsequent poor growth, reduced tuber weight and potato yield, high incidence of poor commercial potato tubers, with low dry matter content and oxidation of tuber post cooking [56].

On the whole, control methods for stubby-root nematodes include those listed for other species as well, i.e. prevention (the use of certified planting material, cleaning soil from machineries and equipments, preventing the movement of animals within infested fields), crop rotation, cultural practices and the use of nematicides [6].

3. Other minor nematode species

Other nematode species, including the sting nematode (*B. longicaudatus*), the spiral nematode (*H. pseudorobustus*), the lance nematode (*H. galeatus*), the stunt nematode (*T. claytoni*) and the dagger nematode (*Xiphinema* spp), among others (**Table 1**), may be of economic importance to potato fields at some regions, for instance, some regions in the USA. Among these ectoparasitic nematode species, *B. longicaudatus* seems to be the most impacting one [59]. Other minor nematode species might be associated with potato, however, with isolated importance

4. Overall strategies for managing nematodes in potato fields

The effective control of potato nematodes are overall difficult and complex due to the particular biology of these plant parasites—they inhabit soil, have a short life cycle, multiply fast and have a large population build up; there are just few plant genotypes resistant to them, and chemical nematicides have limited effect due to their interaction with soil components or are being avoided due to their side effects to human and to the environment [42]. Therefore, control strategies for nematodes affecting potato should be planned carefully in order to succeed. The use of more than one control strategy (integrated management) is advised in order to optimize the control efficiency. Information required for proper nematode management, include: (i) proper diagnosis of nematode species and isolate; (ii) relationship between population density and yield losses; (iii) nematode biology (life cycle, environmental requirements, parasitism); (iv) host range; (v) population dynamics; (vi) efficiency of control methods and (vii) economic feasibility of control methods [21].

Generally used control strategies for potato nematodes are (i) planting in fields free of nematode pests, (ii) the use of certified nematode-free seed potato tubers, (iii) crop rotation and succession with non-host or poor host, (iv) fallow (including elimination of weeds), (v) antagonist plants, (vi) trap plants, (vii) resistant cultivars, (viii) avoidance to disseminate the nematodes, i.e. cleaning of tools and machineries, clean irrigation water and cleaning of

footwear, (ix) planting potato at season that is less favored to nematode reproduction, i.e. dry and cold season, (x) quarantine regulations for exotic nematode species, i.e. potato cyst nematodes *G. pallida* and *G. rostochiensis*, (xi) removal of infected plants, (xii) isolation of infested areas, (xiii) the use of biological control, (xiv) cultural and tillage practices and (xv) the use of chemical nematicides [10, 21, 42, 48].

5. Concluding remarks

Several nematode species are associated with potato and few of them negatively impact yield and tuber quality. Severe yield losses and poor tuber quality have been reported in most regions where potatoes are grown. The importance of these nematode species depends on their adaptation to each geographical region (local climate), plant host factors and management practices of potato crop. Other minor species may be a problem to local regions as well. Nematode species have unique biology, behavior and are usually difficult to be managed or eradicated once they are introduced in a field. In addition, their morphological similarities make them difficult to be diagnosed. Nonetheless, proper nematode identification to species and isolate level are mandatory to choose the proper control method. Overall, these nematode problems in potato are better managed when integrated management practices are used, i.e. exclusion (quarantine regulations, certified plant material, use of clean equipment and machineries), cultural practices (crop rotation, succession, cover crops), genetic control, and ultimately by the use of nematicides. Therefore, for a sustainable cropping of potato cultivars, growers, extension services and researchers must consider these nematodes holistically, the impact they cause and whether these management practices are economically, environmentally and technically sound.

Author details

Fábia S.O. Lima¹, Vanessa S. Mattos², Edvar S. Silva³, Maria A.S. Carvalho¹, Renato A. Teixeira⁴, Janaína C. Silva¹ and Valdir R. Correa^{1*}

*Address all correspondence to: valdir.correia@ifto.edu.br

1 Instituto Federal de Educação, Ciência e Tecnologia do Tocantins, Dianópolis, TO, Brazil

2 Embrapa Recursos Genéticos e Biotecnologia, Brasília, DF, Brazil

3 Instituto Federal de Educação, Ciência e Tecnologia do Acre, Brazil

4 Instituto Federal de Educação, Ciência e Tecnologia do Mato Grosso, Brazil

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