

*Root-lesion nematodes in cereal fields:
importance, distribution, identification,
and management strategies*

**Fouad Mokrini, Nicole Viaene, Lieven
Waeyenberge, Abdelfattah A. Dababat &
Maurice Moens**

**Journal of Plant Diseases and
Protection**

Scientific Journal of the "Deutsche
Phytopathologische Gesellschaft" (DPG) -
the German Society of Plant Protection
and Plant Health

ISSN 1861-3829

J Plant Dis Prot

DOI 10.1007/s41348-018-0195-z



**Journal of
Plant Diseases
and Protection**

 Springer



 Springer

Your article is protected by copyright and all rights are held exclusively by Deutsche Phytomedizinische Gesellschaft. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your article, please use the accepted manuscript version for posting on your own website. You may further deposit the accepted manuscript version in any repository, provided it is only made publicly available 12 months after official publication or later and provided acknowledgement is given to the original source of publication and a link is inserted to the published article on Springer's website. The link must be accompanied by the following text: "The final publication is available at link.springer.com".

Root-lesion nematodes in cereal fields: importance, distribution, identification, and management strategies

Fouad Mokrini¹ · Nicole Viaene^{2,4} · Lieven Waeyenberge² · Abdelfattah A. Dababat⁵ · Maurice Moens^{2,3}

Received: 16 June 2018 / Accepted: 6 October 2018
© Deutsche Phytomedizinische Gesellschaft 2018

Abstract

Root-lesion nematodes of the genus *Pratylenchus* are among the most important nematode pests that limit production of small-grain cereals. Four *Pratylenchus* species, viz. *P. thornei*, *P. neglectus*, *P. penetrans*, and *P. crenatus*, are considered of major economic significance in cereals of which *P. thornei* and *P. neglectus* are the most important and widely distributed species in cereal crops worldwide. However, *P. thornei* is more destructive causing estimated yield losses of up to 50% in the USA and 85% in Australia. This paper provides information regarding the global distribution of *Pratylenchus* species, yield loss due to their attack, their biology and pathogenic relation to plants, the research cutting edges in nematode identification of different *Pratylenchus* species, and their control through cultural practices and resistant varieties as correct identification of root-lesion nematodes can be difficult to achieve, particularly if a quick diagnosis is needed. In this context, in recent years, several molecular techniques for these *Pratylenchus* species have been developed such as quantitative PCR assays which are able to produce precise and rapid identification of several root-lesion nematodes species. So far, many global attempts have been made to control root-lesion nematodes in cereals, including cultural practices and development of resistant varieties. The use of resistant accessions is considered the most economically feasible and environmentally sustainable method. Resistance genes in several lines have been identified and are being used in numerous breeding programmes against root-lesion nematodes species.

Keywords Nematodes · *Pratylenchus* spp. · Cereals · Distribution · Approaches

The importance of cereals and associated root-lesion nematodes

Small-grain cereals include wheat, barley, oats, rye, triticale, rice, and other species that constitute the world's most important source of food. This is due to their great adaptability, permitting successful colonization in every type of ecological habitat, relative ease of cultivation, tillering habit giving higher yield per unit area, and good nutritive values (Vasil 1999). These crops supply 20% of calories and account for more than half of all harvested crop areas in the world (Dababat et al. 2015). About 70% of land devoted to crops production is planted by cereals. Current production levels and trends will not be sufficient to fulfil the projected global demand generated by increasing populations (Ray et al. 2013). For wheat, global production will need to be increased by 60% to meet the estimated demand in 2050 (Ackerman and Stanton 2008). Additional gains in productivity of small-grain cereals will continue to

✉ Fouad Mokrini
fmokrini.inra@gmail.com

✉ Abdelfattah A. Dababat
a.dababat@cgiar.org

¹ National Institute for Agricultural Research (INRA), UR - Integrated Crop Protection, Rue FAR, Inezgane, Agadir, Morocco

² Plant, Crop Protection, Flanders Research Institute for Agriculture, Fisheries and Food (ILVO), Burg. Van Gansberghelaan 96, 9820 Merelbeke, Belgium

³ Faculty of Bio-Science Engineering, Ghent University, Coupure Links 653, 9000 Ghent, Belgium

⁴ Department of Biology, Ghent University, K.L. Ledeganckstraat 35, 9000 Ghent, Belgium

⁵ International Maize and Wheat Improvement Center (CIMMYT), P.K. 39, 06511 Emek, Ankara, Turkey

depend upon developments of new technologies and cereal cultivars, and identifying and addressing the production constraints associated with shifting climate patterns, declining availability of certain fertilizer nutrients, salinization of some currently irrigated land, reduced availability of water in some regions, and yield reductions caused by biotic constraints including diseases, insect pests, weeds, and nematodes.

Plant-parasitic nematodes are one of the main biotic causes of plant stress and yield loss of wheat worldwide (Nicol and Rivoal 2008). Globally, crop losses associated with plant-parasitic nematodes are estimated at 12.6%, representing annual monetary losses of 216 billion US \$ (Nyaku et al. 2017). In Southern and Western Australia, Root-lesion nematodes (RLNs) damage is estimated to cause losses in the order of \$190 million per annum. Actual losses may even be higher because no data are available from the many countries where nematologist expertise is lacking. Moreover, yield losses due to nematodes are often neglected because of lack of conspicuous aboveground symptoms.

Global distribution of the root-lesion nematodes

RLNs belonging to the genus of *Pratylenchus* rank second behind the cyst nematodes in terms of their economic importance in wheat production systems (Castillo and Vovlas 2007). At least eight species of RLNs affect roots of cereals (Rivoal and Cook 1993). Among them, *P. thornei*, *P. neglectus*, *P. penetrans*, and *P. crenatus* have a worldwide distribution, and sometimes coexist (Nicol et al. 2003; Smiley and Nicol 2010).

The geographic distribution of RLN species depends mostly on both the prevalence of host plants supporting reproduction and abiotic factors (mainly temperature) (Castillo and Vovlas 2007). In the Pacific Northwest of the USA (Oregon, Washington, Idaho), RLN species have been identified in more than 90% of dryland wheat fields with predominance of *P. neglectus* and *P. thornei* (Smiley et al. 2004). In the northern grains region of Australia (Queensland and northern New South Wales), the presence of *P. thornei* and *P. neglectus* has been known since the 1960s and yield loss in wheat caused by *P. thornei* has been demonstrated since the late 1970s (Thompson et al. 2008). However, *P. thornei* is the predominant species of RLNs in wheat and causes estimated annual losses of \$33 million (Brennan and Murray 1989). Recently, Thompson et al. (2016) reported that the RLN (*P. thornei*) is a major pathogen to wheat production in the subtropical northern grain region of eastern Australia. Vanstone et al. (2008) reported that both *P. thornei* and *P. neglectus* are the two

most important root-lesion nematodes affecting broad acre crops in the southern cropping region of Australia. Al-Banna et al. (2015) reported the presence of both *P. thornei* and *P. neglectus* in different wheat producing regions in Jordan. Several studies reported that the spring wheat yields elsewhere in the world have been reduced by as much as 32% by *P. neglectus* and 69% by *P. thornei* (McDonald and Nicol 2005; Thompson et al. 2008). Similar yield losses from these species have been reported for spring wheat in Oregon (Smiley et al. 2005). Armstrong et al. (1993) reported that the winter wheat yields were reduced by 32% by *P. thornei* in Colorado. In the Isparta province of Turkey, three *Pratylenchus* species (*P. thornei*, *P. neglectus*, and *P. scribneri*) have been identified in wheat (Sogut and Devran 2011). Yield losses due to *P. thornei* are estimated at 20% on wheat in Turkey (Toktay 2008). In Iran, eight species of RLNs including *P. brachyurus*, *P. coffeae*, *P. crenatus*, *P. neglectus*, *P. penetrans*, *P. pseudopratensis*, *P. thornei*, and *P. zae* were reported from maize, wheat, barley, and rice (Pourjam et al. 1998). *P. neglectus*, *P. thornei*, *P. pseudopratensis*, and *P. penetrans* were reported from wheat fields in Iran (Ghaderi et al. 2010). Pourjam et al. (1999) reported that *P. thornei* and *P. neglectus* are the most common species of RLNs in Iran. *P. penetrans* also parasitizes wheat and barley, resulting in yield loss of 10–19% in Canada (Nicol and Rivoal 2008). In Morocco, RLNs are the most important group of nematodes in different cereal-growing areas followed by nematodes of the *Heterodera avenae* group (Mokrini et al. 2012, 2017). Recently, Mokrini et al. (2016) reported the presence of four species, viz. *P. penetrans*, *P. thornei*, *P. pinguicaudatus*, and *P. pseudocoffeae*, in different wheat-growing areas of Morocco. Sikora (1988) identified *P. neglectus* and *P. penetrans* in addition to *P. thornei* on wheat and barley in Northern Africa and all these as well as *P. zae* in Western Asia.

Life cycle of the root-lesion nematodes

RLN species are migratory endoparasites (Moens and Perry 2009). All mobile life stages of RLN species are parasitic as both adults and juveniles can penetrate, migrate, and feed within roots (Bridge and Starr 2007). As is typical of other plant-parasitic nematodes, RLN species develop within the egg to the J1 that moults to J2, which then hatches from the egg (Davis and MacGuidwin 2000). The nematodes further moult through stages three (J3) and four (J4) to become fully developed adults. Each subsequent moult results in an increase in size and sexual development (Luc et al. 2005). Mobile juveniles and adult stages can enter and leave roots. They may become entirely embedded within root tissue and migrate from cell to cell within that

tissue and spend most of their life cycle in host plant roots, but can also be found at the root surface and in adjacent soil. Females can deposit eggs in the roots and in the soil (Pudasaini et al. 2008). Eggs are released into the soil during root degradation (Castillo and Vovlas 2007). Lesion nematodes appear to be attracted to host roots, especially to the region of root hair production and the root tip (Peng and Moens 1999). There are differences in the sites and mechanisms of root penetration by different species of RLN in various hosts. *P. penetrans* explores the root by rubbing its lip region along the surface of epidermal cells and protracting its stylet enough to touch but not penetrate the walls (Zunke 1990). In lucerne and clover, *P. penetrans* preferred to penetrate the main roots where lateral roots ruptured the cortex and migrated through the cortex of main roots into lateral roots (Townshend et al. 1989). In other studies, *P. penetrans* aggregated and penetrated in the zone of root elongation of turf grasses (Troll and Rohde 1966). Castillo et al. (1998) found that both females and juveniles of *P. thornei* penetrated the roots of chickpea without any preference of site.

Pratylenchus thornei and *P. neglectus* are parthenogenic (De Waele and Elsen 2002), i.e. females produce fertile eggs without copulation with a male. By contrast, *P. penetrans* is an amphimictic species, i.e. male and female must mate before fertile eggs are produced. Populations of *P. penetrans* therefore include nearly equal proportions of males and females (Smiley and Nicol 2010). Long-term survival under adverse conditions can occur at the egg stage (Castillo and Vovlas 2007).

RLN can complete their life cycle in 45–65 days depending on the species, the amount of available food sources, temperature, host species, and moisture (Taylor et al. 2000). The optimum conditions for development vary with the species. *Pratylenchus* spp. can complete three to six generations within the roots during one crop-growing season (Taylor et al. 2000). On the basis of laboratory observations, life cycle duration has been estimated for several nematode–host plant combinations. The time required to complete the life cycle varies considerably depending on temperature and moisture. In red clover, *P. penetrans* completed a generation in 54–65 days and produced 16–35 eggs per female at a rate of 1–2 eggs per day at 24 °C (Turner and Chapman 1972). The generation time of *P. penetrans* in vitro was estimated as 46, 38, 28, 26, and 23 days at 17, 20, 25, 27, and 30 °C, respectively (Mizukubo and Adachi 1997). On carrot callus, the complete life cycle of *P. coffeae* at 30 °C was 27–28 days, that of *P. penetrans* at 24 °C was 34–35 days, and that of *P. loosi* at 20 °C was 45–46 days (Wu et al. 2002). Similarly, the life cycle of *P. thornei* was completed in about 25–35 days on carrot discs at 20–25 °C (Castillo et al. 1995).

Symptoms

Root lesions are the main symptoms on plants invaded by RLN species, and they cause degradation of cells in the epidermis and cortex of underground plant organs. This reduces the amount of root branching and the ability of roots to absorb water and nutrients (Smiley and Nicol 2010). Wheat roots infested with RLN display sloughing of cortical and epidermal cells, degradation of lateral roots, and loss of root hairs (Vanstone et al. 1998). Generally, infected cereal roots are browning as lesions rapidly coalesce to produce extensive areas of discolorations. Aboveground symptoms are non-specific. Overall, affected plants appear stunted with premature yellowing of older leaves, reduced tillering, and lower weight (Smiley and Nicol 2010; Castillo and Vovlas 2007). These symptoms are often confused with nutrient deficiencies, drought, root disease, or barley yellow dwarf (Taylor et al. 1999; Smiley and Nicol 2010) or associated with other pathogens (Evans and Haydock 1993). For instance, fields with high populations of RLNs often have plant canopies that are irregular in height and maturation, as also occurs in plants affected by *Rhizoctonia* root rot (Smiley and Nicol 2010). Penetration of root tissues by RLN results in lesions that favour greater colonization by root-rotting fungi and by saprophytic bacteria, fungi, and nonparasitic nematodes (Moens and Perry 2009). These secondary organisms cause more intense rotting and discoloration than that caused by the RLNs alone. Cortical degradation and reduced root branching often are not visible until plants are 6 or more weeks old, and these root symptoms are often confused with those caused by *Pythium* or *Rhizoctonia* root rot (Smiley and Nicol 2010). Colonization of *Fusarium oxysporum* in chickpea has been shown to increase with increasing population density of *P. thornei* (Castillo et al. 1998). More root lesions can occur when *P. neglectus*-infested wheat plants are co-infested with various fungal pathogens, including *Pythium irregulare*, which causes damping off, and *Gaeumannomyces graminis*, the agent responsible for take-all disease (Taheri et al. 1994).

Differences in temporal developments of symptoms of *P. penetrans* invasion were observed on different hosts. For example, lesions in the proximal parts of the seminal roots of wheat appeared only after 6 weeks after inoculation with *P. thornei* (Baxter and Blake 1968). However, lesions on strawberry roots appeared 17 days after inoculation when inoculated with *P. penetrans* (Townshend 1963).

Identification of root-lesion nematodes

RLNs contain 97 valid species distributed in temperate and tropical environments (Handoo et al. 2008). Traditionally, identification of RLN species based on morphology and morphometrics of females and males (when present) is a challenging task that demands considerable skills. However, diversity in morphology and morphometrics among and within the species has been reported frequently as a result of different environmental conditions, including host plant (e.g. Román and Hirschmann 1969; Doucet et al. 2001). This morphological diversity makes diagnosing of *Pratylenchus* species time-consuming and difficult to achieve, especially in the case of mixed species populations (Mokrini et al. 2016). Nevertheless, accurate identification of *Pratylenchus* species is needed as an initial step in designing effective control. This is especially important when searching for potential source of host plant resistance against RLN species.

Species-specific PCR

Within the last few years, nematode identification based on morphology and morphometrics has been supplemented with molecular observations. Waeyenberge et al. (2000), De Luca et al. (2004), and Subbotin et al. (2006) demonstrated that DNA-based methods provide efficient tools for a precise and rapid identification of RLN species. PCR using species-specific primers constitutes a major step forward in the development of diagnostic technology, which has successfully been used for sensitive detection of RLN species. Several articles report the development and use of species-specific primers for the molecular identification of RLN species. Species-specific primers to detect *P. penetrans* in a conventional PCR have been developed (Uehara et al. 1998a; Al-Banna et al. 2004; Waeyenberge et al. 2009). However, these primers are not suitable to quantify the species. Many studies have been done for molecular identification of *P. thornei* by species-specific primers (Al-Banna et al. 2004; Carrasco-Ballesteros et al. 2007; Yan et al. 2008). Al-Banna et al. (2004) reported that PNEG/D3B designed from the D2D3 expansion region of 28S rRNA discriminated *P. neglectus* from *P. brachyurus*, *P. scribneri*, *P. penetrans*, *P. thornei*, and *P. vulnus*. The primer set (PNEG-F1/D3B5) modified by Yan et al. (2008) could also specifically identify *P. neglectus* in soil by conventional PCR. Moreover, other species-specific primers were reported for detection of *P. coffeae*, *P. loosi*, *P. brachyurus*, *P. crenatus*, *P. zaeae*, and *P. scribneri* (Al-Banna et al. 2004; Uehara et al. 1998b; Mekete et al. 2011). Recently, Huang and Yan (2017) developed specific

detection of the root-lesion nematode *P. scribneri* using conventional PCR.

Quantitative real-time PCR

The main objective of quantification of plant-parasitic nematodes is monitoring the nematodes population for the estimation of the damage threshold (Barker and Noe 1987). The correct identification and quantification of RLN species is a fundamental step in nematode control strategies. However, the identification of RLNs based on morphology and morphometric traits is time-consuming and requires specialized skills. Moreover, RLN species are frequently present in mixed populations, which make their identification and quantification even more difficult. Therefore, molecular tools are useful for the identification and discrimination between species and for their precise quantification. It was demonstrated that species-specific PCR assays provide an efficient tool for an accurate, rapid, and sensitive detection of *P. penetrans* or *P. thornei* (Uehara et al. 1998a; Al-Banna et al. 2004; Carrasco-Ballesteros et al. 2007; Yan et al. 2008; Waeyenberge et al. 2009). However, none of the species-specific primers were developed for quantification purposes, yet quantification is very essential in breeding programmes and extension activities. Recently, quantitative PCR (RTqPCR) strategies have been developed for *P. zaeae* (Berry et al. 2008), *P. neglectus* (Yan et al. 2013), and *P. thornei* (Yan et al. 2012). RTqPCR allows continuous monitoring of the sample during PCR using hybridization probes. Within this region, the number of cycles needed to obtain fluorescence above the background (Ct) is compared between samples and standards with known quantities of DNA. These data then can be used for quantification of the samples (King-smorth et al. 2003).

More recently, a number of publications investigating this technology for nematode enumeration have been published. Sato et al. (2007) could detect a single *P. penetrans* individual in a sample with an abundant number of free-living nematodes using SYBR Green I-based RTqPCR method. Mokrini et al. (2013) detected a single nematode of *P. penetrans* when mixed with 80 individuals of *P. thornei*. Yan et al. (2012) developed a real-time PCR method for quantification of *P. thornei* from DNA extracts of soil using primers designed from the internal transcribed spacer region (ITS) of rDNA. Mokrini et al. (2014) developed a real-time PCR assay for *P. thornei* using sequences of the 1,4-endoglucanase gene and reported that the developed assay was able to detect and quantify *P. thornei* in mixed populations of *Pratylenchus* spp. where visual identification of individual nematodes at species level is extremely difficult. Sato et al. (2011) estimated the

number of *P. penetrans* in the samples from different radish fields using a RTqPCR assay. Qiu et al. (2007) briefly reported a qPCR method for *P. vulnus*. Recently, Huang and Yan (2017) developed a real-time PCR assay for *P. scribneri*.

Management of *Pratylenchus* species on wheat

The choice of management tactic to reduce damage caused by root-lesion nematodes depends upon many factors. All tactics require accurate diagnosis of the species and population levels of *Pratylenchus* as assessed from soil and root samples taken from any given field. Action thresholds vary among species of RLNs and crops depending upon geographic location, crop value, and the potential for disease complexes (Davis and MacGuidwin 2000; Castillo and Vovlas 2007). The damage thresholds of some species of RLN associated with cereals were determined in several studies (Table 1). Assessment of potential crop damage caused by *Pratylenchus* is usually based on population densities in soil at the time of planting, but also on densities in roots during the growing season.

The main purpose of controlling RLN is to avoid having significant yield losses. There are many reports about the different methods to reduce population densities of RLN (Thompson et al. 2009; May et al. 2016).

Cultural practices

Cultural methods offer some control, but are often of limited effectiveness. To be of significance, they need to be integrated with other control measures. The use of crop rotation is a limited option for RLN, due to their polyphagous nature (Nicol and Rivoal 2008). Successful use of rotation requires a thorough understanding of the effectiveness of a particular rotation. Little information is available about the role of crop rotation in controlling RLN in wheat, although some field and laboratory work has been

undertaken to better understand the hosting ability of cereals and leguminous crops to *P. thornei* and *P. neglectus* (Vanstone et al. 1998; Lasserre et al. 1994; Nicol 1996). Nevertheless, some effective rotations have been developed. For example, in Sonora (Mexico), populations of *P. thornei* in wheat fields were reduced by rotations that include corn, cotton, or soybean for 2 consecutive years (Van Gundy et al. 1974). In Queensland (Australia), wheat is rotated with the barley cv. Clipper to reduce populations of *P. thornei* (O'Brien 1983; Owen et al. 2010, 2014; Thompson et al. 2012a). Control of *P. zaeae* has been reported on rice by crop rotation with non-host crops such as legumes, e.g. mung bean (*Vigna radiata*) and black gram (*Vigna mungo*) (Prasad and Rao 1978). The principle for the use of crop rotation to reduce RLN densities is that monoculture of a host plant usually results in increased population density and consequent yield losses (Castillo and Vovlas 2007). However, some long-term monoculture experiences indicate that monoculture may also reduce RLN populations (Castillo and Vovlas 2007). Andersen (1975) showed that *P. crenatus* and *P. neglectus* reached highest numbers in the first 3 years of barley monoculture, after which population densities decreased gradually and stabilized at a lower level.

Di Vito et al. (1991) showed that the solarization of soil with polyethylene film for 6–8 weeks in chickpea fields reduced *P. thornei* populations by 50%. Tillage is often considered as an option for control of soil-borne nematodes (Haak et al. 1993; López-Fando and Bello 1995; Thompson et al. 2010).

Other management practices are less effective in managing RLN populations. Field sanitation during the fallow phase is as important as during the in-crop phase, because species of RLN multiply on many weed species in the genera *Avena*, *Brassica*, *Bromus*, *Malva*, and *Rumex* (Vanstone and Russ 2001). Smiley et al. (2004) reported that the presence of susceptible weeds or crop species between planted crops allows RLN to increase population density over a greater interval of the cropping system. Van Gundy et al. (1974) indicated that delayed planting to mid-November in Sonora Mexico resulted in wheat plants

Table 1 Damage threshold densities of cereal–*Pratylenchus* combinations

<i>Pratylenchus</i> spp.	Cereals	Damage threshold (nematodes/cm ³ soil)	References
<i>P. crenatus</i>	Oat	0.33	Barker and Olthof (1976)
<i>P. neglectus</i>	Barley	1.5	Rivoal and Cook (1993)
<i>P. thornei</i>	Wheat	0.5–1	Rivoal and Cook (1993)
<i>P. thornei</i>	Wheat	0.42	Nicol and Ortiz-Monasterio (2004)
<i>P. thornei</i>	Wheat	2.5	Thompson et al. (1993)
<i>P. thornei</i>	Wheat	3	Nicol et al. (1999)

growing in soil < 15 °C such that nematode reproduction was slowed and the wheat gained a competitive advantage. This concept was extended by modelling an optimum time of sowing wheat in the subtropical grain region of eastern Australia such that *P. thornei* reproduction was limited by lower soil temperatures (Thompson 2015).

Fertilization with inorganic sources of nitrogen has also been observed to modify populations of *Pratylenchus* spp. Dmowska and Ilieva (1995) reported that RLN species were more abundant in plots of barley fertilized with nitrogen over 22 years than in non-fertilized plots.

Resistance and tolerance

The use of resistant and tolerant cultivars is considered the most economically and environmentally acceptable means for control of RLN (Castillo et al. 1998). RLN species readily multiply on a susceptible wheat cultivar to high population densities, which decrease wheat growth and yield; on a resistant cultivar, the reproduction is much reduced with less yield loss. By contrast, a tolerant cultivar still has the capacity to grow and yield well in the presence of high numbers of nematodes (Thompson et al. 1999). The first source of superior tolerance to *P. thornei* in wheat lines was identified through targeted screening of cultivars. Tolerant cultivars such as Pelsart (Brennan et al. 1994), Sunvale (Ellison et al. 1995), and Baxter (Thompson et al. 1999) were used to minimize the effects of RLNs. These tolerant lines offered a 30% yield increase compared to other commercial cultivars available at the time (Thompson et al. 1995). Ideally, the resistance should be combined with tolerance. The most detailed research on breeding for tolerance and resistance to *Pratylenchus* spp. has been carried out in Australia, where it was shown that a tolerant wheat variety grown in nematode-free fields or after nematicide treatment is a good option for controlling RLN (Thompson et al. 2008). The soil-borne pathogen programme at CIMMYT Turkey annually screens about 1000 accessions of wheat from the CIMMYT Mexico spring wheat programme and the Turkey—CIMMYT—ICARDA International Winter Wheat Improvement Program (www.iwwip.org) under growth room, greenhouse, and field conditions at various locations in Turkey. Cultivars are also screened for multiple disease resistance, such as resistance to different species of root-lesion nematodes (e.g. *P. thornei* and *P. neglectus*) (Toktay et al. 2013) and the most resistant lines then distributed to international collaborators to be used in their breeding programmes.

Many sources of resistant wheat germplasm have been reported for RLN (Thompson and Haak 1997; Taylor et al. 2000; Toktay et al. 2012). Resistance in wheat against *P. thornei* (Vanstone et al. 1998; Thompson et al. 1999, 2009)

and *P. neglectus* (Thompson et al. 1989) has been identified. In Australia, the first significant source of resistance to *P. thornei* was the bread wheat line GS50a selected from a severely infested field of the variety Gatcher (Thompson and Clewett 1986). Thompson et al. (1999) showed that this line reduced RLN reproduction by more than tenfold. Sheedy and Thompson (2009) investigated 274 accessions of Iranian wheat landraces and identified 25 accessions that were more resistant than 'GS50a'. Thompson et al. (2009) found additional sources of *P. thornei* resistance from screening wheat accession collections from West Asian and North African regions.

Resistance to *P. neglectus* has been investigated less than resistance to *P. thornei* because the latter species is the most frequent RLN detected on cereals in the world. For *P. neglectus*, the resistant locus, (*Rlnn1*) located on chromosome 7AL and originating from the Australian variety 'Excalibur', has been identified and validated (Williams et al. 2002). As both RLN species are often found in the same field in mixed populations (Thompson et al. 2010), the development of wheat cultivars with resistance to both species is desirable. However, it should be noted that wheat cultivars with resistance or tolerance to *P. thornei* are not necessarily resistant or tolerant to *P. neglectus* and vice versa, since resistance and tolerance to each species is genetically independent (Smiley and Nicol 2010); this probably also applies to other species that infest wheat.

Molecular markers can provide evidence to address fundamental questions on the genetics of root-lesion nematodes resistance in wheat and to assist in breeding for nematode resistant wheat cultivars. Several advancements have occurred in marker and QTL analysis technology in the last decade since the last reported RLN species resistance QTL in wheat. These advancements can be used in genetic mapping to uncover the number of genes involved in resistance and to understand the genetic mechanisms of how the resistance to nematode invasion is conferred by each gene. Several studies showed that resistance to RLN is inherited in a quantitative manner (Thompson and Seymour 2011; Thompson et al. 2012b; Dababat et al. 2016). Resistances to RLN have been reported in accessions of wheat by several researchers (Sheedy and Thompson 2009; Mokrini et al. 2018). Many putative quantitative trait loci (QTL) for RLN resistance were identified (Table 2).

Conclusion

Accurate identification of the nematode species present in the field and knowledge of their population density are essential when designing effective control measures. As is common for other nematode species, RLN species are traditionally identified on the basis of their morphology and

Table 2 QTL associated with *P. thornei* and *P. neglectus* resistance in wheat

<i>Pratylenchus</i> spp.	Origin	Chromosome/QTL	References	
<i>P. thornei</i>	CPI133872 × Janz (ITMI) W-7984 × Opata85	QRInt.lrc-2B.1	Zwart et al. (2005)	
		2BS	Zwart et al. (2006)	
		6DS		
	CPI133872 × Janz	QRInt.lrc-2B.1	Zwart et al. (2010)	
		QRInt.lrc-6D.1	Zwart et al. (2010)	
		QRInt.lrc-6D.2	Zwart et al. (2010)	
		Sokoll × Krichauff	QRInt.sk-2A	Linsell et al. (2014)
			QRInt.sk-2B.1	
			QRInt.sk-2B.2	
	AUS13124 × Janz (AUS13124 and AUS4926) × Janz (AUS13124 and AUS4926) × Janz AUS4926 × Janz	1B	Schmidt et al. (2005)	
		2B		
		3B		
		6D		
<i>P. neglectus</i>	CPI133872 × Janz CPI133872 × Janz CPI133872 × Janz CPI133872 × Janz CPI133872 × Janz Tammin × Excalibus	QRlnc.lrc-2B.1	Zwart et al. (2010)	
		QRlnc.lrc-3D.1		
		QRlnc.lrc-4B.1		
		QRlnc.lrc-4D.1		
		QRlnc.lrc-6D.1		
		Rlnc1/7AL	Williams et al. (2002)	

The parents of the mapping population are shown

morphometrics. Unfortunately, this is time-consuming and hardly applicable when species mixtures need to be identified and quantified. PCR-based DNA analysis is powerful to detect, distinguish, and identify species of RLN, and it can be an excellent tool complementing the traditional identification. The control of RLN diseases is achieved using different approaches, including cultural practices, crop rotation, and genetic resistance and tolerance. The use of resistant cultivars, i.e. cultivars that have the capacity to prevent or reduce nematode multiplication, is considered one of the most effective and economical methods for managing nematodes in different cropping systems including rainfed and irrigated areas.

Acknowledgements The research was financially supported by Islamic Development Bank (IDB) and a Special Research Fund (BOF) scholarship from Ghent University.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Human and animal rights This article does not contain any studies with human participants or animals performed by any of the authors.

References

- Ackerman F, Stanton EA (2008) Can climate change save lives? A comment on economy-wide estimates of the implications of climate change. *Hum Health Ecol Econ* 66:8–13
- Al-Banna L, Ploeg AT, Williamson VM, Kaloshian I (2004) Discrimination of six *Pratylenchus* species using PCR and species-specific primers. *J Nematol* 36:142–146
- Al-Banna L, Al Abded A, Fattash I, Khrfan W, Lafi H, Abu Shweimeh, Mazrawi D, Abu Al Ragheb (2015) Current status of cyst nematodes attacking cereals in Jordan. In: Proceedings of the fifth international cereal nematode initiative workshop, Ankara, pp 12–15
- Andersen HJ (1975) *Pratylenchus* population densities in barley monocultures. *Nord Jordbrugsforsk* 57:1129–1130
- Armstrong JS, Peairs FB, Pilcher SD, Russell CC (1993) The effect of planting time, insecticides, and liquid fertilizer on the Russian wheat aphid (Homoptera: Aphididae) and the lesion nematode (*Pratylenchus thornei*) on winter wheat. *J Kans Entomol Soc* 66:69–73
- Barker KR, Noe JP (1987) Establishing and using threshold population levels. In: Veech JA, Dickson DW (eds) *Vistas on nematology*. Society of Nematologists, Hyattsville, pp 75–81
- Barker KR, Olthof THA (1976) Relationships between nematode population densities and crop responses. *Annu Rev Phytopathol* 14:327–353
- Baxter RI, Blake CD (1968) *Pratylenchus thornei* a cause of root necrosis in wheat. *Nematologica* 14:331–361
- Berry SD, Fargette M, Spaul VW, Morand S, Cadet P (2008) Detection and quantification of root-knot nematode

- (*Meloidogyne javanica*), lesion nematode (*Pratylenchus zeae*) and dagger nematode (*Xiphinema elongatum*) parasites of sugarcane using real-time PCR. *Mol Cell Probes* 22:168–176
- Brennan JP, Murray GM (1989) Australian wheat disease: assessing their economic importance. *Agric Sci* 2:26–35
- Brennan PS, Martin DJ, Thompson JP (1994) *Triticum aestivum* ssp. *vulgare* (bread wheat) cv. Pelsart. *Aust J Exp Agric* 34:864–865
- Bridge J, Starr JL (2007) Plant parasitic nematodes of agricultural importance. A color hand book. Academic Press/Elsevier, New York
- Carrasco-Ballesteros S, Castillo P, Adams BJ, Pérez-Artés E (2007) Identification of *Pratylenchus thornei*, the cereal and legume root-lesion nematode, based on SCAR-PCR and satellite DNA. *Eur J Plant Pathol* 118:115–125. <https://doi.org/10.1007/s10658-007-9110-3>
- Castillo P, Vovlas N (2007) *Pratylenchus* (Nematoda, Pratylenchidae): diagnosis, biology, pathogenicity and management. *Nematol Monogr Perspect* 6:1–530
- Castillo P, Trapero-Casas JL, Jiménez-Díaz RM (1995) Effect of time, temperature, and inoculum density on reproduction of *Pratylenchus thornei* in carrot disk cultures. *J Nematol* 27:120–124
- Castillo P, Vovlas N, Jiménez-Díaz RM (1998) Pathogenicity and histopathology of *Pratylenchus thornei* populations on selected chickpea genotypes. *Plant Pathol* 47:370–376
- Dababat AA, Imren M, Gul Erginbas O, Ashrafi S, Yavuzaslanoglu E, Toktay T, Pariyar SH, Elekcioğlu H, Morgounov A, Mekete T (2015) The importance and management strategies of cereal cyst nematodes, *Heterodera* spp., in Turkey. *Euphytica* 202:173–188
- Dababat AA, Ferney GBH, Erginbas-Orakci G, Dreisigackee S, Imree M, Toktay H, Elekcioğlu HI, Mekete T, Nicol JM, Ansari O, Ogbonnaya F (2016) Association analysis of resistance to cereal cyst nematodes (*Heterodera avenae*) and root lesion nematodes (*Pratylenchus neglectus* and *P. thornei*) in CIMMYT advanced spring wheat lines for semi-arid conditions. *Breed Sci* 66:692–702. <https://doi.org/10.1270/jsbbs.15158>
- Davis EL, MacGuidwin AE (2000) Lesion nematode disease. The Plant Health Instructor. <https://doi.org/10.1094/phi-i-2000-1030-02>
- De Luca F, Fanelli E, Di Vito M, Reyes A, De Giorgi C (2004) Comparison of the sequences of the D3 expansion of the 26S ribosomal genes reveals different degrees of heterogeneity in different populations and species of *Pratylenchus* from the Mediterranean region. *Eur J Plant Pathol* 110:949–957
- De Waele D, Elsen A (2002) Migratory endoparasites: *Pratylenchus* and *Radopholus* species. In: Starr JL, Cook R, Bridge J (eds) In plant resistance to parasitic nematodes. CAB International, Wallingford, pp 175–206
- Di Vito M, Greco N, Saxena MC (1991) Effectiveness of soil solarization for control of *Heterodera ciceri* and *Pratylenchus thornei* on chickpea in Syria. *Nematol Mediterr* 19:109–111
- Dmowska E, Ilieva K (1995) The effect of prolonged diverse mineral fertilization on nematodes inhabiting the rhizosphere of spring barley. *Eur J Soil Biol* 31:189–198
- Doucet ME, Lax P, Di Rienzo JA, Pinochet J, Baujard P (2001) Temperature-induced morphological variability in an isolate of *Pratylenchus vulnus* Allen & Jensen, 1951 (Nematoda: Tylenchida). *Nematology* 3:18
- Ellison FW, Brown GN, Mares DJ, Moore SG, O'Brien L (1995) Registration of Australian winter cereal cultivars *Triticum aestivum* ssp. *vulgare* (bread wheat) cv. Sunvale. *Aust J Exp Agric* 35:416
- Evans K, Haydock PPJ (1993) Interactions of nematodes with root-rot fungi. In: Wajid Khan M (ed) Nematode interactions. Champan Hall, London, pp 104–133
- Ghaderi R, Karegar A, Banihashemi Z, Taghavi M (2010) Distribution and population fluctuation of root-lesion nematodes, *Pratylenchus* spp., in irrigated wheat and corn fields in Marvdasht, Fars province. *Iran J Plant Pathol* 45:95–98
- Haak MI, Peck DM, Thompson JP (1993) Numbers of *Pratylenchus thornei* and *P. neglectus* are altered by frequent tillage and stubble retention. In: Vanstone VA, Taylor SP, Nicol JM (eds) Proceedings of the 9th *Pratylenchus* workshop, APPS conference, Hobart, pp 69–73
- Handoo Z, Carta L, Skantar A (2008) Taxonomy, morphology and phylogenetics of coffee-associated root-lesion nematodes, *Pratylenchus* spp. In: Souza RS (ed) Plant-parasitic nematodes of coffee. Springer, Dordrecht, pp 29–50
- Huang D, Yan D (2017) Detection of the root-lesion nematode *Pratylenchus scribneri* using conventional and real-time PCR. *Plant Dis* 101(2):359–365. <https://doi.org/10.1094/PDIS-07-16-1013-RE>
- Kingsnorth CS, Kingsnorth AJ, Lyons PA, Chwaesczynska DM, Asher MJC (2003) Real-time analysis of *Polymyxa beta* GST expression in infected sugar beet. *Mol Plant Pathol* 4:171–176
- Lasserre F, Rivoal R, Cook R (1994) Interactions between *Heterodera avenae* and *Pratylenchus neglectus* on wheat. *J Nematol* 26:336–344
- Linsell KJ, Rahman MS, Taylor JD, Davey RS, Gogel BJ, Wallwork H, Forrest KL, Hayd MJ, Taylor SP, Oldach KH (2014) QTL for resistance to root lesion nematode (*Pratylenchus thornei*) from a synthetic hexaploid wheat source. *Theor Appl Genet* 127:1409–1421
- López-Fando C, Bello A (1995) Variability in soil nematode populations due to tillage and crop rotation in semi-arid Mediterranean agrosystems. *Soil Tillage Res* 36:59–72
- Luc M, Sikora RA, Bridge J (2005) Plant parasitic nematodes in subtropical and tropical agriculture. CABI Pub, Wallingford
- May DB, Johnson WA, Zuck PC, Chen CC, Dyer AT (2016) Assessment and management of root lesion nematodes in Montana wheat production. *Plant Dis* 100(10):2069–2079
- McDonald AH, Nicol JM (2005) Nematode parasites of cereals. In: Luc M, Sikora RA, Bridge J (eds) Plant parasitic nematodes in subtropical and tropical agriculture. CABI Publishing, Wallingford, pp 131–191
- Mekete T, Reynolds K, Lopez-Nicora HD, Gray ME, Niblack TL (2011) Distribution and diversity of root-lesion nematode (*Pratylenchus* spp.) associated with *Miscanthus × giganteus* and *Panicum virgatum* used for biofuels, and species identification in a multiplex polymerase chain reaction. *Nematology* 13:673–686
- Mizukubo T, Adachi H (1997) Effect of temperature on *Pratylenchus penetrans* development. *J Nematol* 29:306–314
- Moens M, Perry RN (2009) Migratory plant endoparasitic nematodes: a group rich in contrasts and divergence. *Annu Rev Phytopathol* 47:313–332
- Mokrini F, Waeyenberge L, Viaene N, Moens M (2012) Occurrence of nematodes of the *Heterodera avenae* group and *Pratylenchus* spp. on wheat and barley in Morocco. In: 31st International symposium of the European Society of nematologists, Adana, pp 23–27
- Mokrini F, Waeyenberge L, Viaene N, Abbad Andaloussi F, Moens M (2013) Quantitative detection of the root-lesion nematode, *Pratylenchus penetrans*, using qPCR. *Eur J Plant Pathol* 137(2):403–413. <https://doi.org/10.1007/s10658-013-0252-1>
- Mokrini F, Waeyenberge L, Viaene N, Abbad Andaloussi F, Moens M (2014) The β -1,4-endoglucanase gene is suitable for the molecular quantification of the root-lesion nematode, *Pratylenchus thornei*. *Nematology* 16(7):789–796. <https://doi.org/10.1163/15685411-00002808>

- Mokrini F, Waeyenberge L, Viaene N, Abbad Andaloussi F, Moens M (2016) Diversity of root-lesion nematodes (*Pratylenchus* spp.) associated with wheat (*Triticum aestivum* and *T. durum*) in Morocco. *Nematology* 18(7):781–801
- Mokrini F, Viaene N, Waeyenberge L, Dababat AA, Moens M (2017) Characterization of cereal cyst nematodes (*Heterodera* spp.) in Morocco based on morphology, morphometrics and rDNA-ITS sequence analysis. *J Plant Prot Res* 57(3):219–227
- Mokrini F, Viaene N, Waeyenberge L, Dababat AA, Moens M (2018) Investigation of resistance to *Pratylenchus penetrans* and *P. thornei* in international wheat lines and its durability when inoculated together with the cereal cyst nematode *Heterodera avenae*, using qPCR for nematode quantification. *Eur J Plant Pathol*. <https://doi.org/10.1007/s10658-018-1420-0>
- Nicol JM (1996) The distribution, pathogenicity and population dynamics of *Pratylenchus thornei* (Sher and Allen, 1954) on wheat in south Australia, Ph.D. thesis. The University of Adelaide, Adelaide
- Nicol JM, Ortiz-Monasterio I (2004) Effect of root lesion nematode on wheat yields and plant susceptibility in Mexico. *Nematology* 6:485–493
- Nicol JM, Rivoal R (2008) Global knowledge and its application for the integrated control and management of nematodes on wheat. In: Ciancio A, Mukerji KG (eds) *Integrated management and biocontrol of vegetable and grain crops nematodes*, vol 2. Springer, Dordrecht, pp 243–287
- Nicol JM, Davies KA, Hancock TW, Fisher JM (1999) Yield loss caused by *Pratylenchus thornei* on wheat in South Australia. *J Nematol* 31:367–376
- Nicol J, Rivoal R, Taylor S, Zaharieva M (2003) Global importance of cyst (*Heterodera* spp.) and lesion nematodes (*Pratylenchus* spp.) on cereals: Distribution, yield loss, use of host resistance and integration of molecular tools. In: Cook R, Hunt DJ (eds) *Proceedings of the fourth international Congress of nematology*, 8–13 June 2002, Tenerife, Spain. *Nematology Monographs and Perspectives*, vol 2. Brill, Leiden, pp 1–19
- Nyaku ST, Affokpon A, Danquah A, Brentu FC (2017) Harnessing useful rhizosphere microorganisms for nematode control. In: Shah MM, Mahamood M (eds) *Nematology—concepts, diagnosis and control*. InTech, London, pp 153–182. <https://doi.org/10.5772/intechopen.69164>
- O'Brien PC (1983) A further study on the host range of *Pratylenchus thornei*. *Australas Plant Pathol* 12:1–3
- Owen KJ, Clewett TG, Thompson JP (2010) Pre-cropping with canola decreased *Pratylenchus thornei* populations, arbuscular mycorrhizal fungi, and yield of wheat. *Crop Pasture Sci* 61:399–410
- Owen KJ, Clewett TG, Thompson JP (2014) Wheat biomass and yield increased when populations of the root-lesion nematode (*Pratylenchus thornei*) were reduced through sequential rotation of partially-resistant winter and summer crops. *Crop Pasture Sci* 65:227–241
- Peng Y, Moens M (1999) Effects of surface sterilisation and cold storage on in vitro behaviour of *Pratylenchus penetrans*. *Nematology* 1(6):647–653
- Pourjam E, Kheiri A, Geraert E, Alizadeh A (1998) Occurrence of some *Pratylenchus* species in Iran. In: *Proceedings of the 13th Iranian plant protection congress*, vol 2. Plant Diseases, p 318
- Pourjam E, Kheiri A, Geraert E, Alizadeh A (1999) Variations in Iranian populations of *Pratylenchus neglectus* and *P. thornei* (Nematoda: Pratylenchidae). *Iran J Plant Pathol* 35:23–27
- Prasad JS, Rao SY (1978) Influence of crop rotations on the population densities of the root-lesion nematode, *Pratylenchus indicus* in rice and rice soils. *Ann Zool Ecol Anim* 10:627–633
- Pudasaini MP, Viaene N, Moens M (2008) Hatching of the root-lesion nematode, *Pratylenchus penetrans*, under the influence of temperature and host. *Nematology* 10:47–54
- Qiu J, Westerdahl BB, Williamson VM (2007) Detection and quantification of the root-lesion nematode *Pratylenchus vulnus* using real-time PCR. *J Nematol* 39:95–96
- Ray DK, Mueller ND, West PC, Foley JA (2013) Yield trends are insufficient to double global crop production by 2050. *PLoS ONE* 8:e66428
- Rivoal R, Cook R (1993) Nematode pests of cereals. In: Evans K, Trudgill DL, Webster JM (eds) *Plant parasitic nematodes in temperate agriculture*. CABI Publishing, Wallingford, pp 259–303
- Román J, Hirschmann H (1969) Morphology and morphometrics of six species of *Pratylenchus*. *J Nematol* 1:363–386
- Sato E, Min YY, Sgirakashi T, Wada S, Toyota K (2007) Detection of the root-lesion nematode, *Pratylenchus penetrans* (Cobb), in a nematode community using real-time PCR. *J Nematol* 37:38–92
- Sato E, Suga Y, Kisaki C, Toyota K, Miyake K, Takada A, Takeuchi A, Matsuura A (2011) Quantification of *Pratylenchus penetrans* in radish fields using a combination method of soil compaction and real-time PCR to determine the economic threshold. *Soil Sci Plant Nutr* 57(2):213–220
- Schmidt AL, McIntyre CL, Thompson J, Seymour NP, Liu CJ (2005) Quantitative trait loci for root lesion nematode (*Pratylenchus thornei*) resistance in Middle-Eastern landraces and their potential for introgression into Australian bread wheat. *Aust J Agric Res* 56:1059–1068
- Sheedy JG, Thompson JP (2009) Resistance to the root-lesion nematode *Pratylenchus thornei* of Iranian landrace wheat. *Australas Plant Pathol* 38:478–489
- Sikora RA (1988) Plant parasitic nematodes of wheat and barley in temperate and temperate semi-arid regions—a comparative analysis. In: Saxena MC, Sikora RA, Srivastava JP (eds) *Nematodes parasitic to cereals and legumes in temperate semi-arid regions*. ICARDA, Aleppo, pp 46–48
- Smiley RW, Nicol JM (2010) Nematodes which challenge global wheat production. In: Carver BF (ed) *Wheat science and trade*. Wiley Blackwell, New York, pp 171–187
- Smiley RW, Merrifield K, Patterson LM, Whittaker RG, Gourlie JA, Easley SA (2004) Nematodes in dryland field crops in the semiarid Pacific Northwest United States. *J Nematol* 36:54–68
- Smiley RM, Whittaker RG, Gourlie JA, Easley SA, Ingham RE (2005) Plant parasitic nematodes associated with reduced wheat yield in Oregon, *Heterodera avenae*. *J Nematol* 37:297–307
- Sogut MA, Devran Z (2011) Distribution and molecular identification of root-lesion nematodes in temperature fruit orchards of Turkey. *Nematotopica* 41:91–98
- Subbotin SA, Sturhan D, Chizhov VN, Vovlas N, Baldwin JG (2006) Phylogenetic analysis of Tylenchida Thorne, 1949 as inferred from D2 and D3 expansion fragments of the 28S rRNA gene sequences. *Nematology* 8:455–474
- Taheri A, Hollamby GJ, Vanstone VA (1994) Interaction between root lesion nematode, *Pratylenchus neglectus* (Rensch 1924) Chitwood and Oteifa 1952, and root rotting fungi of wheat. *N Z J Crop Hortic Sci* 22:181–185
- Taylor SP, Vanstone VA, Ware AH, McKay AC, Szot D, Russ MH (1999) Measuring yield loss in cereals caused by root lesion nematodes (*Pratylenchus neglectus* and *P. thornei*) with and without nematicides. *Aust J Agric Res* 50:617–622
- Taylor SP, Hollaway GJ, Hunt CH (2000) Effect of rotational field crops on population densities of *Pratylenchus neglectus* and *P. thornei* in southeastern Australia, part 1: *P. neglectus*. *Suppl J Nematol* 32:591–599
- Thompson JP (2015) Modelling population densities of root-lesion nematode (*Pratylenchus thornei*) from soil profile temperatures to choose an optimum sowing date for wheat in a subtropical region. *Field Crops Res* 183:50–55

- Thompson JP, Clewett TG (1986) Research on root-lesion nematode: occurrence and wheat varietal reaction. Queensland Wheat Research Institute Biennial Report for 1982–84. Queensland Department of Primary Industries, Toowoomba, pp 32–35
- Thompson JP, Haak MI (1997) Resistance to root lesion nematode (*Pratylenchus thornei*) in *Aegilops tauschii* Coss., the D-genome donor to wheat. Aust J Agric Res 48:553–559
- Thompson JP, Seymour NP (2011) Inheritance of resistance to root-lesion nematode (*P. thornei*) in wheat landraces and cultivars from the West Asia and North Africa (WANA) region. Crop Pasture Sci 62:82–93
- Thompson JP, Mackenzie J, Clewett TG (1989) Rapid coring of clay topsoils for microbiological analyses. Austral Plant Pathol 18:1–2
- Thompson JP, Clewett TG, O'Reilly MM (1993) Tolerance and resistance in wheat to *Pratylenchus thornei*. In: *Pratylenchus* workshop, 9th Biennial conference of the Australasian Plant Pathology Society, Hobart, Tasmania, pp 43–48
- Thompson JP, Clewett MT, O'Reilly GM, Brennan PS (1995) Disease reactions of selected cultivars. Root lesion nematode. Queensland Wheat Variety Trials 1994, Queensland Department of Primary Industries, pp 60–64
- Thompson JP, Brennan PS, Clewett TG, Sheedy JG, Seymour NP (1999) Progress in breeding wheat for tolerance and resistance to root-lesion nematode (*Pratylenchus thornei*). Austral Plant Pathol 28:45–52
- Thompson JP, Owen KJ, Stirling GR, Bell MJ (2008) Root-lesion nematodes (*Pratylenchus thornei* and *P. neglectus*): a review of recent progress in managing a significant pest of grain crops in northern Australia. Austral Plant Pathol 37:235–242
- Thompson JP, O'Reilly MM, Clewett TG (2009) Resistance to the root-lesion nematode *Pratylenchus thornei* in wheat landraces and cultivars from the West Asia and North Africa (WANA) region. Crop Pasture Sci 60(12):1209–1217
- Thompson JP, Clewett TG, Sheedy JG, Reen RA, O'Reilly MM, Bell KL (2010) Occurrence of root-lesion nematodes (*Pratylenchus thornei* and *P. neglectus*) and stunt nematode (*Merlinius brevidens*) in the northern grain region of Australia. Austral Plant Pathol 39:254–264
- Thompson JP, Mackenzie J, Sheedy GH (2012a) Root-lesion nematode (*Pratylenchus thornei*) reduces nutrient response, biomass and yield of wheat in sorghum–fallow–wheat cropping systems in a subtropical environment. Field Crops Res 137:126–140
- Thompson JP, Zwart RS, Butler D (2012b) Inheritance of resistance to root-lesion nematodes (*Pratylenchus thornei* and *P. neglectus*) in five doubled-haploid populations of wheat. Euphytica 188:209–219
- Thompson JP, Rostad RH, Whish JPM (2016) Survival of root-lesion nematodes (*Pratylenchus thornei*) after wheat growth in a vertisol is influenced by rate of progressive soil desiccation. Ann Appl Biol 170:78–88
- Toktay H (2008) Bazı Yazlık Buğday Çeşitlerinin *Pratylenchus thornei* Sher et Allen (Tylenchida: Pratylenchidae)'ye Karşı Dayanıklılığının Araştırılması. Çukurova Üniversitesi Fen Bilimleri Enstitüsü, (Basılmamış) Doktora Tezi, Adana (Turkey), 117 S. (Resistance of Some Spring Wheat Against *Pratylenchus thornei* Sher Et Allen Tylenchida: Pratylenchidae, Ph.D. thesis. University of Cukurova, Institute of Nature of Science, Adana, p 117
- Toktay H, Yavuzaslanoğlu E, İmren M, Nicol JM, Elekcioğlu IH, Dababat AA (2012) Screening for resistance to *Heterodera filipjevi* (Madzhidov) Stelter (Tylenchida: Heteroderidae) and *Pratylenchus thornei* (Sher & Allen) (Tylenchida: Pratylenchidae) sister lines of spring wheat. Turk J Entomol 36:455–461
- Toktay H, İmren M, Elekcioğlu IH, Dababat AA (2013) Evaluation of Turkish wild Emmers (*Triticum dicoccoides* Koern.) and wheat varieties for resistance to the root lesion nematodes (*Pratylenchus thornei* and *Pratylenchus neglectus*). Turk J Entomol 39(3):219–227
- Townshend JL (1963) The pathogenicity of *Pratylenchus penetrans* to strawberry. Can J Plant Sci 43:75–78
- Townshend JL, Stobbs L, Carter R (1989) Ultrastructural pathology of cells affected by *Pratylenchus penetrans* in alfalfa roots. J Nematol 21:530–539
- Troll J, Rohde RA (1966) Pathogenicity of *Pratylenchus penetrans* and *Tylenchorhynchus claytoni* on turfgrasses. Phytopathology 56:995–998
- Turner DR, Chapman RA (1972) Infections of seedlings of alfalfa and red clover by concomitant populations of *Meloidogyne incognita* and *Pratylenchus penetrans*. J Nematol 4:280–286
- Uehara T, Mizukubo T, Kushida A, Momota Y (1998a) Identification of *Pratylenchus penetrans* (Cobb) by PCR using ITS-based species-specific primers. Jpn J Nematol 28:1–7
- Uehara T, Mizukubo T, Kushida A, Momota Y (1998b) Identification of *Pratylenchus coffeae* and *P. loosi* using specific primers for PCR amplification of ribosomal DNA. Nematologica 44:357–368
- Van Gundy SD, Jose Gustavo Perez B, Stolzy LH, Thomason JJ (1974) A pest management approach to the control of *Pratylenchus thornei* on wheat in Mexico. J Nematol 6:107–116
- Vanstone VA, Russ MH (2001) Ability of weeds to host the root lesion nematodes *Pratylenchus neglectus* and *P. thornei*. I. Grass weeds. Austral Plant Pathol 30:245–250
- Vanstone VA, Rathjen AJ, Ware AH, Wheeler RD (1998) Relationship between root lesion nematodes (*Pratylenchus neglectus* and *P. thornei*) and performance of wheat varieties. Aust J Exp Agric 38:181–189
- Vanstone VA, Hollaway GJ, Stirling GR (2008) Managing nematode pests in the southern and western regions of the Australian cereal industry: continuing progress in a challenging environment. Austral Plant Pathol 37:220–234
- Vasil IK (1999) Molecular improvement of epidemiology. In: Leonard K, Dry W (eds) Cereal crops. Advances in cellular and molecular biology of plants, vol 5. Kluwer/Spriyer, Dordrecht, p 402
- Waeyenberge L, Ryss A, Moens M, Pinochet J, Vrain TC (2000) Molecular characterisation of 18 *Pratylenchus* species using ribosomal DNA restriction fragment length polymorphism. Nematology 2:135–142
- Waeyenberge L, Viaene N, Moens M (2009) Species-specific duplex PCR for the detection of *Pratylenchus penetrans*. Nematology 11(6):847–857
- Williams KJ, Taylor SP, Bogacki P, Pallotta M, Bariana HS, Wallwork H (2002) Mapping of the root-lesion nematode (*Pratylenchus neglectus*) resistance gene *Rlnn1* in wheat. Theor Appl Genet 104:874–879
- Wu HY, Tsay TT, Lin YY (2002) Identification and biological study of *Pratylenchus* spp. isolated from the crops in Taiwan. Plant Pathol Bull 11:123–136
- Yan G, Smiley RW, Okubara PA, Skantar A, Easley SA, Sheedy JG, Thompson AL (2008) Detection and discrimination of *Pratylenchus neglectus* and *P. thornei* in DNA extracts from soil. Plant Dis 92:1480–1487
- Yan G, Smiley RW, Okubara PA (2012) Detection and quantification of *Pratylenchus thornei* in DNA extracted from soil using real-time PCR. Phytopathology 102:14–22
- Yan GP, Smiley RW, Okubara PA, Skantar AM, Reardon CL (2013) Developing a real-time PCR assay for detection and quantification of *Pratylenchus neglectus* in soil. Plant Dis 97:757–764

- Zunke U (1990) Observations on the invasion and endoparasitic behavior of the root lesion nematode, *Pratylenchus penetrans*. *J Nematol* 22:309–320
- Zwart RS, Thompson JP, Godwin ID (2005) Identification of quantitative trait loci for resistance to two species of root-lesion nematode (*Pratylenchus thornei* and *P. neglectus*) in wheat. *Aust J Agric Res* 56:345–352
- Zwart RS, Thompson JP, Sheedy JG, Nelson CJ (2006) Mapping quantitative trait loci for resistance to *Pratylenchus thornei* from synthetic hexaploid wheat in the International Triticeae Mapping Initiative (ITMI) population. *Aust J Agric Res* 57:525–530
- Zwart RS, Thompson JP, Milgate AW, Bansal UK, Williamson PM, Raman H, Bariana HS (2010) QTL mapping of multiple foliar disease and root-lesion nematode resistances in wheat. *Mol Breed* 26:107–124