

# Chapter 8

## Nematodes Which Challenge Global Wheat Production

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### SUMMARY

- 1) Effects of cereal cyst (*Heterodera*) and root-lesion (*Pratylenchus*) nematodes on wheat are difficult to identify and control. Symptoms are non-specific and easily confused with stress from nutrient deficiency, drought, or disease.
- 2) Multiple species of *Heterodera* and *Pratylenchus* are capable of damaging wheat. Identification of species is difficult and procedures based on comparative morphology can be unreliable. Identification of species is now assisted by molecular tools.
- 3) *Heterodera* species discussed in this chapter reproduce only on hosts within the Poaceae, and individual species are highly heterogeneous for virulence to specific host genotypes. Many pathotypes occur within *H. avenae*, and the same is anticipated for *H. filipjevi* and *H. latipons*. No pathotypic variation within either *P. neglectus* or *P. thornei* has been reported on wheat, but both species multiply in a wide range of monocot and dicot hosts. Mixtures of *Heterodera* species or pathotypes, and *Pratylenchus* species, may occur within individual fields.
- 4) Field sanitation is important because these nematodes multiply on many weed species and volunteer cereals. Cereal cyst nematode can be controlled by rotating wheat with a noncereal, a resistant cultivar, or with weed-free fallow. Root-lesion nematode is best managed by rotating resistant and tolerant wheat cultivars with other poor hosts.
- 5) Resistance and tolerance are genetically independent, and cultivars resistant or tolerant to one species are not necessarily resistant or tolerant to another species. Root-lesion nematode resistance is quantitative and cereal cyst nematode is controlled by single-gene resistance. Molecular markers have been developed to identify genes and quantitative trait loci for resistance in seedlings.
- 6) Molecular tests to identify and quantify nematodes in commercial soil testing laboratories will allow more effective surveys of populations. Greater collaboration is needed between research institutions, organizations, and countries.

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### INTRODUCTION

Plant-parasitic nematodes are tiny but complex animals (unsegmented roundworms) anatomically differentiated for feeding, digestion, locomotion, and reproduction (Barker et al., 1998). Most species are transparent, vermiform (eel-shaped), and 0.5 to 2 mm long.

They puncture cells and damage plants mechanically and chemically, reducing plant vigor, inducing lesions, rots, deformations, galls, or root knots, and predisposing plants to infection by root-infecting fungi. World crop production is thought to be reduced 10% by damage from plant-parasitic nematodes (Whitehead 1997).

Plant-parasitic nematode species that live in the soil represent one of the most difficult pest problems to identify, demonstrate, and control. A particular challenge is to clearly identify damage by cereal nematodes, as the symptoms are non-specific and easily confused with other ailments such as nitrogen deficiency, water availability, and other disease. Farmers, pest management advisors, and scientists routinely underestimate or fail to recognize their impact on wheat.

Procedures to sample, extract, identify, and quantify plant-parasitic nematodes are both technically challenging and time consuming. Extensive training is necessary to distinguish genera and species (Varma 1995; Mai and Mullin 1996; Siddiqi 2000), which is essential for implementation of appropriate management strategies.

The damage threshold, defined as the number of nematodes to give a specific yield loss, is determined by both environmental and genotypic factors. The threshold generally is decreased when plant growth is stressed by drought, poor soil nutrition, impediments to root penetration, or adverse temperature. The threshold is increased by partial or full resistance reactions by a given cultivar. Damage caused by cereal nematode is likely to be greater where limited rotation or cultivar options exist, especially in rainfed cereal monoculture, including “rotations” of winter wheat with summer fallow. Unlike the visually obvious and more vastly studied cereal rusts, the global knowledge of economic importance is less well known and understood due to difficulties working with soil-inhabiting nematodes.

The most important plant-parasitic species affecting wheat are in the genera *Heterodera* (cyst), *Pratylenchus* (root-lesion), *Meloidogyne* (root knot), *Ditylenchus* (stem), *Tylenchorhynchus* and *Merlinius* (stunt), *Paratrichodorus* (stubby-root), and *Anguina* (seed-gall) (Rivoal and Cook 1993; McDonald and Nicol 2005; Nicol and Rivoal 2007; Bockus et al., 2009).

This chapter will focus on two nematodes of primary global importance to wheat. The global distribution of cereal cyst nematode species and

pathotypes is clearly a major economic constraint to rainfed wheat production systems, especially where monocultures are dominant. Root-lesion nematode species are also important but appear to have a more restricted distribution.

## CEREAL CYST NEMATODE

Cyst nematodes are the most studied plant-parasitic nematodes on wheat (Cook and Noel 2002; Nicol 2002; Nicol et al., 2003). Although the ‘*Heterodera avenae* group’ (Handoo 2002) is a complex of 12 species and intraspecific pathotypes that invade roots of cereals and grasses, three main species are the most economically important: *Heterodera avenae*, *H. filipjevi*, and *H. latipons* (Rivoal and Cook 1993, McDonald and Nicol 2005).

*Heterodera avenae* is economically important in temperate wheat-producing regions throughout the world, including North and South Africa, East and West Asia, Australia, Europe, the Indian Subcontinent, the Middle East, and North America. *Heterodera latipons* occurs mostly throughout the Mediterranean region but also in Asia and Europe. This species was recently described as widespread and economically important in key wheat growing provinces of China (Peng et al., 2007). *Heterodera filipjevi* was recently detected in North America (Smiley et al., 2008) and also has an increasingly recognized wide distribution across northern Europe and continental climates of Central and West Asia, as well as the Middle East and Indian Subcontinent. Only one species is generally identified in most regions but mixtures of species may also occur in individual fields (Abidou et al., 2005).

Less prevalent species of cyst nematode associated with wheat include *H. arenaria*, *H. bifenestra*, *H. hordecalis*, *H. mani*, *H. pakistanensis*, *H. pratensis*, *H. zaeae*, and *Punctodera punctata*.

## Symptoms and epidemiology

Plants with roots heavily damaged by *H.*

*avenae* appear initially as pale green seedlings that lack vigor (Color Plate 16). Mature plants are often severely stunted (Color Plate 17). Plants with visual damage often occur in patches but may also occur over entire fields, particularly under monocultures of susceptible cereals and when combined with inadequate plant nutrition or other stress.

Symptoms on roots are specific to host species. Wheat (*Triticum* species) and barley (*Hordeum vulgare* L.) roots invaded by *Heterodera avenae* branch excessively at locations where juveniles invade, resulting in a bushy or knotted appearance (Color Plate 18a). Root symptoms often do not become recognizable until one to three months after planting, depending upon climatic conditions and spring or winter wheat growth habit. Oat (*Avena sativa* L.) roots invaded by *H. avenae* are shortened and thickened but do not exhibit the knotted symptom.

*Heterodera* species complete only one generation per crop season. Juveniles penetrate epidermal and cortical cells of young root segments in the zone of elongation. They enter the stele, where they induce the formation of a specialized feeding cell called a syncytium. Females are fertilized by males and 100-600 eggs are retained in the female body.

Mature females become sedentary and embedded in the root. The presence of the white swollen female body (0.5-2mm; about the size of a pin head) is diagnostic. It can be seen around the flowering time of wheat. One or more females are generally visible at the point of abnormal root proliferation. They protrude from the root surface, glisten when wet, and are white-gray. They are best viewed by washing a root sample and observing under low magnification (Color Plate 18b), because their presence among knotted roots is often obscured by adhering soil. The females are attached loosely and are easily dislodged when soil is washed from roots.

Upon death of host roots the female body wall dies and hardens into a resistant dark-brown cyst of a similar size as a soil particle. These cysts mostly dislodge into the soil as the wheat roots decompose. The cyst protects eggs and

juveniles during periods between hosts. Eggs inside cysts may remain viable for several years. Emergence of juveniles from brown cysts requires a period of dormancy (diapause) that differs among species and climatic regions. Diapause characteristics must be understood before damage by these nematodes can be effectively managed. Emergence of juveniles is triggered by specific interactions among soil temperature and moisture, and these conditions may be overcome to some extent by exudates from host roots (Ismail et al., 2000; Scholz and Sikora 2004; McDonald and Nicol 2005). Well-established infestations exhibit ecotypic differences in which peak numbers of infective juveniles in soil generally coincide with the traditional wheat sowing and seedling growth stages in each geographic region (Rivoal and Cook 1993).

Cereal cyst nematode is not strongly restricted by soil type but damage is often greatest in light-textured, well-drained soils such as sands. The damage threshold varies with soil type, climate, and cultivar, and with nematode species, virulence, and ecotype characteristics. These variable influences on plant damage make it difficult to directly relate initial populations with reduction in grain yield (Bonfil et al., 2004).

### Causal organisms

The most economically important cyst nematode species on wheat include *H. avenae* Wollenweber, *H. latipons* Franklin, and *H. filipjevi* (Madzhidov) Stone. Two important nematodes previously reported as *H. avenae* have been re-classified. The so-called Gotland strain of *H. avenae* is now accepted as *H. filipjevi* (Bekal et al., 1997; Ferris et al., 1999), making this species more reported than previously thought. Most recently, *H. avenae* pathotype Ha13 in Australia was re-described as *H. australis* (Subbotin et al., 2002); that designation has not yet been widely accepted.

Identification of cereal cyst nematodes is complex and has traditionally been based on comparative morphology and diagnostic keys (Luc et al., 1988; Handoo 2002). Techniques

based on protein or DNA differences using RFLP are now available to facilitate identification to a species level and to study phylogenetic relationships (Subbotin et al., 1996, 1999, 2000, 2001, 2003; Bekal et al., 1997; Andrés et al., 2001a,b; Mokabli et al., 2001; Rivoal et al., 2003). Further work is needed to convert these RFLP-based primers into the more cost- and time-efficient PCR-based probes.

One of the major challenges to controlling cereal cyst nematodes is occurrence of individuals within species and also among populations from different regions that is highly variable in virulence and in reproductive capacity (fitness) characteristics on the same host (Rivoal et al., 2001; Mokabli et al., 2002). Moreover, individual species within the *H. avenae* group are highly heterogeneous with respect to virulence to specific host genotypes (Cook and Rivoal 1998; Cook and Noel 2002; McDonald and Nicol 2005).

Virulence groups (pathotypes) are differentiated (Cook and Noel 2002; McDonald and Nicol 2005) by testing unknown populations against a matrix of cereals in “The International Cereal Test Assortment for Defining Cereal Cyst Nematode Pathotypes”, which was developed by Andersen and Andersen (1982). The test distinguishes three primary groups based on host resistance reactions of three barley cultivars carrying the resistance genes *Rha1*, *Rha2*, and *Rha3*. Additional barley, oat, and wheat differentials are used to define pathotypes within each group. The most widely distributed *H. avenae* populations in Europe, North Africa, and Asia are in groups 1 and 2 (Al-Hazmi et al., 2001; Cook and Noel 2002; Mokabli et al., 2002; McDonald and Nicol 2005). Pathotypes in group 3 are prevalent in Australia, Europe, and North Africa (Rivoal and Cook 1993; Mokabli et al., 2002). Unfortunately, the pathotype concept is incomplete because it was established to differentiate northern European populations of *H. avenae* and is increasingly incapable of clearly defining resistance reactions achieved with populations in other regions. For instance, three undescribed pathotypes were recently reported from China (Nicol and Rivoal 2007; Peng et al.,

2007), and the existing pathotype matrix does not define North American populations (Smiley, unpublished data). The Test Assortment therefore greatly underestimates polymorphism for *H. avenae* (Cook and Noel 2002; McDonald and Nicol 2005), *H. latipons*, and *H. filijevi*. The Test Assortment needs to be revised to capture new sources of resistance and pathogen variation.

## Management

To achieve effective control of cereal cyst nematodes it is necessary to reduce the population below the economic threshold for damage. This requires definitive studies on population dynamics and yield losses on representative local cultivars under natural field conditions. Cultural practices based on rotational combinations of non-hosts (non-cereals), resistant cultivars, and clean fallow can effectively control these nematodes. Restricting hosts to 50% of the time in heavier soils and 25% in lighter soils can cause dramatic reductions in the population of *H. avenae*. However, these management strategies each require a full understanding of the virulence and diapause characteristics for the local nematode populations, and of the effectiveness and durability of the resistance gene(s) deployed against that nematode population.

The use of host-plant resistance is one of the most effective methods of controlling cereal nematodes. Resistance is defined as the ability of the host to inhibit nematode multiplication (Cook and Evans 1987). Ideally resistance should be combined with tolerance, which is the ability of the host plant to maintain yield potential in the presence of the nematode (Cook and Evans 1987). The use of cultivars that are both resistant and tolerant offers the best control option, in addition to being environmentally sustainable and requiring no additional equipment or cost. However, the use of resistance requires a sound knowledge of the virulence spectrum for the targeted species and pathotypes. Wheat cultivars resistant to *H. avenae* populations in one region may be fully susceptible to populations in other

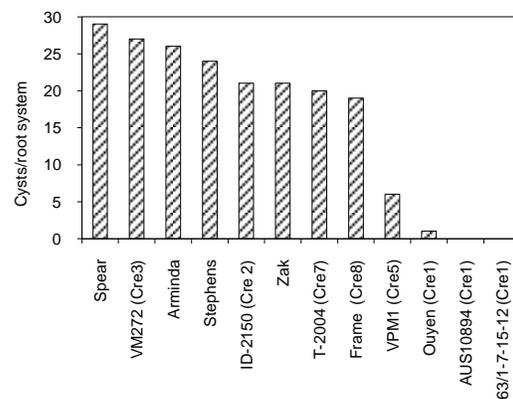
regions. This was shown for Australian cultivars evaluated in Israel (Bonfil et al., 2004) and for the cultivar Raj MR1 in India, which is effective in Rajasthan but not in the Punjab (A.K. Singh, personal communication). Also, although not frequently reported, repeated plantings of wheat, barley, and oat cultivars with a single gene for resistance to *H. avenae* have led to selection of new virulent pathotypes over prolonged time periods, overcoming host plant resistance (Lasserre et al., 1996; Cook and Noel 2002), in addition to possibly increasing damage from root-lesion nematode (Lasserre et al., 1994).

It is also possible to manage damage by rotating resistant cereals with susceptible crop species. However, local knowledge of resistance reactions is essential for effective use of this practice. For instance, rye (*Secale cereale* L.) and certain cultivars of triticale (*Triticosecale rimpaui* Wittm.) are resistant. Oat is resistant to *H. avenae* in Australia and several Mediterranean countries but susceptible in northern Europe (McDonald and Nicol 2005). Moreover, resistant cultivars from one region may be exposed to mixtures of species in other regions, as exemplified in Israel by oat cultivars that are resistant to *H. avenae* and susceptible to *H. latipons* (Mor et al., 1992).

Host resistance will continue to be the most profitable and easily applied management procedure. However resistance will only be used by farmers if the cultivars also contain a level of tolerance (yield performance) which is comparable to other commonly cultivated wheat cultivars. Sources of resistance to *H. avenae* populations worldwide have been collated and reviewed and, where possible, have had their genetic location and gene designation reported (Table 8.1) (Rivoal et al., 2001; Nicol 2002; Nicol et al., 2003; McDonald and Nicol 2005; Nicol and Rivoal 2007). All of the sources of resistance reported against cereal cyst nematode to date feature single-gene inheritance. Six *Cre* genes for *H. avenae* resistance in wheat (*Cre2* to *Cre7*) and the *Rkn2* gene for resistance to both *H. avenae* and *Meloidogyne naasi* (Jahier et al., 1998) were derived from *Aegilops* species. Other resistance genes were derived from *Triticum*

*aestivum* (*Cre1* and *Cre8*) and *Secale cereale* (*CreR*). Several other sources of resistance (*CreX* and *CreY*) are also reported, but their genetic control and gene designation are still unknown. Most of these resistance genes have been introgressed into hexaploid wheat.

The *Cre1* gene is highly effective against populations of *H. avenae* from Europe, North Africa, and North America (Fig. 8.1) and moderately effective or ineffective to populations in Australia and Asia (Rivoal et al., 2001; Mokabli et al., 2002). Populations of *H. filipjevi* in India and *H. latipons* in Syria differ in virulence to the *Cre1* gene, compared with *H. avenae* (Mokabli et al., 2002). In Turkey, the *Cre1* gene appears affective against *H. filipjevi*, but *Cre3* is not. The *Cre3* gene is effective against Australian populations (Vanstone et al., 2008) but not European populations of *H. avenae* (de Majnik et al., 2003; Safari et al., 2005) or *H. filipjevi* in Turkey. The *Cre2* and *Cre4* resistance genes from *Aegilops* and an unidentified resistance gene from the wheat line AUS4930 offer promise against an array of *Heterodera* species and pathotypes (Nicol et al., 2001). An International Root Disease Resistance Nursery containing seven of the known *Cre* genes is coordinated by CIMMYT to establish the value of these genes in different regions of the world.



**Fig. 8.1** Relative number of cysts for an Oregon population of *Heterodera avenae* developing on root systems of 12 wheat cultivars or lines; the identity of a *Cre* resistance gene is indicated if present.

Table 8.1 Principal sources of genes used to breed wheat for resistance to the cereal cyst nematode *Heterodera avenae* [Ha], unless stated otherwise.

| Cereal Species                                       | Cultivar or Line                     | Origin  | Resistance Gene(s) <sup>a,b</sup>   | Response to Pathotypes <sup>b,c</sup>  | Use in Cultivars                              |
|--|--------------------------------------|---|---|--|---|
| <b>Wheat</b>   |                                      |   |   |  |   |
| <i>Triticum aestivum</i>                             | Loros, AUS10894                      | ? <sup>d</sup>                                  | <b>Cre1<sup>e</sup></b> (formerly <i>Ccn1</i> ), on chromosome 2BL                | pR to several pathotypes   | NW Europe, Australia; NW USA under evaluation |
|  | Katylil                              | Australia                                       | <i>Ccn1</i>   | S, India   | Australia                                     |
|  | Festiguay                            | Australia                                       | <i>Cre8</i> (Formerly <i>CreF</i> ) on chromosome 7L? Recent analysis suggests 6B | pR to <i>Ha13</i>  | Australia                                     |
|  | AUS4930 = 'Iraq 48'                  | Iraq  | possibly identical genetic location as <i>Cre1</i> ; also resistance to Pt        | R to several pathotypes and <i>Heterodera</i> species and Pt                             | Australia, France, CIMMYT; under evaluation   |
|  | Molineux                             | Australia                                       | chromosome 1B (14% resistance)  | R to <i>Ha13</i>   | Australia                                     |
|  | Raj MR1 (Raj Molya Rodhak1)          | landrace from Nidge, Turkey<br>AUS 15854 x J-24 | one dominant gene   | R only to some populations of <i>H. avenae</i> , appears S to Indian <i>H. filipjevi</i> | Released cultivar in northern India in 2002   |
| <i>Triticum durum</i>                                | Psathias 7654, 7655, Sansome, Khapli | ?   | ?   | S to some pathotypes, pR to others   |   |
| <b>Triticale and rye</b>                             |                                      |   |   |  |   |
| <i>Triticosecale</i>                                 | T701-4-6                             | Australia                                       | <i>CreR</i> on chromosome 6RL   | R to <i>Ha13</i>   | Australia                                     |
|  | Drira (=Ningadhu)                    | Australia                                       | ?   | R to <i>Ha13</i>   | Australia                                     |
|  | Tahara                               | Australia                                       | ?   | R to <i>Ha13</i>   |   |
|  | Salvo                                | Poland  | ?   |  | UK  |
| <i>Secale cereale</i>                                | R173 Family                          |   | <i>CreR</i> on chromosome 6RL   | R to <i>Ha13</i>   | Australia                                     |
| <b>Wild grass relatives of wheat</b>                 |                                      |   |   |  |   |
| <i>Aegilops tauschii</i>                             | CPI 110813                           | Central Asia                                    | <i>Cre4</i> on chromosome 2DL   | R to <i>Ha13</i>   | Australian synthetic hexaploid lines          |
| <i>Aegilops tauschii</i>                             | AUS18913                             | ?   | <b>Cre3</b> on chromosome 2DL   | R to <i>Ha13</i>   | Australian advanced breeding lines            |
| <i>Aegilops peregrina</i> (= <i>Ae. variabilis</i> ) | 1                                    |   | <i>Cre(3S)</i> with <i>Rkn2</i> on chromosome 3S; <i>CreX</i> , not yet located   |  |   |
| <i>Aegilops longissima</i>                           | 18                                   | ?   | ?   | R to four French pathotypes and <i>Meloidogyne naasi</i>                                 | France  |
| <i>Aegilops geniculata</i>                           | 79; MZ1, MZ61, MZ77, MZ124           | ?   |   | R and pR to several pathotypes   | France – under evaluation                     |
| <i>Aegilops triuncialis</i>                          | TR-353                               | ?   | <i>Cre7</i> (formerly <i>CreAet</i> )   | R and pR to several pathotypes   | France – under evaluation                     |
| <i>Aegilops ventricosa</i>                           | VPM 1                                |   | <i>Cre5</i> (formerly <i>CreX</i> ), on chromosome 2AS                            | R to several pathotypes  | Spain – under evaluation                      |
|  | 11; AP-1, H-93-8                     |   | <i>Cre2</i> (formerly <i>CreX</i> ) on genome N <sup>v</sup>                      |  |   |
|  | 11; AP-1, H-93-8, H-93-35            |   | <i>Cre6</i> , on chromosome 5N <sup>v</sup>                                       |  |   |

<sup>a</sup> Sources: Reviews and references in Rivoal and Cook (1993), Cook and Rivoal (1998), McDonald and Nicol (2005), and Nicol and Rivoal (2007).<sup>b</sup> Characterized single-gene resistance to cereal cyst nematode.<sup>c</sup> R = resistant, pR = partially resistant, S = susceptible.<sup>d</sup> ? = no published scientific studies conducted.<sup>e</sup> Marker implemented in commercial breeding program – refer to Ogonnaya et al. (2001b).

Molecular markers have been developed to identify genes for resistance to *H. avenae* in barley and wheat (Eastwood et al., 1994; Williams et al., 1994, 2006; Kretschmer et al., 1997; Barr et al., 1998; Paull et al., 1998; Eagles et al., 2001; Ogbonnaya et al., 2001a,b; Martin et al., 2004; Barloy et al., 2007). Some of these markers have been used in marker-assisted selection and for pyramiding genes for resistance.

Practices other than crop rotation and planting resistant cultivars are less efficient; however components of these strategies could still form part of an integrated pest management approach to nematode control. Other cultural methods (Nicol and Rivoal 2007) include manipulating the sowing time to minimize the impact of the major hatching period, as when winter wheat is planted during autumn in cool, temperate regions where the major hatch occurs during spring. *Heterodera avenae* populations can also be reduced by planting a susceptible host as a trap crop prior to the major hatching period, thereby encouraging a maximum hatching efficiency by a plant stand that is then killed before new cysts are developed. The greatest crop loss occurs when nutrients or water become limiting for maximum plant growth potential at any point during the growing season. Crop damage is therefore minimized by supplying optimal plant nutrition (Color Plate 16) and, where possible, supplemental water during intervals of drought.

Biological control products are not commercially available, but *H. avenae* populations in some locations are maintained below an economic threshold by fungal and bacterial parasites of eggs and juveniles (Kerry 1987; Kerry and Crump 1998; Ismail et al., 2001).

A low rate of nematicide application can provide effective and economical control of cereal cyst nematode in wheat (Brown 1987). However, current environmental concerns associated with these chemicals eliminate them as a viable alternative for use by farmers. They will, however, continue to be an important research tool for studying yield loss and

population dynamics.

Once introduced into a region or country it is very difficult to minimize the spread of cyst nematodes. They are efficiently disseminated by all means of soil movement, including minute amounts of soil that contaminate equipment, by animals and plant products, and by soil that is moved by water and wind. Rapid dissemination together with increased reporting of *H. avenae* is especially well illustrated in China, where this nematode was first reported in 1987 and is now reported in at least eight provinces (Nicol and Rivoal 2007; Peng et al., 2007). Likewise, *H. avenae* was first reported in the western USA in 1974 and is now reported in at least seven states (Smiley et al., 1994, 2005c).

## ROOT-LESION NEMATODE

At least eight species in the genus *Pratylenchus* are parasitic to wheat (De Waele and Elsen 2002; Nicol 2002; Nicol et al., 2003; McDonald and Nicol 2005; Castillo and Vovlas 2007). Four species (*P. crenatus*, *P. neglectus*, *P. penetrans*, and *P. thornei*) occur throughout the world in temperate cereal-producing regions.

*Pratylenchus neglectus* and *P. thornei* are the species most often associated with yield loss in wheat and are emphasized in this chapter. One or both species occur in Australia, Europe, the Indian Subcontinent, the Mediterranean Basin, the Middle East, West Asia, North Africa, and North America (Nicol and Rivoal 2007). *Pratylenchus thornei* is considered the most economically important species on wheat and has reduced yields as much as 85% in Australia, 37% in Mexico, 70% in Israel, and 50% in the USA (Armstrong et al., 1993; Nicol and Ortiz-Monasterio 2004; Smiley et al., 2005a). *Pratylenchus neglectus* also causes losses up to 37% in the USA (Smiley et al., 2005b).

## Symptoms and epidemiology

*Pratylenchus* species are migratory root endoparasites capable of multiplying in a wide range of monocot and dicot host species (Loof

1978; Vanstone and Russ 2001a,b; Vanstone et al., 2008). They live freely in soil and may become entirely embedded in root tissue but never lose the ability to migrate within the root or back into soil.

Root-lesion nematodes puncture and migrate through root epidermal and cortical cells (Color Plate 19a). Tissue degradation results in lesions that favor greater colonization by root-rotting fungi. These activities reduce the ability of roots to produce branches and absorb water and nutrients. Cortical degradation and reduced branching (Color Plate 19b) often are not visible until plants are six or more weeks old, and these symptoms are often confused with root rots caused by *Pythium* and *Rhizoctonia*. Interactions of root-lesion nematodes, fungal pathogens, other plant-parasitic nematodes, and insect pests have been reported (Lasserre et al., 1994; Taheri et al., 1994; Smiley et al., 2004a,b).

Foliar symptoms are non-specific (Van Gundy et al., 1974; Orion et al., 1984; Doyle et al., 1987; Thompson et al., 1995; Smiley et al., 2005a,b). Intolerant plants with roots heavily damaged by root-lesion nematodes may exhibit poor vigor, yellowing and premature death of lower leaves, stunting, reduced tillering, and reduced grain yield and grain quality. Damaged wheat plants are less capable of extracting soil water and exhibit stress and wilting earlier than undamaged plants as soil moisture becomes limiting for plant growth. Plants that become infested while growing under drought stress are more likely to suffer yield loss (Nicol and Ortiz-Monasterio 2004).

*Pratylenchus* species associated with wheat are not strongly restricted by soil type and may attain damaging population levels even in the very driest (250 mm annual precipitation) rainfed wheat-producing regions. Large populations have been detected throughout the depth of root growth in deep soils (Taylor and Evans 1998; Thompson et al., 1999; Ophel-Keller et al., 2008). *Pratylenchus* species can survive in an inactive, dehydrated state (anhydrobiosis) in roots and soil during dry conditions (Glazer and Orion 1983; Talavera and Vanstone 2001). Individuals entering host roots after emerging

from anhydrobiosis multiply more rapidly than individuals that have not been subjected to dormancy. Populations of *Pratylenchus* often decline during long fallow periods between crops but high rates of survival have also been reported (Orion et al., 1984; Talavera and Vanstone 2001).

### Causal organisms

*Pratylenchus neglectus* (Rensch) Filipjev Schuurmanns & Stekhoven and *P. thornei* Sher & Allen often occur as mixtures in the same soil. Both species are parthenogenic, with males generally being rare or absent. In contrast, species such as *P. penetrans* (Cobb) Filipjev and Schuurmanns Stekhoven are amphimictic, with populations having both males and females.

All species of *Pratylenchus* retain a vermiform body shape (Color Plate 19a) with many being about 0.5 mm long and 0.02 mm in diameter. Life cycles range from 45 to 65 days depending on species and environmental variables. Females deposit about one egg per day in root tissue or in soil. First-stage juveniles molt to second-stage juveniles within the egg. One second-stage juvenile emerges from each egg about one week after the egg was deposited. Two additional molts within 35 to 40 days result in the adult stage. All juvenile and adult stages are parasitic. The number of nematodes in root tissue increases exponentially through the growing season.

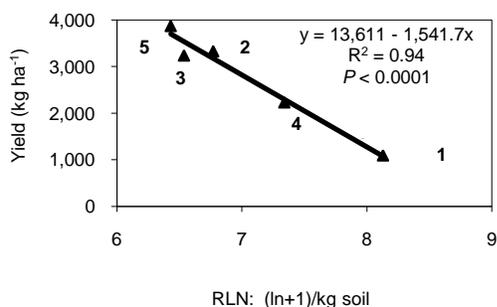
Identification of *Pratylenchus* to the species level is an essential prerequisite for most control strategies. However, identification is difficult because the few morphological characteristics of taxonomic value for differentiating *Pratylenchus* species are, without exception, replete with large ranges of intraspecific variation, often including overlapping ranges and shapes. Therefore, procedures to differentiate species based on comparative morphology (Loof 1978; Filho and Huang 1989; Handoo and Golden 1989) are always difficult and can be unreliable. Modern techniques are based on detection of differences of proteins or DNA (Ibrahim et al., 1995; Ouri and Mizukubo 1999; Uehara et al., 1999; Andrés

et al., 2000; Waeyenberge et al., 2000; Carta et al., 2001; Al-Banna et al., 2004; Carrasco-Ballesteros et al., 2007; Castillo and Vovlas 2007). The PCR or RFLP procedures are particularly useful for identifying species. Species-targeted real-time PCR procedures have been developed to differentiate and quantify *P. neglectus* and *P. thornei* in a single DNA extract from soil (G. Yan and Smiley, unpublished data).

Biological diversity among populations has been reported for six *Pratylenchus* species (De Waele and Elsen 2002), including *P. neglectus* on potato (Hafez et al., 1999) but not for *P. thornei*. The potential impact of *P. neglectus* heterogeneity or pathotypes on wheat has not been reported, but results from screening specific wheat and barley genotypes against populations of both *P. neglectus* and *P. thornei* in Australia, Mexico, Turkey, and the USA have thus far been uniform for both species across all countries, as have been observations from crop rotation experiments and commercial practices.

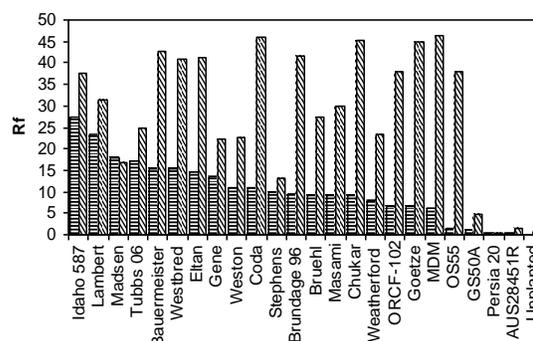
**Management**

Management of root-lesion nematodes is best approached by integrating crop rotations (Fig. 8.2) and planting wheat cultivars that are both resistant (Fig. 8.3) and tolerant (Fig. 8.4). Rotations alone are somewhat limited due to the

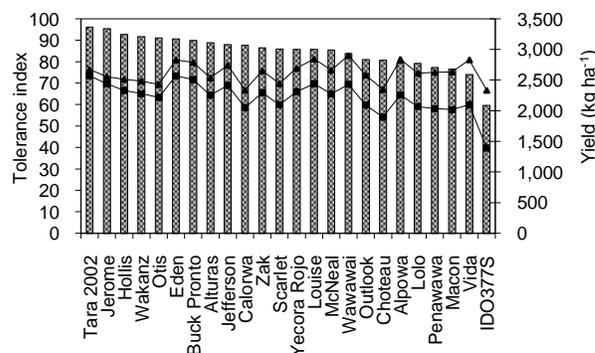


**Fig. 8.2** Relationship between numbers of root-lesion nematodes (RLN) and grain yield for winter wheat in five crop-rotation and tillage-management treatments in a 300-mm precipitation zone of Oregon (USA); means across 3 years for no-till annual winter wheat (1), rotations of winter wheat with cultivated fallow (2) or with chemical fallow (3), rotation of no-till winter wheat and no-till winter pea (4), and rotation of no-till winter wheat, no-till spring barley, and chemical fallow (5).

polyphagous nature of *P. neglectus* and *P. thornei*. The greatest long-term production efficiency will therefore be achieved with wheat cultivars that are both resistant and tolerant to the most economically important *Pratylenchus* species in a region or to both species where mixtures occur (Thompson et al., 2008; Vanstone et al., 2008). However, cultivars with resistance to *P. neglectus* are not necessarily resistant to *P. thornei* (Fig. 8.3), and vice versa (Farsi et al., 1995). Cultivars tolerant to *P. neglectus* are not necessarily tolerant to *P. thornei*, and vice versa.



**Fig. 8.3** Reproductive factor (Rf) for *Pratylenchus thornei* (left) and *P. neglectus* (right) in 20 Pacific Northwest (USA) winter wheat cultivars, in 3 lines carrying genes for resistance, and in unplanted soil; Rf =  $P_f P_i^{-1} \times 100$ , where  $P_f$  = final number after 16 weeks' growth and  $P_i$  = initial population in soil (750 nematodes per kilogram).



**Fig. 8.4** Tolerance index (bars) and grain yield for Pacific Northwest (USA) spring wheat cultivars produced in untreated soil (■) or in soil treated with nematicide (▲) to reduce numbers of *Pratylenchus neglectus*; grain yield in untreated soil correlated with tolerance index ( $R^2 = 0.80$ ,  $P < 0.0001$ ).

Furthermore, resistance and tolerance to each of these root-lesion nematode species are genetically independent; a cultivar can be resistant and intolerant, susceptible and tolerant, or another combination.

Successive or frequent crops of susceptible wheat cultivars elevate populations of *P. neglectus* and *P. thornei* and increase the level of risk to subsequent intolerant crops. Many cultivars of mustard [*Brassica juncea* (L.) Czern., *Sinapsis alba* L.], canola (*Brassica napus* L.), lentil (*Lens culinaris* Medik.), and chickpea (*Cicer arietinum* L.) also increase the population of *P. neglectus* or *P. thornei*, or both, with multiplication capacities differing greatly for each combination of *Pratylenchus* species and host cultivar (Bernard and Montgomery-Dee 1993; Castillo et al., 1998; Potter et al., 1999; Fatemy et al., 2006).

Crops that restrict multiplication of *P. neglectus* and/or *P. thornei*, such as some cultivars of barley, safflower (*Carthamus tinctorius* L.), triticale, flax (*Linum usitatissimum* L.) and field pea (*Pisum sativum* L.), reduce the nematode population and improve the yield potential for subsequent intolerant wheat crops (Van Gundy et al., 1974; Heide 1975; Esmenjaud et al., 1990; Lasserre et al., 1994; Farsi et al., 1995; Thompson et al., 1995; Hollaway et al., 2000; Taylor et al., 2000; Riley and Kelley 2002; Smiley et al., 2004b). However, results from these studies indicate hosting ability is species- and cultivar-specific, both within legumes and cereals. Therefore, hosting-ability studies must be conducted with local cultivars.

Wheat cultivars exhibiting tolerance to *P. neglectus* and *P. thornei* have been deployed effectively in Australia (Vanstone et al., 1998, 2008; Thompson et al., 1999, 2008; Nicol et al., 2001), and studies are underway in the USA to identify tolerant germplasm (Fig. 8.4). However, tolerance alone is not considered an effective long-term management strategy.

Resistance is the most important and economical strategy for reducing populations of root-lesion nematodes. Unlike the single-gene inheritance of cereal cyst nematode resistance, root-lesion nematode resistance is quantitative

and controlled by several genes, making the prospect of developing effective resistance more challenging. However, many sources of resistance to *P. thornei* have been identified in commercial wheat cultivars, in Middle East landrace lines, and in wheat relatives such as *Aegilops* species (Table 8.2) (Thompson and Haak 1997; Thompson et al., 1999; Nicol et al., 1999, 2001, 2003; Nombela and Romero 1999; Hollaway et al., 2000; Zwart et al., 2004, 2005; Tokay et al., 2006; Sheedy et al., 2008). Several lines are especially interesting in that they exhibit resistance to both *P. neglectus* and *P. thornei* (Zwart et al., 2005; Nicol et al., 2007; Sheedy et al., 2007, 2008). Introgression of dual-resistance sources (Fig. 8.3) into commercial cultivars would eliminate the need for farmers to identify *Pratylenchus* to the species level before selecting a resistant cultivar. Also of particular interest are lines that convey high levels of both tolerance and resistance to *P. thornei* or *P. neglectus*.

Phenotypic identification of resistance, coupled with molecular biology, has been used to investigate the genetic control and location of resistance genes, and the identification of resistance markers. Quantitative trait loci (QTLs) for resistance to *P. thornei* have been identified on chromosomes 1B, 2B, 3B, 4D, 6D, and 7A (Schmidt et al., 2005; Zwart et al., 2005, 2006; Tokay et al., 2006). The *P. neglectus* resistance gene *Rlnn1* occurs on chromosome 7A, and a molecular marker can identify its presence in seedlings (Williams et al., 2002). A resistance gene for *P. neglectus* was also identified on chromosome 4D (Zwart et al., 2005).

Research on resistance to *P. neglectus* and *P. thornei* has included development of simple sequence repeat (SSR) markers for tracking QTLs in breeding programs. Associations between markers and resistance reactions have been sufficiently consistent to demonstrate the potential for applying marker-assisted selection to the improvement of *Pratylenchus* resistance in wheat. This process is actively practiced by Australian and CIMMYT International wheat breeding programs, using the *Rlnn1* marker (Williams et al., 2002).

Table 8.2 Principal sources of genes used to breed wheat for resistance to root-lesion nematodes *Pratylenchus neglectus* (*Pn*) and *P. thornei* (*Pt*).

| Cereal Species             | Cultivar or Line                        | Origin                                   | Resistance Gene(s) <sup>a,b</sup> | Response to Pathotypes <sup>b,c</sup>                     | Use in Cultivars                        |
|----------------------------|---|--|-----------------------------------|---|---|
| <i>Triticum aestivum</i>   | GS50a                                   | Australia - reselection from cv. Gatcher | Major QTL mapped to 6D            |   | Australia                               |
|                            | AUS4930= Iraq 48                        | Iraq                                     | QTLs mapped to 1B, 2B, and 6D     | R to <i>Pt</i> but also portrays R to <i>Ha</i>           | Australia, CIMMYT – under investigation |
|                            | Reselection of Excalibur                | Australian cv. Excalibur                 | QTL mapped to 7AL                 | R to <i>Pn</i> ( <b><i>Rlnn1</i></b> ), on chromosome 7AL | Australia, CIMMYT                       |
|                            | Croc_1/ <i>Ae. tausch.</i> (224)//Opata | Primary synthetic                        | QTLs mapped to 1B and 3B          | R to <i>Pt</i>  | CIMMYT                                  |
|                            | CPI133872                               | Primary synthetic                        | QTLs mapped to 2B, 4D, 6A, 6D     | R to <i>Pt</i> and <i>Pn</i>                              | Australia                               |
|                            | W-7984 x Opata 85                       |  | QTLs mapped to 2B and 6D          | R to <i>Pt</i>  | Australia                               |
|                            | AUS4926                                 | Middle eastern landrace                  | QTLs mapped to 1B, 2B, 3B, and 6D | R to <i>Pt</i>  | Australia                               |
|                            | AUS13124                                | Middle eastern landrace                  | QTLs mapped to 2B, 3B, 6D, and 7A | R to <i>Pt</i>  | Australia                               |
| <i>Aegilops tauschii</i>   | CPI 110872                              |  |                                   | R to <i>Pt</i> and <i>Pn</i>                              |   |
| <i>Aegilops geniculata</i> | MZ10, MZ61, MZ96, MZ144                 | Middle East and West Asia                |                                   | pR to <i>Pt.</i> , several also portray R to <i>Ha</i>    |   |

<sup>a</sup> Sources: Reviews and references in Rivoal and Cook (1993), Cook and Rivoal (1998), McDonald and Nicol (2005), and Nicol and Rivoal (2007).

<sup>b</sup> Characterized QTLs associated with multigenic resistance to root-lesion nematodes.

<sup>c</sup> R = resistant, pR = partially resistant, *Ha* = *Heterodera avenae*.

Other management practices are less effective in managing *Pratylenchus* populations. Field sanitation during the fallow phase is as important as during the in-crop phase, because *Pratylenchus* species multiply on many weed species in the genera *Avena*, *Brassica*, *Bromus*, *Carrichtera*, *Emex*, *Heliotropium*, *Hordeum*, *Malva*, *Raphanus*, *Rumex*, and *Tribulis* (Vanstone and Russ 2001a,b) and on volunteer cereals including oat, wheat, and triticale (Forge et al., 2000). The presence of susceptible weeds or crop species between planted crops allows *Pratylenchus* to increase population density over a greater interval of the cropping system (Smiley et al., 2004b).

Tillage has reportedly increased, decreased, or had no effect on populations of *Pratylenchus* in wheat (Smiley et al., 2004b). In North America it appears that the greatest impact of conservation cropping systems will be associated with the frequency of host crops or weeds rather than the

presence, absence, or intensity of tillage. While cultivation and fallow have appeared to reduce populations of *P. neglectus* and *P. thornei* (Orion et al., 1984; Thompson 1992; Nombela et al., 1998; Smiley et al., 2004b; Strausbaugh et al., 2004), these interpretations were based mostly upon soil samples collected at shallow depth. Shallow samples accurately characterize *Pratylenchus* populations in shallow soils but not in many deep soils where these nematodes may be found as deep as 150 cm and where peak populations may vary from shallow to as deep as 60 to 90 cm depending upon variables such as intensity of surface cultivation or seasonal rainfall (Taylor and Evans 1998; Thompson et al., 1999; Ophel-Keller et al., 2008).

The reproductive rate for *P. thornei* increases as soil temperature increases from 15°C to 20°C (Castillo et al., 1996). Irrigated wheat yield in *P. thornei*-infested fields was improved by delaying

planting by one month, presumably because seedlings overwintered with lower populations than for early planting (Van Gundy et al., 1974). In a contrasting use of temperature treatment, mulching a field with polyethylene film for 6 to 8 weeks over the hot summer period suppressed *P. thornei* populations by 50% (Di Vito et al., 1991).

As with cereal cyst nematode, *Pratylenchus neglectus* and *P. thornei* are often more damaging to crops in drier than wetter regions. The economic threshold for damage is expected to be lower for low-rainfall environments than for crops produced with supplemental irrigation or in areas of greater precipitation especially during the growing season (Orion et al., 1984; Castillo et al., 1995; Nicol and Ortiz-Monasterio 2004).

Chemical nematicides are effective and are widely used in research (Taylor et al., 1999; Thompson et al., 1995; Smiley et al., 2005a,b) but are not economically feasible, registered, or environmentally appropriate for managing these parasites on wheat. Biological control agents are not commercially available for *Pratylenchus* species on wheat. Bacterial parasites of *Pratylenchus* have been reported (Ornat et al., 1999) but are unlikely to be successfully adapted for managing these migratory species that are well adapted to highly diverse soils and climates.

Green-manure crops can be used to sanitize soil through bio-fumigation in regions where water is not a limiting factor for wheat growth. Several *Pratylenchus* species are capable of multiplying in roots of sudan grass [*Sorghum drummondii* (Nees ex Steud.) Millsp. & Chase] and many *Brassica* species. Populations may remain high where these crops are grown to maturity for seed or forage harvest. However, when green tissue from some of these crops is incorporated into soil it is, in some cases, capable of reducing the elevated population to pre-plant levels or below (Bernard and Montgomery-Dee 1993; Potter et al., 1998, 1999; Forge et al., 2000).

## FUTURE PERSPECTIVES

In most regions, and especially in the developing world, the impact of cereal cyst and

root-lesion nematodes on wheat yield has not been documented, because extraction of nematodes is not a normal practice for the husbandry of wheat. Even where nematodes are known to be damaging the identity of the species and pathotype (for cyst nematodes) complex is often poorly defined.

More intensive surveys are required to more clearly identify (i) areas where cereal cyst and root-lesion nematodes are present, (ii) species and pathotypes, (iii) occurrences of mixed populations, and (iv) the magnitude and frequency of yield loss. Further development of molecular identification and quantification techniques and adoption of these procedures by commercial soil diagnostic laboratories will allow more rapid and effective surveys of populations in areas where nematodes are currently not monitored. A commercial testing program in South Australia is of particular interest (Ophel-Keller et al., 2008). A DNA extract from soil is used to quantitatively estimate inoculum levels of multiple fungal pathogens and populations of several nematode species, including *H. avenae*, *P. neglectus*, and *P. thornei*. Levels of disease risk, established from many years of collected field population and yield loss data, are communicated back to farmers through a network of agronomic advisors.

Many wheat breeding programs are not breeding for resistance to cereal cyst and root-lesion nematodes. Reasons may include a lack of understanding of the importance of the issue, limited financial, technical or institutional support for this disciplinary research, or lack of field test sites with adequate uniformity of infestation and absence of significant impacts by other parasitic nematode species and soilborne fungal pathogens. Additional wheat production efficiency and profitability will be attained by improving the level of nematode resistance and tolerance in wheat cultivars produced on highly infested fields.

Development of additional and improved molecular markers will allow more rapid integration of resistance into commercial cultivars. Genetic transformations may also aid in the development of nematode-resistant germplasm. For cyst nematodes, molecular techniques will also facilitate greater precision in studies of resistance mechanisms (Seah et al.,

2000; Andrés et al., 2001a; Montes et al., 2003, 2004).

Global complementation among regional or national research programs has proven to be highly beneficial for identifying and deploying germplasm with higher levels of resistance and tolerance to cereal cyst and root-lesion nematodes. However, these global efforts currently lack effective funding and coordination, limiting the ability to realize the benefits already known to exist. Greater collaboration is therefore needed between advanced research institutions, international organizations such as CIMMYT and ICARDA, and scientists in countries where these nematodes are known to be a problem. These collaborative efforts will provide greater understanding of the complexity, economic importance, and control of *Heterodera* and *Pratylenchus* populations, and of pathotype evolution or selection for *Heterodera* species.

## REFERENCES

- Abidou, H., A. El-Ahmed, J.M. Nicol, N. Bolat, R. Rivoal, and A. Yahyaoui. 2005. Occurrence and distribution of species of the *Heterodera avenae* group in Syria and Turkey. *Nematol. Mediter.* 33:195-201.
- Al-Banna, L., A.T. Ploeg, V.M. Williamson, and I. Kaloshian. 2004. Discrimination of six *Pratylenchus* species using PCR and species-specific primers. *J. Nematol.* 36:142-146.
- Al-Hazmi, A.S., R. Cook, and A.A.M. Ibrahim. 2001. Pathotype characterisation of the cereal cyst nematode, *Heterodera avenae*, in Saudi Arabia. *Nematology* 3:379-382.
- Andersen, S., and K. Andersen. 1982. Suggestions for determination and terminology of pathotypes and genes for resistance in cyst-forming nematodes especially *Heterodera avenae*. *EPPO Bull.* 12:379-386.
- Andrés, M., T. Melillo, A. Delibes, M.D. Romero, and T. Bleve-Zacheo. 2001a. Changes in wheat root enzymes correlated with resistance to cereal cyst nematodes. *New Phytol.* 152:343-354.
- Andrés, M.F., J. Pinochet, A. Hernández-Dorrego, and A. Delibes. 2000. Detection and analysis of inter- and intraspecific diversity of *Pratylenchus* spp. using isozyme markers. *Plant Pathol.* 49:640-649.
- Andrés, M.F., M.D. Romero, M.J. Montes, and A. Delibes. 2001b. Genetic relationships and isozyme variability in the *Heterodera avenae* complex determined by isoelectric focusing. *Plant Pathol.* 50:270-279.
- Armstrong, J.S., F.B. Peairs, S.D. Pilcher, and C.C. Russell. 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, K.R., G.A. Pederson, and G.L. Windham (ed.) 1998. Plant and nematode interactions. ASA, Madison, WI.
- Barloy, D., J. Lemoine, P. Abelard, A.M. Tanguy, R. Rivoal, and J. Jahier. 2007. Marker-assisted pyramiding of two cereal cyst nematode resistance genes from *Aegilops variabilis* in wheat. *Mol. Breed.* 20:31-40.
- Barr, A.R., K.J. Chalmers, A. Karakousis, J.M. Kretschmer, S. Manning, R.C.M. Lance, J. Lewis, S.P. Jefferies, and P. Langridge. 1998. RFLP mapping of a new cereal cyst nematode resistance locus in barley. *Plant Breed.* 117:185-187.
- Bekal, S., J.P. Gauthier, and R. Rivoal. 1997. Genetic diversity among a complex of cereal cyst nematodes inferred from RFLP analysis of the ribosomal internal transcribed spacer region. *Genome* 40:479-486.
- Bernard, E.C., and M.E. Montgomery-Dee. 1993. Reproduction of plant parasitic nematodes on winter rapeseed (*Brassica napus* spp. *oleifera*). *J. Nematol.* 25(4S):863-868.
- Bockus, W.W., R.L. Bowden, R.M. Hunger, W.L. Morrill, T.D. Murray, and R.W. Smiley (ed.) 2009. Compendium of wheat diseases and insects. 3rd ed. APS Press, St. Paul, MN.
- Bonfil, D.J., B. Dolgin, I. Mufradi, and S. Asido. 2004. Bioassay to forecast cereal cyst nematode damage to wheat in fields. *Precision Agric.* 5:329-344.
- Brown, R.H. 1987. Control strategies in low-value crops. p. 351-387. *In* R.H. Brown and B.R. Kerry (ed.) *Principals and practice of nematode control in crops*. Academic Press, Sydney, Australia.
- Carrasco-Ballesteros, S., P. Castillo, B.J. Adams, and E. Pérez-Artés. 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.
- Carta, L.K., A.M. Skantar, and Z.A. Handoo. 2001. Molecular, morphological and thermal characters of 19 *Pratylenchus* spp. and relatives using the D3 segment of the nuclear LSU rRNA gene. *Nematropica* 31:195-209.
- Castillo, P., A. Gomez-Barcina, and R.M. Jiménez-Díaz. 1996. Plant parasitic nematodes associated with chickpea in southern Spain and effect of soil temperature on reproduction of *Pratylenchus thornei*. *Nematologica* 42:211-219.
- Castillo, P., R.M. Jiménez-Díaz, A. Gomez-Barcina, and N. Vovlas. 1995. Parasitism of the root-lesion nematode *Pratylenchus thornei* on chickpea. *Plant Pathol.* 44:728-733.
- Castillo, P., and N. Vovlas. 2007. *Pratylenchus*, Nematoda, Pratylenchidae: Diagnosis, biology, pathogenicity and management. *Nematol. Monogr. Perspect.* 6:1-530.
- Castillo, P., N. Vovlas, and R.M. Jiménez-Díaz. 1998. Pathogenicity and histopathology of *Pratylenchus thornei* populations on selected chickpea genotypes. *Plant Pathol.* 47:370-376.
- Cook, R., and K. Evans. 1987. Resistance and tolerance. p. 179-231. *In* R.H. Brown and B.R. Kerry (ed.) *Principles*

- and practice of nematode control in crops. Academic Press, Sydney, Australia.
- Cook, R., and G.R. Noel. 2002. Cyst nematodes: *Globodera* and *Heterodera* species. p. 71-105. In J.L. Starr, R. Cook, and J. Bridge (ed.) Plant resistance to parasitic nematodes. CAB Int., Wallingford, UK.
- Cook, R., and R. Rivoal. 1998. Genetics of resistance and parasitism. p. 322-352. In S.B. Sharma (ed.) The cyst nematodes. Chapman and Hall, London, UK.
- de Majnik, J., F.C. Ogbonnaya, O. Moullet, and E.S. Lagudah. 2003. The Cre1 and Cre3 nematode resistance genes are located at homeologous loci in the wheat genome. *Mol. Plant-Microbe Interact.* 16:1129-1134.
- De Waele, D., and A. Elsen. 2002. Migratory endoparasites: *Pratylenchus* and *Radopholus* species. p. 175-206. In J.L. Starr, R. Cook, and J. Bridge (ed.) Plant resistance to parasitic nematodes. CAB Int., Wallingford, UK.
- Di Vito, M., N. Greco, and M.C. Saxena. 1991. Effectiveness of soil solarization for control of *Heterodera ciceri* and *Pratylenchus thornei* on chickpeas in Syria. *Nematol. Mediter.* 19:109-111.
- Doyle, A.D., R.W. McLeod, P.T.W. Wong, S.E. Hetherington, and R.J. Southwell. 1987. Evidence for the involvement of the root-lesion nematode *Pratylenchus thornei* in wheat yield decline in northern New South Wales. *Aust. J. Exp. Agric.* 27:563-570.
- Eagles, H.A., H.S. Bariana, F.C. Ogbonnaya, G.J. Rebetzke, G.L. Hollamby, R.J. Henry, P.H. Henschke, and M. Carter. 2001. Implementation of markers in Australian wheat breeding. *Aust. J. Agric. Res.* 52:1349-1356.
- Eastwood, R.F., E.S. Lagudah, and R. Appels. 1994. A directed search for DNA sequences tightly linked to cereal cyst nematode resistance genes in *Triticum tauschii*. *Genome* 37:311-319.
- Esmenjaud, D., R. Rivoal, and H. Marzin. 1990. Numbers of *Pratylenchus* spp., (Nematoda) in the field on winter wheat in different cereal rotations. *Nematologica* 36:317-226.
- Farsi, M., V.A. Vanstone, J.M. Fisher, and A.J. Rathjen. 1995. Genetic variation in resistance to *Pratylenchus neglectus* in wheat and triticales. *Aust. J. Exp. Agric.* 35:597-602.
- Fatemy, S., E. Abootorabi, N. Ebrahimi, and F. Aghabeigi. 2006. First report of *Pratylenchus neglectus* and *P. thornei* infecting canola and weeds in Iran. *Plant Dis.* 90:1555.
- Ferris, V.R., S.A. Subbotin, A. Ireholm, Y. Spiegel, J. Faghini, and J.M. Ferris. 1999. Ribosomal DNA sequence analysis of *Heterodera filipjevi* and *H. latipons* isolates from Russia and comparisons with other nematode isolates. *Rus. J. Nematol.* 7:121-125.
- Filho, A.C.C., and C.S. Huang. 1989. Description of *Pratylenchus pseudofallax* n.sp. with a key to species of the genus *Pratylenchus* Filipjev, 1936 (Nematoda: Pratylenchidae). *Revue Nématol.* 12:7-15.
- Forge, T.A., R.E. Ingham, D. Kaufman, and J.N. Pinkerton. 2000. Population growth of *Pratylenchus penetrans* on winter cover crops grown in the Pacific Northwest. *J. Nematol.* 32:42-51.
- Glazer, I., and D. Orion. 1983. Studies on anhydrobiosis of *Pratylenchus thornei*. *J. Nematol.* 15:333-338.
- Hafez, S.L., A. Al-Rehiyani, M. Thornton, and P. Sundararaj. 1999. Differentiation of two geographically isolated populations of *Pratylenchus neglectus* based on their parasitism of potato and interaction with *Verticillium dahliae*. *Nematotropica* 29:25-36.
- Handoo, Z.A. 2002. A key and compendium to species of the *Heterodera avenae* Group (Nematoda: Heteroderidae). *J. Nematol.* 34:250-262.
- Handoo, Z.A., and A.M. Golden. 1989. A key and diagnostic compendium to the species of the genus *Pratylenchus* Filipjev, 1936 (lesion nematodes). *J. Nematol.* 21:202-218.
- Heide, A. 1975. Studies on the population dynamics of migratory root nematodes in cereal monocultures as well as in alternating cereal growing. *Archiv für Phytopathologie und Pflanzenschutz* 11:225-232.
- Hollaway, G.J., S.P. Taylor, R.F. Eastwood, and C.H. Hunt. 2000. Effect of field crops on density of *Pratylenchus neglectus* and *P. thornei* in southeastern Australia: Part 2. *P. thornei*. *J. Nematol.* 32(4S):600-608.
- Ibrahim, S.K., R.N. Perry, and R.M. Webb. 1995. Use of isoenzyme and protein phenotypes to discriminate between six *Pratylenchus* species from Great Britain. *Ann. Appl. Biol.* 126:317-327.
- Ismail, S., R.P. Schuster, and R.A. Sikora. 2000. Factors affecting dormancy of the Mediterranean cereal cyst nematode *Heterodera latipons* on barley. *Meded.-Fac. Landb. Toeg. Biolog. Wetens., Univ. Gent.* 65(2b):529-535.
- Ismail, S., R.A. Sikora, and R.P. Schuster. 2001. Occurrence and diversity of egg pathogenic fungi of the Mediterranean cereal cyst nematode *Heterodera latipons*. *Meded.-Fac. Landb. Toeg. Biolog. Wetens., Univ. Gent.* 66(2b):645-653.
- Jahier, J., R. Rivoal, M.Q. Yu, P. Abélard, A.M. Tanguy, and D. Barloy. 1998. Transfer of genes for resistance to cereal cyst nematode from *Aegilops variabilis* Eig to wheat. *J. Gen. Breed.* 52:253-257.
- Kerry, B.R. 1987. Biological control. p. 233-263. In R.H. Brown and B.R. Kerry (ed.) Principles and practice of nematode control in crops. Academic Press, Sydney, Australia.
- Kerry, B.R., and D.H. Crump. 1998. The dynamics of the decline of the cereal cyst nematode, *Heterodera avenae*, in four soils under intensive cereal production. *Fundamental Appl. Nematol.* 21:617-625.
- Kretschmer, J.M., K.J. Chalmers, S. Manning, A. Karakousis, A.R. Barr, A.K.M.R. Islam, S.J. Logue, Y.W. Choe, S.J. Barker, R.C.M. Lance, and P. Langridge. 1997. RFLP mapping of the Ha2 cereal cyst nematode resistance gene in barley. *Theor. Appl. Genet.* 94:1060-1064.
- Lasserre, F., F. Gigault, J.P. Gauthier, J.P. Henry, M. Sandmeier, and R. Rivoal. 1996. Genetic variation in natural populations of the cereal cyst nematode (*Heterodera avenae* Woll.) submitted to resistant and susceptible cultivar of cereals. *Theor. Appl. Genet.* 93:1-8.
- Lasserre, F., R. Rivoal, and R. Cook. 1994. Interactions between *Heterodera avenae* and *Pratylenchus neglectus* on wheat. *J. Nematol.* 26:336-344.

- Loof, P.A.A. 1978. The genus *Pratylenchus* Filipjev, 1936 (Nematoda: Pratylenchidae): A review of its anatomy, morphology, distribution, systematics and identification. Swed. Univ. Agric. Sci., Res. Infor. Centre, Uppsala, Sweden.
- Luc, M., A.R. Maggenti, and R. Fortuner. 1988. A reappraisal of Tylenchina (Nemata): 9. The family Heteroderidae Filip'ev & Schuurmans Stekhoven, 1941. *Revue Nématol.* 11:159-176.
- Mai, W.F., and P.G. Mullin. 1996. Plant parasitic nematodes: A pictorial key to genera. Cornell Univ. Press, Ithaca, NY.
- Martin, E.M., R.F. Eastwood, and F.C. Ogonnaya. 2004. Identification of microsatellite markers associated with the cereal cyst nematode resistance gene *Cre3* in wheat. *Aust. J. Agric. Res.* 55:1205-1211.
- McDonald, A.H., and J.M. Nicol. 2005. Nematode parasites of cereals. p. 131-191. *In* M. Luc, R.A. Sikora, and J. Bridge (ed.) *Plant parasitic nematodes in subtropical and tropical agriculture*. CAB Int., Wallingford, UK.
- Mokabli, A., S. Valette, J.-P. Gauthier, and R. Rivoal. 2002. Variation in virulence of cereal cyst nematode populations from North Africa and Asia. *Nematology* 4:521-525.
- Mokabli, A., S. Valette, and R. Rivoal. 2001. Différenciation de quelques espèces de nématodes à kystes des céréales et des graminées par électrophorèse sur gel d'acétate de cellulose. *Nematol. Mediter.* 29:103-108.
- Montes, M.J., I. López-Braña, and A. Delibes. 2004. Root enzyme activities associated with resistance to *Heterodera avenae* conferred by gene *Cre7* in a wheat/*Aegilops triuncalis* introgression line. *J. Plant Physiol.* 161:493-495.
- Montes, M.J., I. López-Braña, M.D. Romero, E. Sin, M.F. Andrés, J.A. Martín-Sánchez, and A. Delibes. 2003. Biochemical and genetic studies of two *Heterodera avenae* resistance genes transferred from *Aegilops ventricosa* to wheat. *Theor. Appl. Genet.* 107:611-618.
- Mor, M., E. Cohn, and Y. Spiegel. 1992. Phenology, pathogenicity and pathotypes of cereal cyst nematodes, *Heterodera avenae* Woll. and *H. latipons* (Nematoda: Heteroderidae) in Israel. *Nematologica* 38:444-501.
- Nicol, J.M. 2002. Important nematode pests of cereals. p. 345-366. *In* B.C. Curtis, S. Rajaram, and G. Macpherson (ed.) *Bread wheat: Improvement and production*. FAO Plant Production and Protection Series, No. 30. FAO, Rome, Italy.
- Nicol, J.M., N. Bolat, A. Bagci, R.T. Trethowan, M. William, H. Hekimhan, A.F. Yildirim, E. Şahin, H. Elekçioğlu, H. Toktay, B. Tunali, A. Hede, S. Taner, H.J. Braun, M. van Ginkel, M. Keser, Z. Arisoy, A. Yorgancılar, A. Tulek, D. Erdurmus, O. Buyuk, and M. Aydogdu. 2007. The international breeding strategy for the incorporation of resistance in bread wheat against the soil borne pathogens (dryland root rot and cyst and lesion nematodes) using conventional and molecular tools. p. 125-137. *In* H.T. Buck, J.E. Nisi, and N. Salomón (ed.) *Wheat production in stressed environments*. Springer, Dordrecht, The Netherlands.
- Nicol, J.M., K.A. Davies, T.W. Hancock, and J.M. Fisher. 1999. Yield loss caused by *Pratylenchus thornei* on wheat in South Aust. *J. Nematol.* 31: 367-376.
- Nicol, J.M., and I. Ortiz-Monasterio. 2004. Effects of the root-lesion nematode, *Pratylenchus thornei*, on wheat yields in Mexico. *Nematology* 6:485-493.
- Nicol, J.M., and R. Rivoal. 2007. Global knowledge and its application for the integrated control and management of nematodes on wheat. p. 243-287. *In* A. Ciancio and K.G. Mukerji (ed.) *Integrated management and biocontrol of vegetable and grain crops nematodes*. Springer, Dordrecht, The Netherlands.
- Nicol, J., R. Rivoal, S. Taylor, and M. Zaharieva. 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. *Nematol. Monogr. Perspect.* 2:1-19.
- Nicol, J.M., R. Rivoal, R.M. Trethowan, M. van Ginkel, M. Mergoum, and R.P. Singh. 2001. CIMMYT's approach to identify and use resistance to nematodes and soil-borne fungi, in developing superior wheat germplasm. p. 381-389. *In* Z. Bedö and L. Láng (ed.) *Wheat in a global environment*. Kluwer Acad. Publ., The Netherlands.
- Nombela, G., A. Navas, and A. Bello. 1998. Effects of crop rotations of cereals with vetch and fallow on soil nematofauna in central Spain. *Nematologica* 44:63-80.
- Nombela, G., and M.D. Romero. 1999. Host response to *Pratylenchus thornei* of a wheat line carrying the *Cre2* gene for resistance to *Heterodera avenae*. *Nematology* 1:381-388.
- Ogonnaya, F.C., S. Seah, A. Delibes, J. Jahier, I. López-Braña, R.F. Eastwood, and E.S. Lagudah. 2001a. Molecular-genetic characterisation of a new nematode resistance gene in wheat. *Theor. Appl. Genet.* 102:623-629.
- Ogonnaya, F.C., N.C. Subrahmanyam, O. Moullet, J. de Majnik, H.A. Eagles, J.S. Brown, R.F. Eastwood, J. Kollmorgen, R. Appels, and E.S. Lagudah. 2001b. Diagnostic DNA markers for cereal cyst nematode resistance in bread wheat. *Aust. J. Agric. Res.* 52:1367-1374.
- Ophel-Keller, K., A. McKay, D. Hartley, Herdina, and J. Curran. 2008. Development of a routine DNA-based testing service for soilborne diseases in Australia. *Australasian Plant Pathol.* 37:243-253.
- Orion, D., J. Amir, and J. Krikun. 1984. Field observations on *Pratylenchus thornei* and its effects on wheat under arid conditions. *Rev. Nématol.* 7:341-345.
- Ornat, C., S. Verdejo-Lucas, F.J. Sorribas, and E.A. Tzortzakakis. 1999. Effect of fallow and root destruction on survival of root-knot and root-lesion nematodes in intensive vegetable cropping systems. *Nematotropa* 29:5-16.
- Ouri, Y., and T. Mizukubo. 1999. Discrimination of seven *Pratylenchus* species (Nematoda: Pratylenchidae) in Japan by PCR-RFLP analysis. *Appl. Entomol. Zool.* 34:205-211.
- Paull, J.G., K.J. Chalmers, A. Karakousis, J.M. Kretschmer, S. Manning, and P. Langridge. 1998. Genetic diversity in Australian wheat varieties and breeding material based on RFLP data. *Theor. Appl. Genet.* 96:435-446.
- Peng, D., D. Zhang, J.M. Nicol, S. Chen, L. Waeyenberge, M. Moens, H. Li, W. Tang, and I.T. Riley. 2007.

- Occurrence, distribution and research situation of cereal cyst nematode in China. p. 350-351. *In Proc. Int. Plant Protection Conf.*, 16th. Glasgow, Scotland, UK. 15-18 Oct. 2007. Br. Crop Prod. Council, Alton, Hampshire, UK.
- Potter, M.J., K. Davies, and A.J. Rathjen. 1998. Suppressive impact of glucosinolates in *Brassica* vegetative tissues on root lesion nematode *Pratylenchus neglectus*. *J. Chem. Ecol.* 24:67-80.
- Potter, M.J., V.A. Vanstone, K.A. Davies, J.A. Kirkegaard, and A.J. Rathjen. 1999. Reduced susceptibility of *Brassica napus* to *Pratylenchus neglectus* in plants with elevated root levels of 2-phenylethyl glucosinolate. *J. Nematol.* 31:291-298.
- Riley, I.T., and S.J. Kelley. 2002. Endoparasitic nematodes in cropping soils of Western Australia. *Aust. J. Exp. Agric.* 42:49-56.
- Rivoal, R., S. Bekal, S. Valette, J.-P. Gauthier, M.B.H. Fradj, A. Mokabli, J. Jahier, J. Nicol, and A. Yahyaoui. 2001. Variation in reproductive capacity and virulence on different genotypes and resistance genes of Triticeae, in the cereal cyst nematode species complex. *Nematology* 3:581-592.
- Rivoal, R., and R. Cook. 1993. Nematode pests of cereals. p. 259-303. *In* K. Evans, D.L. Trudgill, and J.M. Webster (ed.) *Plant parasitic nematodes in temperate agriculture*. CAB Int., Wallingford, UK.
- Rivoal, R., S. Valette, S. Bekal, J.-P. Gauthier, and A. Yahyaoui. 2003. Genetic and phenotypic diversity in the graminaceous cyst nematode complex, inferred from PCR-RFLP of ribosomal DNA and morphometric analysis. *Eur. J. Plant Pathol.* 109:227-241.
- Safari, E., N.N. Gororo, R.F. Eastwood, J. Lewis, H.A. Eagles, and F.C. Ogbonayya. 2005. Impact of *Cre1*, *Cre8* and *Cre3* genes on cereal cyst nematode resistance in wheat. *Theor. Appl. Genet.* 110:567-572.
- Schmidt, A.L., C.L. McIntyre, J. Thompson, N.P. Seymour, and C.J. Liu. 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.
- Scholz, U., and R.A. Sikora. 2004. Hatching behaviour and life cycle of *Heterodera latipons* Franklin under Syrian agro-ecological conditions. *Nematology* 6:245-256.
- Seah, S., C. Miller, K. Sivasithamparam, and E.S. Lagudah. 2000. Root responses to cereal cyst nematode (*Heterodera avenae*) in hosts with different resistance genes. *New Phytol.* 146:527-533.
- Sheedy, J.G., R.W. Smiley, S.A. Easley, and A.L. Thompson. 2007. Resistance reaction of Pacific Northwest spring wheat and barley cultivars to root-lesion nematode; *Pratylenchus neglectus*. p. CF022. *In* Plant disease management reports. Vol 1. APS Press, St. Paul, MN.
- Sheedy, J.G., R.W. Smiley, S.A. Easley, and A.L. Thompson. 2008. Resistance of Pacific Northwest spring wheat and barley cultivars to root-lesion nematode; *Pratylenchus thornei*. p. N007. *In* Plant disease management reports. Vol 2. APS Press, St. Paul, MN.
- Siddiqi, M.R. 2000. *Tylenchida: Parasites of plants and insects*. 2nd ed. CAB Int., Wallingford, UK.
- Smiley, R.W., J.A. Gourlie, R.G. Whittaker, S.A. Easley, and K.K. Kidwell. 2004a. Economic impact of Hessian fly (Diptera: Cecidomyiidae) on spring wheat in Oregon and additive yield losses with Fusarium crown rot and lesion nematode. *J. Econ. Entomol.* 97:397-408.
- Smiley, R.W., R.E. Ingham, W. Uddin, and G.H. Cook. 1994. Crop sequences for winter wheat in soil infested with cereal cyst nematode and fungal pathogens. *Plant Dis.* 78:1142-1149.
- Smiley, R.W., K. Merrifield, L.-M. Patterson, R.G. Whittaker, J.A. Gourlie, and S.A. Easley. 2004b. Nematodes in dryland field crops in the semiarid Pacific Northwest United States. *J. Nematol.* 36:54-68.
- Smiley, R.W., R.G. Whittaker, J.A. Gourlie, and S.A. Easley. 2005a. *Pratylenchus thornei* associated with reduced wheat yield in Oregon. *J. Nematol.* 37:45-54.
- Smiley, R.W., R.G. Whittaker, J.A. Gourlie, and S.A. Easley. 2005b. Suppression of wheat growth and yield by *Pratylenchus neglectus* in the Pacific Northwest. *Plant Dis.* 89:958-968.
- Smiley, R.W., R.G. Whittaker, J.A. Gourlie, S.A. Easley, and R.E. Ingham. 2005c. Plant-parasitic nematodes associated with reduced wheat yield in Oregon: *Heterodera avenae*. *J. Nematol.* 37:297-307.
- Smiley, R.W., G.P. Yan, and Z.A. Handoo. 2008. First record of the cereal cyst nematode *Heterodera filipjevi* in Oregon. *Plant Dis.* 92:1136.
- Strausbaugh, C.A., C.A. Bradley, A.C. Koehn, and R.L. Forster. 2004. Survey of root diseases of wheat and barley in southeastern Idaho. *Can. J. Plant Pathol.* 26:167-176.
- Subbotin, S.A., H.J. Rumpfenhorst, and D. Sturhan. 1996. Morphological and electrophoretic studies on populations of the *Heterodera avenae* complex from the former USSR. *Rus. J. Nematol.* 4:29-38.
- Subbotin, S.A., D. Sturhan, H.J. Rumpfenhorst, and M. Moens. 2002. Description of the Australian cereal cyst nematode *Heterodera australis* sp. n. (Tylenchida: Heteroderidae). *Rus. J. Nematol.* 10:139-148.
- Subbotin, S.A., D. Sturhan, H.J. Rumpfenhorst, and M. Moens. 2003. Molecular and morphological characterization of the *Heterodera avenae* species complex (Tylenchida: Heteroderidae). *Nematology* 5:515-538.
- Subbotin, S.A., A. Vierstraete, P. De Ley, J. Rowe, L. Waeyenberge, M. Moens, and J.R. Vanfleteren. 2001. Phylogenetic relationships within the cyst-forming nematodes (Nematoda, Heteroderidae) based on analysis of sequences from the ITS regions of ribosomal DNA. *Mol. Phylogenet. Evol.* 21:1-16.
- Subbotin, S.A., L. Waeyenberge, and M. Moens. 2000. Identification of cyst forming nematodes of the genus *Heterodera* (Nematoda: Heteroderidae) based on the ribosomal DNA-RFLP. *Nematology* 2:153-164.
- Subbotin, S.A., L. Waeyenberge, I.A. Molokanova, and M. Moens. 1999. Identification of *Heterodera avenae* group species by morphometrics and rDNA-RFLPs. *Nematology* 1:195-207.
- Taheri, A., G.J. Hollamby, and V.A. Vanstone. 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.
- Talavera, M., and V.A. Vanstone. 2001. Monitoring *Pratylenchus thornei* densities in soil and roots under resistant (*Triticum turgidum durum*) and susceptible (*Triticum aestivum*) wheat cultivars. *Phytoparasitica* 29:29-35.
- Taylor, S.P., and M.L. Evans. 1998. Vertical and horizontal distribution of and soil sampling for root lesion nematodes (*Pratylenchus neglectus* and *P. thornei*) in South Australia. *Australasian Plant Pathol.* 27:90-96.
- Taylor, S.P., G.J. Hollaway, and C.H. Hunt. 2000. Effect of field crops on population densities of *Pratylenchus neglectus* and *P. thornei* in southeastern Australia: Part I. *P. neglectus*. *J. Nematol.* 32(4S):591-599.
- Taylor, S.P., V.A. Vanstone, A.H. Ware, A.C. McKay, D. Szot, and M.H. Russ. 1999. Measuring yield loss in cereals caused by root lesion nematodes (*Pratylenchus neglectus* and *P. thornei*) with and without nematicide. *Aust. J. Agric. Res.* 50:617-622.
- Thompson, J.P. 1992. Soil biotic and biochemical factors in a long-term tillage and stubble management experiment on a vertisol: 2. Nitrogen deficiency with zero tillage and stubble retention. *Soil Tillage Res.* 22:339-361.
- Thompson, J.P., P.S. Brennan, T.G. Clewett, J.G. Sheedy, and N.P. Seymour. 1999. Progress in breeding wheat for tolerance and resistance to root-lesion nematode (*Pratylenchus thornei*). *Australasian Plant Pathol.* 28:45-52.
- Thompson, J.P., and M.I. Haak. 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, J.P., J. Mackenzie, and R. Amos. 1995. Root-lesion nematode (*Pratylenchus thornei*) limits response of wheat but not barley to stored soil moisture in the Hermitage long-term tillage experiment. *Aust. J. Exp. Agric.* 35:1049-1055.
- Thompson, J.P., K.J. Owen, G.R. Stirling, and M.J. Bell. 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. *Australasian Plant Pathol.* 37:235-242.
- Tokay, H., C.L. McIntyre, J.M. Nicol, H. Ozkan, and H.İ. Elekçioğlu. 2006. Identification of common root-lesion nematode (*Pratylenchus thornei* Sher et Allen) loci in bread wheat. *Genome* 49:1319-1323.
- Uehara, T., A. Kushida, and Y. Momota. 1999. Rapid and sensitive identification of *Pratylenchus* spp. using reverse dot blot hybridization. *Nematology* 1:549-555.
- Van Gundy, S.D., J.G. Perez, L.H. Stolzy, and I.J. Thomason. 1974. A pest management approach to the control of *Pratylenchus thornei* on wheat in Mexico. *J. Nematol.* 6:107-116.
- Vanstone, V.A., G.J. Hollaway, and G.R. Stirling. 2008. Managing nematode pests in the southern and western regions of the Australian cereal industry: Continuing progress in a challenging environment. *Australasian Plant Pathol.* 37:220-234.
- Vanstone, V.A., A.J. Rathjen, A.H. Ware, and R.D. Wheeler. 1998. Relationship between root lesion nematodes (*Pratylenchus neglectus* and *P. thornei*) and performance of wheat varieties. *Aust. J. Exp. Agric.* 38:181-188.
- Vanstone, V.A., and M.H. Russ. 2001a. Ability of weeds to host the root lesion nematodes *Pratylenchus neglectus* and *P. thornei*: I. Grass weeds. *Australasian Plant Pathol.* 30:245-250.
- Vanstone, V.A., and M.H. Russ. 2001b. Ability of weeds to host the root lesion nematodes *Pratylenchus neglectus* and *P. thornei*: II. Broad-leaf weeds. *Australasian Plant Pathol.* 30:251-258.
- Varma, M.K. 1995. Dictionary of plant nematology. Vedams Books Int., New Delhi.
- Waeyenberge, L., A. Ryss, M. Moens, J. Pinochet, and T.C. Vrain. 2000. Molecular characterization of 18 *Pratylenchus* species using rDNA restriction fragment length polymorphism. *Nematology* 2:135-142.
- Whitehead, A.G. 1997. Plant nematode control. CAB Int., Wallingford, UK.
- Williams, K.J., J.M. Fisher, and P. Langridge. 1994. Identification of RFLP markers linked to the cereal cyst nematode resistance gene (*Cre*) in wheat. *Theor. Appl. Genet.* 89:927-930.
- Williams, K.J., S.P. Taylor, P. Bogacki, M. Pallotta, H.S. Bariana, and H. Wallwork. 2002. Mapping of the root lesion nematode (*Pratylenchus neglectus*) resistance gene *Rln1* in wheat. *Theor. Appl. Genet.* 104:874-879.
- Williams, K.J., K.L. Willmore, S. Olson, M. Matic, and H. Kuchel. 2006. Mapping a novel QTL for resistance to cereal cyst nematode in wheat. *Theor. Appl. Genet.* 112:1480-1486.
- Zwart, R.S., J.P. Thompson, and I.D. Godwin. 2004. Genetic analysis of resistance to root-lesion nematode (*Pratylenchus thornei*) in wheat. *Plant Breed.* 123:209-212.
- Zwart, R.S., J.P. Thompson, and I.D. Godwin. 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, R.S., J.P. Thompson, J.G. Sheedy, and J.C. Nelson. 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.

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**Plate 16** Visual symptoms of cereal cyst nematode (*Heterodera avenae*) damage on spring wheat are masked by a “doubled” fertilizer rate applied along the field border, in foreground; roots from this field are shown as Plate 18a (courtesy R.W. Smiley).



**Plate 17** Cereal cyst nematode (*Heterodera avenae*) causing patchy growth of winter wheat on a flat field (courtesy R.W. Smiley).



(a) (b)

**Plate 19** Root-lesion nematode on wheat, showing (a) root cortex tissue stained to reveal an adult *Pratylenchus thornei* female (0.5 mm long) and eggs (courtesy R.W. Smiley), and (b) reduced root branching and cortical degradation by *P. neglectus* (courtesy V.A. Vanstone).



(a)



(b)

**Plate 18** Cereal cyst nematode (*Heterodera avenae*) on wheat roots, showing (a) abnormal branching of seedling roots at sites of invasion by juveniles (courtesy R.W. Smiley), and (b) cysts of adult females attached to mature roots (courtesy R.H. Brown).