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Root-lesion nematodes of potato: current status of diagnostics, pathogenicity and management

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ABSTRACT

Root-lesion nematodes of the genus *Pratylenchus* are migratory endoparasites with worldwide economic impact on several important crops including potato, where certain species like *P. penetrans*, *P. neglectus* and *P. scribneri* reduce the yield and quality of potato tubers. Morphological identification of *Pratylenchus* spp. is challenging, and recent advancements in molecular techniques provide robust and rapid diagnostics to differentiate species without need of specialist skills. However, the fact that molecular diagnostics are not available for all *Pratylenchus* species means that there are limitations in worldwide application. In general, root-lesion nematodes are difficult to manage once introduced into

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agricultural land and damage can be related to pathogenicity and population densities. In addition, root-lesion nematodes interact with fungi such as *V. dahliae*, resulting in disease complexes that enhance the damage inflicted on the potato crop. Management interventions are often focused on limiting nematode reproduction before planting crops and include the application of nematicides, and cultural practices such as crop rotation, cover crops, biofumigation, and biological control. Understanding the limitations of the available crop protection strategies is important and there are many gaps for further study. This review discusses the status of the diagnosis, distribution, pathogenicity and management of the main species of root-lesion nematodes, reported to infect potatoes worldwide, and highlights areas for potential future research.

INTRODUCTION

Potato (*Solanum tuberosum* L.) is an herbaceous annual plant belonging to the *Solanaceae* family, ranked as the fifth most important staple food crop in the world, and grown in over 130 countries, in almost all climatic conditions (FAO, 2018). Potatoes are subject to a plethora of different pests and diseases including plant parasitic nematodes that reduce the yield and quality of tubers, which impact their marketability (Mugniéry & Philips, 2007).

Root-lesion nematodes of the genus *Pratylenchus* Filipjev, 1936 are migratory endoparasites with worldwide economic impact on several important crops such as cereals, coffee, vegetables and potato (Sasser & Freckman, 1987; Castillo & Vovlas, 2007). To date, according to taxonomic studies, there are 101 valid species of root-lesion nematodes described (Janssen *et al.*, 2017a), but only *P. alleni*, *P. andinus*, *P. brachyurus*, *P. coffeae*, *P. crenatus*, *P. flakkensis*, *P. neglectus*, *P. penetrans*, *P. scribneri* and *P. thornei* are associated with potatoes (Oostenbrink 1958, 1961; Brodie *et al.*, 1993; Ingham *et al.*, 2005; Scurrah *et al.*, 2005; Castillo & Vovlas, 2007; Yan *et al.*, 2016).

MORPHOLOGICAL AND MOLECULAR CHARACTERIZATION OF THE MAIN *PRATYLENCHUS* SPP. INFECTING POTATOES

Morphological identification of root-lesion nematode

The genus *Pratylenchus* is characterized by a lip region that is flattened anteriorly, usually continuous with the body contour and with a strong sclerotization (Geraert, 2013). The lateral line incisures are four to six, deirids are absent, whilst phasmids are near to the middle of the tail. The stylet

is typically around 15-20 μm in length with basal knobs that can vary in shape according to species or also between individuals (Tarte & Mai, 1976; Mizukubo & Minagawa, 1991). The pharyngeal glands overlap the intestine ventrally and metacarpus is muscular, and oval to round. The reproductive system is monoprodelfic, and only the anterior genital tract has a spermatheca with a functional ovary, and a postvulval uterine sac present. The vulva is situated posteriorly, usually at 70–80% of the total body length (Loof, 1960, 1991; Geraert, 1983; Luc, 1987; Handoo & Golden, 1989; Ryss, 2002). Female tail is sub-cylindrical to conoid with smooth or annulated terminus (Castillo & Vovlas, 2007; Geraert, 2013).

Morphological identification of *Pratylenchus* species is usually based on female morphology as they have more diagnostic characters than male, which are rare or unknown for a substantial number of species (Loof, 1991). Certain characters have taxonomic validity such as number of lip region annuli, number of lateral incisures, vulva position, length of post-vulval uterine sac, tail shape and presence/absence of males (Table 1). For example, a clavate tail with annulated tip shape and the presence of a strong musculature at the secretory-excretory (SE) pore are features generally observed only with *P. crenatus* (Karssen & Bolk, 2000). *Pratylenchus neglectus* is similar to *P. crenatus*, but generally has a smooth tail tip and poorly developed musculature at the SE pore. However, *P. neglectus* has large variability between some populations in stylet knob and tail shape, complicating the identification (Mizukubo & Minagawa, 1991). Indeed, the diagnosis of root-lesion nematodes is challenging, mainly due to the low interspecific variation and conversely the high intraspecific variation that exists for certain important morphological characters, such as shape of the spermatheca, vulva position and tail shape, that confound species discrimination (Castillo & Vovlas, 2007; Geraert, 2013; Janssen *et al.*, 2017a). For example, populations of *P. penetrans* from different geographical locations have a high level of morphological variation, mainly in the tail shape (Tarte & Mai, 1976). The tail tip is useful in distinguishing *P. penetrans* from *P. fallax*, because this is smooth in the case of *P. penetrans* and annulated for *P. fallax*, but they remain difficult to distinguish morphologically from each other (Tarte & Mai, 1976). Despite their similarities, several molecular studies have demonstrated they are separate taxonomic entities (Ibrahim *et al.*, 1995; Waeyenberge *et al.*, 2000; Carta *et al.*, 2001; Handoo *et al.*, 2001; Janssen *et al.*, 2017b), highlighting the importance of molecular diagnostics to overcome the issues of overlapping morphological characters. Further problems to consider are also the presence of more than one species in the same soil sample and, like most nematode taxa, the identification of *Pratylenchus* by microscopy is time consuming and requires taxonomic expertise.

Molecular diagnostics of root-lesion nematodes

Molecular tools can ideally detect a target nematode species within a mixture of non-target nematodes and to distinguish closely related and cryptic species (Powers, 2004). To obtain a robust identification, it is important to combine classical taxonomy with molecular diagnostics using different molecular markers from single specimens (Coomans, 2000; Powers, 2004; Janssen *et al.*, 2017a,b). However, misidentification due to the use of sequences which have been incorrectly assigned to a species is a major problem for molecular analysis (Subbotin *et al.*, 2008; Janssen *et al.*, 2017a,b).

Species-specific primers for different *Pratylenchus* spp. have been designed for conventional polymerase chain reaction (PCR) and quantitative PCR (qPCR) (Table 2). The qPCR method allows not only the qualitative detection of target organisms but also the quantification, giving a faster alternative to the identification and counting of nematodes by microscopy. Several qPCR diagnostic assays have been developed based on the internal transcribed spacer (ITS) of rDNA for identification and quantification of *P. crenatus* (Oliveira *et al.*, 2017), *P. penetrans* (Sato *et al.*, 2007, 2010; Goto *et al.*, 2011; Oliveira *et al.*, 2017), *P. neglectus* (Yan *et al.*, 2013; Oliveira *et al.*, 2017) and *P. thornei* (Yan *et al.*, 2017). However, the high variability of ITS sequences in *Pratylenchus* spp. has been demonstrated by several authors (Waeyenberge *et al.*, 2000, 2009; De Luca *et al.*, 2011; Janssen *et al.*, 2017a), increasing the risk of obtaining false-positive reactions (fragments from unknown species not yet investigated) or false-negative reactions due to variation occurring between individuals. Inaccurate quantification might arise due also to some gene sequences being present in multiple copies in each cell of each individual. Furthermore, gene copy numbers can change from one species to another or also amongst different developmental stages (Darby *et al.*, 2013; Roberts *et al.*, 2016; Lopes *et al.*, 2019).

Attention has also been given to the D2-D3 expansion segment of 28S rDNA as a potential target for qPCR methods for detection and quantification of *P. penetrans* (Baidoo *et al.*, 2017; Dauphinais *et al.*, 2018). Both qPCR methods allowed the detection of a single individual of *P. penetrans* without evidence of cross-reaction with other root-lesion nematode species or plant parasitic nematodes. However, these methods showed an overestimation of nematode numbers compared to conventional enumeration under microscope (Baidoo *et al.*, 2017; Dauphinais *et al.*, 2018).

Another promising gene target for the development of a qPCR method is the β -1,4-endoglucanase gene which has been investigated for *P. penetrans* (Mokrini *et al.*, 2013) and *P. thornei* (Mokrini *et al.*, 2014). Mokrini *et al.* (2013) detected a single specimen of *P. penetrans* in mixed populations with *P. thornei*. No amplicons were obtained when the primers were used in presence of 18 *Pratylenchus* species and other plant-parasitic nematodes. Similar results were obtained for the detection and quantification of

P. thornei (Mokrini *et al.*, 2014). In both studies, there were no cases of underestimation or overestimation compared to enumeration under microscope as previously reported by other qPCR methods (Sato *et al.*, 2007, 2010; Goto *et al.*, 2011; Oliveira *et al.*, 2017; Baidoo *et al.*, 2017; Dauphinais *et al.*, 2018). Further tests must be done to check their reproducibility in other laboratories worldwide.

ROOT-LESION NEMATODES INFECTING POTATOES: BIOLOGY, INFECTION, PATHOGENICITY AND DISTRIBUTION

Life cycle of root-lesion nematodes

Generally, the first moult is within the egg where the first-stage juvenile (J1) becomes a second-stage juvenile (J2). The J2 stage remains inside the egg until hatch, usually after one week from egg deposition. Following hatching, the J2 moults into J3 and then J4, within 35 to 40 days, there after moulting into adults, becoming either female or male (Castillo & Volvas, 2007) (Figure 1). Males are common in some species (*P. coffeae* and *P. penetrans*) but are rare or absent in others (*P. crenatus*, *P. neglectus* and *P. thornei*) with the latter species reproducing by parthenogenesis (Duncan & Moens, 2013). When males are present, reproduction is amphimictic. Females lay eggs that can be found in clusters inside roots or also in the surrounding soil (Castillo & Volvas, 2007).

Little is known about the life cycle of root-lesion nematodes under field conditions, with almost all the information available originating from studies conducted in controlled conditions (Turner & Chapman, 1972; Chitimbar & Raski, 1985; Castillo *et al.*, 1995). The time for a complete life cycle is dependent upon the species, temperature and host plant. For example, *P. penetrans* has a life cycle of 54-65 days and each female produces 16-35 eggs at a rate of 1-2 eggs per day in red clover (Turner & Chapman, 1972), whereas *P. thornei* has a shorter life cycle of about 25–35 days on carrot discs (Castillo *et al.*, 1995). Temperature can be an important factor to determine the time of the life cycle. Increasing the temperature from 17 to 30°C decreased the life cycle of *P. penetrans* from 46 to 22 days in ladino clover roots, with 25°C being considered optimal for this species to complete its life cycle in 26 days (Mizukubo & Adachi, 1997). In contrast, Mokrini *et al.* (2019) reported an optimum temperature of 20°C for the reproduction of *P. penetrans* and *P. thornei* on carrot discs.

Crop damage and symptoms caused by root-lesion nematodes on potatoes

Root-lesion nematodes are classified as migratory endoparasites as they can feed and reproduce within the root system, although they may also feed on the root surface without entering the root tissue (Duncan & Moens, 2013). *Pratylenchus* feed directly on roots, tubers and cortical tissues. Both adults and juveniles infect roots entering behind the zone of elongation and feed on parenchyma cells (Castillo *et al.*, 1996). The nematodes degrade cell walls with mechanical movements of the stylet but also by secreting enzymes, which degrade the cytoplasm within cells leading to brown lesions at the points of entry and root migration (Zunke, 1990a,b) (Figure 1). Such lesions typically lead to necrotic areas and cell death with a reduction in root growth (Castillo & Volvas, 2007). Damaged roots impede uptake of water and nutrients, thus plants become stunted and present leaf chlorosis (Duncan & Moens, 2013). Root-lesion nematodes occur in patches (foci) in potato fields (Holgado & Magnusson, 2012). Depending on the species, different symptoms can be present also on potato tubers. For instance, *P. scribneri* causes tubers to have a scabby appearance whilst *P. penetrans* has been associated with wart-like protuberances (Brodie *et al.*, 1993). There are reports of seed potato tubers infected by *P. penetrans* (Olthof & Wolynetz, 1991; Khan & Hussain, 2004; Holgado *et al.*, 2009; Holgado & Magnusson, 2012), *P. neglectus* (Olthof & Wolynetz, 1991), *P. scribneri* (Olthof & Wolynetz, 1991) and *P. brachyurus* (Koen & Hogewind, 1967; Koen, 1969). Infected seed potato tubers may lead to the transfer and subsequent spread in potato fields that were previously uninfested.

Damage thresholds and pathogenicity of root-lesion nematodes on potatoes

Crop damage is often related to population densities, and for this reason, management interventions are focused on limiting nematode reproduction before planting of the crop. Studies on damage thresholds of root-lesion nematodes on potato have been previously published in Canada (Olthof, 1986; Kimpinski & McRae, 1988; Olthof, 1990) and Norway (Holgado *et al.*, 2009). For *P. penetrans* and *P. scribneri* densities of 1-2 nematodes g⁻¹ soil have been reported to cause damage to potatoes (Olthof & Potter, 1973; Riedel *et al.*, 1985; Olthof, 1986) whereas *P. neglectus* can induce damage at densities of around 0.6 nematodes g⁻¹ soil (Olthof, 1990). In Norway, potato growth (cv. Saturna) was correlated negatively with increasing densities of *P. penetrans*, and a damage threshold of 100 nematodes 250 g⁻¹ of soil (0.4 g⁻¹ soil) was estimated to cause a yield reduction of 50% (Holgado *et al.*, 2009). Damage thresholds can vary also according to cultivar and other environmental factors such as soil texture, temperature and moisture (Castillo & Volvas, 2007). For example, Bernard & Laughlin (1976) demonstrated that *P. penetrans* had different effects on yield loss of different cultivars showing that the variety Superior had

a yield loss of 23 - 30% caused by 0.38 nematodes g⁻¹ soil, whereas Kennebec was affected by 0.81 nematodes g⁻¹ soil and Katahdin by 1.5 - 2 g⁻¹ soil. In comparison, Russet Burbank was unaffected by *P. penetrans* at densities of 0.38 - 2 per g⁻¹ soil.

Interactions between root-lesion nematodes and pathogenic fungi

Root-lesion nematodes enter roots of host plants and migrate intracellularly in the cortical tissues causing lesions on roots that provide entry points for other pathogens such as bacteria or fungi (Powelson & Rowe, 1993). These secondary pathogens may increase the severity of root decay caused by root-lesion nematodes. A well-documented nematode-fungus disease complex in potato is the interaction between *Pratylenchus* spp. and *Verticillium dahliae* resulting in the disease complex known as Potato Early Dying (PED) that causes significant reduction in tuber size and yield (Martin *et al.*, 1982; Bowers *et al.*, 1996; Kimpinski *et al.*, 1998; Back *et al.*, 2002; Mahran *et al.*, 2010). *Pratylenchus penetrans* is the main species reported to interact synergistically with *V. dahliae* causing wilt disease (Martin *et al.*, 1982; Riedel *et al.*, 1985; Rowe *et al.*, 1985; Wheeler *et al.*, 1994; Bowers *et al.*, 1996). Controlled studies on the influence of *V. dahliae* and *P. penetrans* on gas exchange of the cultivar Russet Burbank demonstrated that co-infection with both pathogens significantly reduced photosynthesis, stomatal conductance and transpiration of plants, confirming that plant physiology and consequently also development and yield were affected (Saeed *et al.*, 1997, 1998; Rotenberg *et al.*, 2004). Riedel *et al.* (1985) showed that the correct identification of *Pratylenchus* species is important to determine the potential risk of damage to potato, indeed *P. penetrans* interacts synergistically with *V. dahliae* causing wilt disease, whereas *P. crenatus*, *P. neglectus* and *P. scribneri* do not. In addition, Hafez *et al.* (1999) reported that different populations of the same *Pratylenchus* species influenced disease incidence. Indeed, a population of *P. neglectus* from Ontario interacted synergistically with *V. dahliae* on potato causing tuber yield reduction but a population from Idaho did not (Hafez *et al.*, 1999). Botseas & Rowe (1994) showed also that the synergism between *V. dahliae* and *P. penetrans* occurred in potatoes only when the *V. dahliae* subgroup A of the vegetative compatibility group 4 (VCG4A) was involved; in contrast, the subgroup VCG4B did not interact with *P. penetrans*. Environmental factors such as temperature are also important to consider. For example, *P. scribneri* is not typically associated with PED, but at elevated temperatures (> 32 °C) *P. scribneri* interacted with *V. dahliae* increasing disease severity (Riedel *et al.*, 1985).

Although there are numerous studies on the interaction between root-lesion nematodes and *V. dahliae*, less is known about interactions with other pathogens such as *Rhizoctonia solani*, especially on potatoes. *Rhizoctonia solani* has been reported to interact with *Globodera* spp. (Back *et al.*, 2002, 2010), but it is still unclear if a synergistic interaction with *Pratylenchus* spp. on potatoes occurs (Kotcon *et al.*, 1985; Kenyon & Smith, 2007; Björsell *et al.*, 2017; Viketoft *et al.*, 2017).

Distribution of root-lesion nematodes in potato crops

Globally, different species of root-lesion nematodes have been found in soil associated with potatoes (Table 3), with *P. crenatus*, *P. neglectus*, *P. penetrans*, *P. scribneri* and *P. thornei* being the most widely distributed. *Pratylenchus penetrans* is found all over the world associated with over 350 host plants, including weeds (Bélaïr *et al.*, 2007), and has been considered the most damaging species associated with potatoes in Europe (Holgado *et al.*, 2009 ;Van Der Sommen *et al.* 2009; Holgado & Magnusson, 2012; Esteves *et al.*, 2015), North America (Kimpinski, 1979; Brown *et al.*, 1980; Olthof & Wolynetz, 1991) and Australia (Harding & Wicks, 2007). *Pratylenchus crenatus* and *P. neglectus*, mostly recorded on cereals and grasses worldwide (Loof, 1991), have also been reported associated with potatoes in Europe (Van Der Sommen *et al.* 2009; Holgado *et al.*, 2009; Esteves *et al.*, 2015) and North America (Kimpinski, 1979; Olthof *et al.*, 1982; Florini *et al.*, 1987; Kimpinski & Smith, 1988; Olthof & Wolynetz, 1991). *Pratylenchus thornei* has been only been reported associated with potato in Córdoba (Argentina) (Doucet, 1988), Ohio (North America) (Brown *et al.*, 1980) and Portugal (Esteves *et al.*, 2015) but at low densities compared to the other species.

Although there are several reports of *Pratylenchus* spp. on potatoes worldwide (Table 3), there is still the need for further studies to understand their distribution and impact on potato crops in some countries. In the UK, for example, there are reports of root-lesion nematodes from infested peas, bean, carrot, barley and wheat fields (Corbett, 1970; Boag 1979, 1980; Boag & Lopez-Llorca 1989; Boag *et al.*, 1990; Dale & Neilson, 2006), but there is no data regarding the affected areas and their impact on potato production.

MANAGEMENT OF ROOT-LESION NEMATODES ON POTATOES

Crop protection strategies need to facilitate the reduction of the initial nematode population density and minimise reproduction during the growing season. The history of the crop, species of root-lesion nematode and soil texture are important factors to consider in the selection of management strategies for a specific field (Duncan & Moens, 2013). Physical and chemical management of soil, crop rotation,

organic amendments, cover crops, biofumigation, elimination of weeds in the harvest and off season are examples of important cultural practices for the control of root-lesion nematodes (Castillo & Volvas, 2007).

Resistance of root-lesion nematodes on potatoes

Brodie & Plaisted (1993) studied the resistance of different potato cultivars to *P. penetrans* and found that clones least susceptible to *P. penetrans* were also resistant to the Potato Cyst Nematode species, *Globodera pallida* and *G. rostochiensis*. The US cultivar Butte was reported to be resistant to *P. penetrans* and *P. neglectus* (Davis *et al.*, 1992), while cultivars Peconic and Hudson were considered resistant only to *P. penetrans* (Brodie & Plaisted, 1993; Kimpinski & McRae, 1988). In contrast, France & Brodie (1995) found that cultivar Butte was resistant to one *P. penetrans* population from Cornell but susceptible to a population from Long Island. However, many of these cultivars are currently not grown commercially and there are no recent studies on the resistance of potato cultivars against root-lesion nematodes. This highlights the need for up-to-date screening of potato cultivars against root-lesion nematodes.

Chemical control

Chemical treatment is perhaps still the main crop protection method used by farmers to reduce damage caused by nematode feeding. Root-lesion nematodes can be managed with soil fumigants or non-fumigant nematicides (Table 4). Chloropicrin, methyl bromide, dazomet, 1,3-dichloropropene, metham-sodium are alternative fumigant nematicides historically used to treat root-lesion nematodes impacting potato production (Olthof, 1987; Olthof, 1989; Whitehead, 1998). However, the use of fumigant nematicides globally is restricted due to human health safety, environmental concerns and their negative effects on non-target organisms (Haydock *et al.*, 2013). Among all fumigants, only metam-sodium and dazomet are currently permitted for use to manage plant parasitic nematodes in Europe (EFSA, 2011; Lainsbury, 2019). Non-fumigant nematicides like oxamyl, ethoprophos, aldicarb, carbofuran, fensulpathion and disulphoton have been reported to manage *P. penetrans* in potato crops (Bernard & Laughlin, 1976; Kimpinski, 1982; Olthof *et al.*, 1985; Olthof, 1986; Kimpinski & McRae, 1988), but, also in this case, many have been banned and only oxamyl and fosthiazate are currently approved in Europe (EFSA, 2011; Lainsbury, 2019).

Cultural practices:

Crop rotation can be employed for nematode management, but in practice, this is difficult to apply for root-lesion nematodes due to their wide host range. For example, oats (*Avena sativa*) and rye (*Secale cereale*), often used in rotation with potatoes, favour multiplication of root-lesion nematodes (Olthof, 1980; Bélair *et al.*, 2002). Bélair *et al.* (2002) reported that *P. penetrans* not only reproduced on rye but also on brown mustard (*Brassica juncea*), soybean (*Glycine max*), Japanese millet (*Echinochloa frumentacea*), oilseed rape (*B. napus*), buckwheat (*Fagopyrum esculentum*), white mustard (*Sinapsis alba*), foxtail millet (*Setaria italica*), oats (*Avena sativa*), corn (*Zea mays*), bromegrass (*Bromus inermis*) and perennial ryegrass (*Lolium perenne*) under greenhouse conditions. Only forage pearl millet (*Pennisetum glaucum*) was found to decrease the number of *P. penetrans*. In one year rotation, forage pearl millet significantly reduced *P. penetrans* populations, increasing the yield of potato by 10% compared to oats (Bélair *et al.*, 2005). Similarly, both forage pearl millet and marigold reduced *P. penetrans* populations increasing potato yields (Ball-Coelho *et al.*, 2003).

Cover crops grown as inter crops, such as legumes, brassicas and grasses, planted after harvest of the main crop are usually grown through winter until spring when a new main crop is planted. Certain cover crop species, such as marigolds (*Tagetes* spp.), alfalfa (*Medicago sativa*), redtop (*Agrostis alba* L.), and red fescue (*Festuca rubra* L.), can also help to reduce population densities of *Pratylenchus* spp. (Castillo & Vovlas, 2007). For example, marigolds are reported to be effective in the suppression of *P. penetrans* (Reynolds *et al.*, 2000; Alexander & Waldenmaier, 2002; Evenhuis *et al.*, 2004; Pudasaini *et al.*, 2006; Hooks *et al.*, 2010) and can be used in rotation with potato (Alexander & Waldenmaier, 2002; Pudasaini *et al.*, 2006). Kimpinski *et al.* (2000) reported the ability of different *Tagetes* species (*T. patula*, *T. tenuifolia* cvs. NemaKill and Nemanon, *T. patula* spp. *nana* and *T. erecta* cv. Crackerjack) to reduce *P. penetrans* reproduction and to enhance tuber yields by about 14% more than other cover crops such as annual ryegrass, red clover, soybean and meadow fescue. Red clover and soybean cover crops resulted in the highest population densities of root-lesion nematodes and consequently lowest potato tuber yields in rotation with these two crops (Kimpinski *et al.*, 2000).

Biofumigation is an alternative practice that consists of the use of brassica plants to limit the reproduction of the soil-borne pests. The impact of tissue amendments from several varieties of *Brassica napus*, *B. oxyrrhina*, *B. rapa*, *B. nigra*, *B. carinata* and *B. juncea* were found to cause 56–95% mortality of *P. neglectus* under laboratory conditions (Potter *et al.*, 1999). While total glucosinolate content within root amendments had no significant correlation with *P. neglectus* mortality, the level of 2-phenylethyl glucosinolate was significantly correlated with the suppression of *P. neglectus* (Potter *et al.*, 1999). In a

greenhouse and field microplot study, *B. campestris* and *Raphanus sativus* green manures reduced populations of *P. neglectus* by up to 60%, when grown prior to planting potato in the USA (Al-Rehiyani & Hafez, 1998). Significant reductions of *P. penetrans* ranging from 66 to 74% were also reported by Yu *et al.* (2007) using *B. juncea* seed meal and bran soil amendments as biofumigants prior to potato, strawberry and maize planting in greenhouse. Overall, the use of Brassicaceae crops appears to offer a good method for the management of root-lesion nematodes, but further studies are necessary to evaluate its effectiveness in commercial scale agriculture. For example, in a six-year study reported by Korthals *et al.* (2014), *B. juncea* (cv. Energy) was not effective in the management of *P. penetrans* and *V. dahliae*, and even increased nematode populations in some instances.

Biological control

Root-lesion nematodes are considered difficult targets for biological control because they live mainly within plant roots (Stirling, 2014). Moreover, while the use of biological control for nematodes on potatoes has potential, it is not well established and its use in agriculture is limited (Palomares-Rius *et al.*, 2014; Stirling, 2014).

Certain 'trapping' fungi such as *Arthrobotrys oligospora*, *H. rhossiliensis*, *Monacrosporium elliposporum*, *Verticillium balanoides*, *Drechmeria coniospora*, and *Nematoctonus* spp. that produce adhesive conidia have been investigated for potential biological control of *P. penetrans*, but only *H. rhossiliensis* has shown to be effective in potatoes (Timper & Brodie, 1993). In the same study, *A. dactyloides*, *A. aligospora* and *M. elliposporum*, were successful in causing mortality in adults and juveniles of *P. penetrans* under *in-vitro* conditions, but only *H. rhossiliensis* and *M. elliposporum* were capable of causing a reduction of 24-25% in field conditions. Whilst, *V. balanoides*, *D. coniospora*, and *Nematoctonus* spp. were weak or no pathogens of *P. penetrans* (Timper & Brodie, 1993). In another study, *H. rhossiliensis* also caused a 25% reduction of *P. penetrans* entering potato roots with the suppression of nematode penetration (Timper & Brodie, 1994).

There is scant information on the efficacy of bacteria to reduce *Pratylenchus* spp. in potatoes. Sturz & Kimpinski (2004) assessed an *in-vitro* assay to study the effects of different endophytic bacteria isolated from African (*T. erecta*) and French (*T. patula*) marigold on *P. penetrans* mortality. Among forty-nine species of bacteria recovered from these plants, *Microbacterium esteraromaticum*, *Pseudomonas chlororaphis*, *Kocuria varians*, *K. kristinae* and *Tsukamurella paurometabola* showed activity against *P. penetrans* with *M. esteraromaticum* and *K. varians* having the greatest level of *P. penetrans* mortality. Recently, in a study of five potato farms in Colorado, Castillo *et al.* (2017) reported

a correlation between *P. neglectus*, *Meloidogyne chitwoodi* and rhizosphere bacteria, often present in potato soils. This study showed that farms with the fewest nematodes had greatest densities of *Bacillus* spp., *Arthrobacter* spp., and *Lysobacter* spp., whereas farms with greater abundances of *P. neglectus* and *M. chitwoodi* had a lower abundance of bacteria. This may suggest that some soil bacteria play an important role in suppressing *P. neglectus* in potato soils.

CONCLUSION

Root-lesion nematodes are frequently overlooked in potatoes, which may lead to an erosion of yield if they are not detected. Morphological and molecular diagnostics are often used to identify root-lesion nematodes, but the lack of expertise for morphological identification and issues with the available molecular methods, highlight the need for alternative approaches that provide a quick and reliable diagnosis. Correct diagnosis and quantification are a key component of nematode management.

Damage thresholds for *P. penetrans*, *P. neglectus* and *P. scribneri* affecting potatoes have been reported (Olthof & Potter, 1973; Riedel *et al.*, 1985; Olthof, 1986, 1990), but they can vary according to cultivar and environmental factors e.g. soil texture, temperature and moisture. Furthermore, species such as *P. brachyurus*, *P. coffeae*, *P. crenatus* and *P. thornei* have been found in soil associated with potato but there is no information available about their pathogenicity and symptoms on potatoes. Consequently, further work is required on the recognition of clear symptoms caused by different *Pratylenchus* spp. and their impact on the yield of potatoes. Lesions on the roots caused by *Pratylenchus* spp. provide entry points for secondary pathogens such as fungi resulting in interactions that enhance crop damage. Variability in experimental data suggests that interactions between *Pratylenchus* spp. and fungi are complex. Several factors play important roles in this interaction but there are still knowledge gaps on how multiple species of plant parasitic nematodes combine to enhance diseases caused by potato pathogens.

Different measures can be adopted to minimise damage caused by *Pratylenchus* spp., e.g. the application of nematicides, and cultural practices e.g. crop rotation, cover crops, biofumigation, and biological control. Each of these measures has limitations that make decision on their use challenging. Further, the wide host range of some *Pratylenchus* spp. causes problems in the design of crop rotations confounded with a lack of available resistant and tolerant potato cultivars. Cultivar resistance offers a potential solution as it could unlock a sustainable solution for root-lesion nematode management in potatoes. However, this is a long-term process to breed and bring to market a resistant cultivar. As with other plant parasitic nematodes, farmers still rely heavily on nematicides. However, only dazomet,

metham sodium, oxamyl, and fosthiazate are currently available for use against plant parasitic nematodes, including *Pratylenchus* spp., in Europe. Increasingly stringent pesticide legislation makes them unreliable in the long term, and nematologists are focusing their attention on the efficacy of alternative methods to reduce the use of nematicides in agricultural systems. Whilst crop rotation with forage pearl millet, cover crops such as *Tagetes* spp. and biofumigation with Brassicaceae crops have been shown to be the most effective methods for reducing root-lesion nematodes on potato, further studies are necessary to evaluate their effectiveness in agriculture. A multifaceted approach combining different methods may give good long-term field results on the limitation of root-lesion nematodes and this topic certainly needs further studies for a reliable application in agricultural systems.

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DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analysed in this study.

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FIGURE LEGENDS

Figure 1: Life cycle and potato infection by root-lesion nematode.

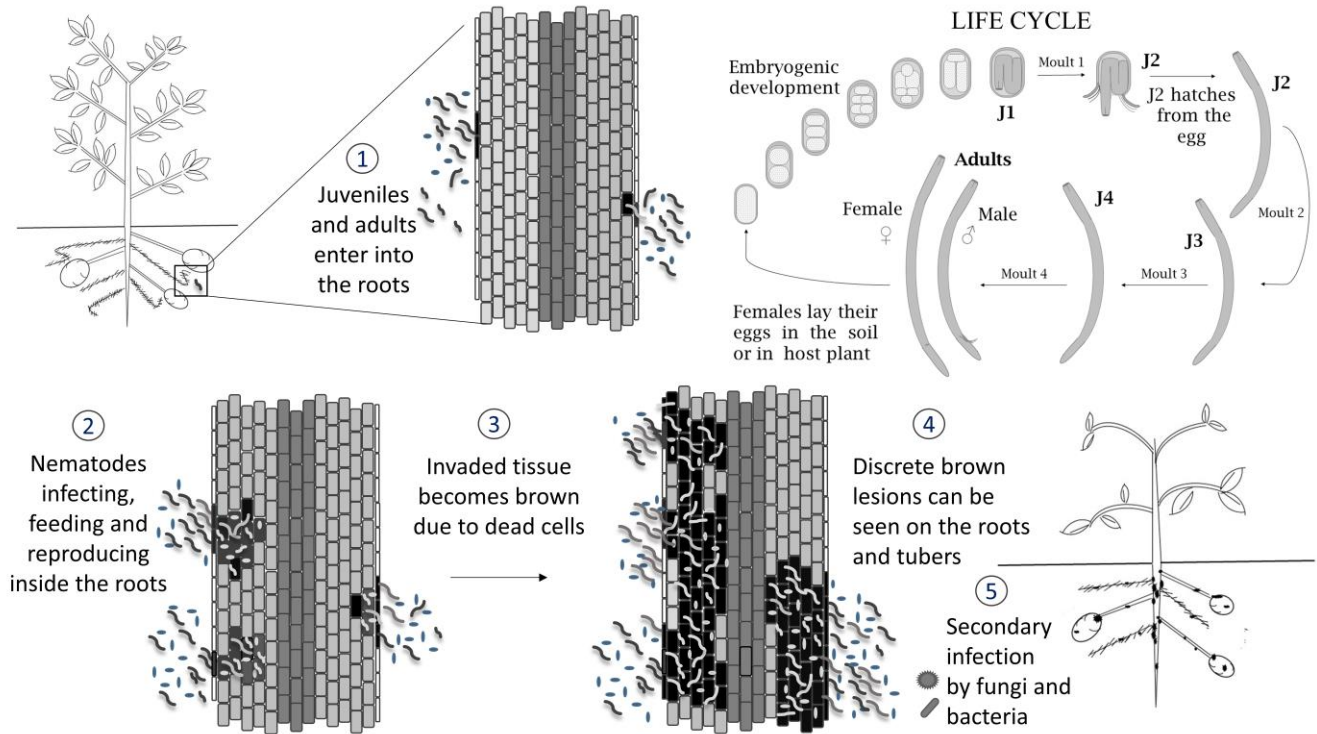


Table 1: Key morphological characters used for the identification of common root-lesion nematodes species associated with potato (adapted from Castillo & Volvas, 2007; Duncan & Moens, 2013; Geraert, 2013)

| <i>Species</i> | Head annuli | Lateral fields | Spermatheca | Post-vulval uterine sac | Tail | Male present |
|----------------------|-------------|----------------|-----------------------------------------------------------|---------------------------------|-------------------------------------------------|--------------|
| <i>P. brachyurus</i> | 2 | 4 | empty | short | conical with rounded, truncate or spiculate tip | no |
| <i>P. coffeae</i> | 2 | 4-5 | large, broadly oval to nearly rounded, usually with sperm | long | bluntly rounded, truncate or indented | yes |
| <i>P. crenatus</i> | 3 | 6 | empty | long | clavate with annulated tip | no |
| <i>P. neglectus</i> | 2 | 4 | empty | short | conical with rounded smooth tip | no |
| <i>P. penetrans</i> | 3 | 4 | round | short | round and smooth tip | yes |
| <i>P. scribneri</i> | 2 | 5-6 | oblong | short | smooth tip | yes |
| <i>P. thornei</i> | 3 | 4 | small, empty | slightly longer than body width | broad with truncate tip | no |

Table 2: Published species-specific primers of ITS rDNA, 28S rDNA and β -1,4-endoglucanase for identification of common *Pratylenchus* spp. on potato. f – forward; r- reverse; * universal primer.

| <i>Pratylenchus</i> Species | DNA region | Primer Sequence (5'-3') | PCR product size (bp) | Molecular Assay | Reference |
|-----------------------------|----------------------------|-------------------------------------------------------------------|-----------------------|------------------|----------------------------------|
| <i>P. brachyurus</i> | 18S rDNA | f -TTGATTACGTCCCTGCCCTT* | 267 | Conventional PCR | Machado <i>et al.</i> (2007) |
| | ITS rDNA | r - GCWCCATCCAAACAAYGAG | | | |
| <i>P. coffeae</i> | ITS rDNA | f – ATGCGCACATTGCATTCA r - GAGCGAGAAAACACCTCTCAC | 632 | Conventional PCR | Uehara <i>et al.</i> (1998a) |
| | ITS rDNA | f – ATGCCACATTGCATTCAGC r - GAGAGAGAAAACACCTCTCAC | 638 | Multiplex PCR | Saeki <i>et al.</i> (2003) |
| <i>P. crenatus</i> | 28S rDNA | f - AAAGCCTGAATGCCCTGAG r - AAATTGAAAGAGGTTCGGTCGT | 610 | Conventional PCR | Mekete <i>et al.</i> (2011) |
| | ITS rDNA | f - TTCTTGACAAGTTCATTGCTTC r - CACTCACGATGTGCTTCTG | 116 | TaqMan qPCR | Oliveira <i>et al.</i> (2017) |
| | β -1,4-endoglucanase | f -TCTCTGGACGGACGTGCTC r - AGGCCCTCCAGGAAGGTGTAC | 381 | Conventional PCR | Peetz & Zasada (2016) |
| <i>P. neglectus</i> | 28S rDNA | f - ATGAAAGTGAACATTGTCTC r - TCGGAAGGAACCAGCTACTA* | 290 | Conventional PCR | Al-Banna <i>et al.</i> (2004) |
| | 28S rDNA | f - CGCAATGAAAGTGAACAATGTC r - AGTTCACCATCTTTCGGGTC | 144 | SYBR green qPCR | Yan <i>et al.</i> (2008) |
| | ITS rDNA | f – GGCAGTGTGCGAAGTGTCCG r -TTAACACCTCAGGCGTCATGTAC | 234 | SYBR green qPCR | Yan <i>et al.</i> (2013) |
| | ITS rDNA | f - ACTGTGCGAAGTGTCCG r - GATCCACCGATAAGGCTAGA | 121 | TaqMan qPCR | Oliveira <i>et al.</i> (2017) |
| | β -1,4-endoglucanase | f - TGACCACAACGCGCAGAACCAC r - GCCACGTCCACGTCTGGGA | 293 | Conventional PCR | Peetz & Zasada (2016) |
| <i>P. penetrans</i> | 28S rDNA | f - TAAAGAATCCGCAAGGATAC r - TCGGAAGGAACCAGCTACTA* | 278 | Conventional PCR | Al-Banna <i>et al.</i> (2004) |
| | 28S rDNA | f - ACATGGTCGACACGGTGATA r - TGTTGCGCAAATCCCTGTTA | 520 | Conventional PCR | Mekete <i>et al.</i> (2011) |
| | 28S rDNA | f - GGTTCCTCGGGCTCATATGGGTTT r - TTTACGCCGAGAGTGGGATTGTG | 111 | SYBR green qPCR | Baidoo <i>et al.</i> (2017) |
| | 28S rDNA | f – GAGACTTTCGAGAAGGCGATATG r - AGGACCGAATTGGCAGAAG | 176 | TaqMan qPCR | Dauphinais <i>et al.</i> (2018) |
| | ITS rDNA | f - ATGATGGAAGTGTCCGCCT r - CCCAAACGACGGTCAAAAGG | 462 | Conventional PCR | Uehara <i>et al.</i> (1998b) |
| | ITS rDNA | f - ATTCCGTCCGTGGTTGCTATG r - GCCGAGTGATCCACCAGTAAG | 134 | SYBR green qPCR | Sato <i>et al.</i> (2007) |
| | ITS rDNA | f - TGACTATATGACACATTTRAACCTTG r - ATATGCTTAAAGTTCAGCGGGT | 660 | Duplex PCR | Waeyenberge <i>et al.</i> (2009) |
| | ITS rDNA | f - AATGTGTCTCGCCCTGAGG r - GCAACCACGGACGGAATAC | 80 | TaqMan qPCR | Oliveira <i>et al.</i> (2017) |
| | β -1,4-endoglucanase | f - CCAACCTCTGCTACACTA r - CAGTGCCGTATTCACTGA | - | TaqMan qPCR | Mokrini <i>et al.</i> (2013) |
| | β -1,4-endoglucanase | f - GGCATTTATGTG(A/C)TCGTGGATTGGC r - GTTGCCATCAGCGCTGACAGTG | 528 | Conventional PCR | Peetz & Zasada (2016) |
| <i>P. scribneri</i> | 28S rDNA | f - AAAGTGAACGTTTCCATTTT r - TCGGAAGGAACCAGCTACTA* | 286 | Conventional PCR | Al-Banna <i>et al.</i> (2004) |
| | 28S rDNA | f - ATGTGTTGCCATGCATCTG r - GTCCAGAACCATTGGACT | 750 | Conventional PCR | Mekete <i>et al.</i> (2011) |
| | ITS rDNA | f - AGTGTGCTATAATTCATGTAAAGTTGC r - TGGCCAGATGCGATTTCGAGAGGTGT | 136 | SYBR green qPCR | Huang & Yan (2017) |
| <i>P. thornei</i> | 28S rDNA | f - GAAAGTGAAGGTATCCCTCG r - TCGGAAGGAACCAGCTACTA* | 288 | Conventional PCR | Al-Banna <i>et al.</i> (2004) |
| | ITS rDNA | f - GTGTGTCGCTGAGCAGTTGTTGCC r - GTTGCTGGCGTCCCCAGTCAATG | 131 | SYBR green qPCR | Yan <i>et al.</i> (2012) |
| | β -1,4-endoglucanase | f - GGATGCGGTCATCAAGGC r - TTGGCTCTGGTGGTTCTG | 88 | TaqMan qPCR | Mokrini <i>et al.</i> (2014) |
| | β -1,4-endoglucanase | f - GGCTGGTCAGGAGTGAAGTCC r - GCCAGTTCACCACTCGTTGG | 364 | Conventional PCR | Peetz & Zasada (2016) |

Table 3: Global distribution of *Pratylenchus* species infesting potato

| <i>Pratylenchus</i> species | Location | References |
|-----------------------------|-----------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| <i>P. brachyurus</i> | South Africa | Koen & Hogewind, 1967 |
| | Zambia | Martin, 1972 |
| <i>P. coffeae</i> | Brazil | Kubo <i>et al.</i> , 2001 |
| <i>P. crenatus</i> | North America: Winsconsin, Ohio, Maine, New York (USA); Prince Edward Island, Ontario (Canada) | Dickerson <i>et al.</i> , 1964; Kimpinski, 1979; Brown <i>et al.</i> , 1980; Olthof <i>et al.</i> , 1982; Florini <i>et al.</i> , 1987; MacGuidwin & Rouse 1990; MacGuidwin & Stanger, 1991; Huettel <i>et al.</i> , 1991 |
| | Australia: South Australia | Harding & Wicks, 2007 |
| | Europe: Belgium, The Netherlands, Portugal | Pelsmaeker & Coomans, 1987; Scholte, 2000; Esteves <i>et al.</i> , 2015 |
| | | |
| <i>P. neglectus</i> | North America Winsconsin, Ohio (USA); Ontario (Canada) | Dickerson <i>et al.</i> , 1964; Brown <i>et al.</i> , 1980; Olthof <i>et al.</i> , 1982; MacGuidwin & Rouse 1990; MacGuidwin & Stanger, 1991 |
| | Australia: South Australia | Harding & Wicks, 2007 |
| | Europe: The Netherlands, Portugal | Van Der Sommen <i>et al.</i> , 2009; Esteves <i>et al.</i> , 2015 |
| <i>P. penetrans</i> | North America Winsconsin, Washington, Minnesota, Ohio (USA); Ontario, Prince Edward Island (Canada) | Dickerson <i>et al.</i> , 1964; Kimpinski, 1979; Brown <i>et al.</i> , 1980; Olthof <i>et al.</i> , 1982; MacGuidwin and Rouse 1990; MacGuidwin & Stanger, 1991; Ingham <i>et al.</i> 2005; Baidoo <i>et al.</i> , 2017 |
| | Australia South Australia | Harding & Wicks, 2007 |
| | Europe Belgium, Portugal, Cyprus, The Netherlands | Pelsmaeker & Coomans, 1987; Abrantes <i>et al.</i> 1987; Philis, 1995; Van Der Sommen <i>et al.</i> , 2009; Esteves <i>et al.</i> , 2015 |
| | Asia Vietnam, Pakistan | Ryss & Fam-Tkhan, 1989; Khan & Hussain, 2004 |
| | | |
| <i>P. thornei</i> | North America Winsconsin, Ohio (USA) | Dickerson <i>et al.</i> , 1964; Brown <i>et al.</i> , 1980; MacGuidwin & Rouse 1990; MacGuidwin & Stanger, 1991; Yan <i>et al.</i> , 2016 |
| <i>P. thornei</i> | North America Winsconsin, Ohio (USA) | Dickerson <i>et al.</i> , 1964; Brown <i>et al.</i> , 1980; MacGuidwin & Rouse 1990; MacGuidwin & Stanger, 1991 |
| | Argentina | Doucet, 1988 |
| | Europe Portugal | Esteves <i>et al.</i> , 2015 |
| | | |

Table 4: Nematicides for management of root-lesion nematodes in Europe. Status under Reg. (EC) No 1107/2009 based on EU Pesticides database (<http://ec.europa.eu/food/plant/pesticides/eu-pesticides-database/public>)

| Active substance | Chemical Group | State of formulation | Status under Reg. (EC) No 1107/2009 |
|--------------------------------------|---------------------------------|--------------------------|-------------------------------------|
| FUMIGANTS | | | |
| 1,3 – Dichloropropene | Halogenated hydrocarbon | Liquid | Not approved |
| Dazomet | Methyl isothiocyanate liberator | Microgranulate | Approved |
| Metam (incl. -potassium and -sodium) | Methyl isothiocyanate liberator | Liquid Liquid | Approved |
| Methyl bromide | Halogenated hydrocarbon | Gas | Not approved |
| CARBAMATES | | | |
| Aldicarb | Oxime carbamate | Microgranulate | Not approved |
| Carbofuran | Carbamate | Microgranulate Liquid | Not approved |
| Oxamyl | Oxime carbamate | Microgranulate Liquid | Approved |
| ORGANOPHOSPATES | | | |
| Cadusafos | Organophosphorus | Liquid Microgranulate | Not approved |
| Ethoprophos | Organophosphorus | Microgranulate | Not approved |
| Fosthiazate | Organophosphorus | Microgranulate | Approved |
| Thionazin | Organophosphorus | Microgranulate | Not approved |