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Important nematode pests

J.M. Nicol

Nematodes are microscopic roundworms that live in many habitats. At least 2 500 species of plant-parasitic nematodes have been described, characterized by the presence of a stylet, which is used for penetration of host plant tissue. Most attack roots and underground parts of plants, but some are able to feed on leaves and flowers.

Plant-parasitic nematodes are of great economic importance. However, because most of them live in the soil, they represent one of the most difficult pest problems to identify, demonstrate and control (Stirling *et al.*, 1998). Their effects are commonly underestimated by farmers, agronomists and pest management consultants, but it has been estimated that some 10 percent of world crop production is lost as a result of plant nematode damage (Whitehead, 1998).

Although many nematodes have been found associated with small-grained cereals, only a few of them are considered economically important. Those of importance include: (i) cereal cyst nematodes, *Heterodera* spp.; (ii) root lesion nematodes, *Pratylenchus* spp.; (iii) root knot nematodes, *Meloidogyne* spp.; (iv) seed gall nematode, *Anguina tritici*; and (v) stem nematode, *Ditylenchus dipsaci*. Each of these is described and discussed below.

Management of nematodes may be approached by using a combination of methods in an integrated pest management system or may involve only one of these methods. Some of the most commonly practised methods will be discussed, including crop rotation, the use of resistant and tolerant cultivars, cultural practices and chemicals. It is important to stress that the most appropriate control method will be determined by the nematode involved and the economic feasibility of implementing the possible control(s). These will be discussed briefly for each nematode.

The purpose of this chapter is to provide an insight into the economically important nematodes on small grains, their currently known distribution and damage potential, and the management options that exist for their control. For further references and illustration of these nematodes, refer to the reviews of Kort (1972), Griffin (1984), Sikora (1988), Swarup and Sosa-Moss (1990) and Rivoal and Cook (1993).

CEREAL CYST NEMATODES

Distribution

The cereal cyst nematodes, *Heterodera* spp., are a group of several closely related species and are considered to be one of the most important groups of plant-parasitic nematodes on a worldwide basis. The most commonly recorded species of economic importance on cereals is *H. avenae*, which has been detected in many countries, including Australia, Canada, Israel, South Africa, Japan and most European countries (Kort, 1972), as well as India (Sharma and Swarup, 1984; Sikora, 1988) and countries within North Africa and West Asia, including Morocco, Tunisia, Pakistan and Libya (Sikora, 1988), and recently Algeria (Mokabli *et al.*, 2001) and Saudi Arabia (Ibrahim *et al.*, 1999). Although its distribution is global, much of the research has been confined to Europe, Canada, Australia and India (Swarup and Sosa-Moss, 1990).

Heterodera avenae is the principal species on temperate cereals (Rivoal and Cook, 1993), while another important cereal species, *H. latipons*, is essentially only Mediterranean in distribution, being found in Syria (Sikora and Oostendorp, 1986; Scholz, 2001), Israel (Kort, 1972; Mor *et al.*, 1992), Cyprus (Sikora, 1988), Italy and Libya (Kort, 1972). However, it is also known to occur in northern Europe (Sabova *et al.*, 1988). Other *Heterodera* species known to be of importance to cereals include: *H. hordecalis* in Sweden, Germany and the United Kingdom (Andersson, 1974; Sturhan, 1982; Cook and York, 1982a); *H. zeae*, which is found in India, Pakistan (Sharma and Swarup, 1984; Maqbool, 1988) and Iraq (Stephan, 1988); *H. filipjevi* in Russia (Balakhnina, 1989) and Turkey (Nicol *et al.*, unpublished data); and various others, including *H. mani*, *H. bifenestra* and *H. pakistanensis*, and an unrelated species of cyst nematode, *Punctodera punctata* (Sikora, 1988). Other cyst nematode species have been found on cereals, but they have not been shown to be economically important. Most of these species are difficult to differentiate easily and require a strong taxonomic understanding of morphological traits of cysts or juveniles. Recent molecular techniques, such as random fragment length polymorphism (RFLP) of the ribosomal DNA, have enabled solid taxonomic differentiation among several entities of the cereal cyst nematode complex (Bekal *et al.*, 1997; Subbotin *et al.*, 2000).

Biology

The host range of *H. avenae* is restricted to graminaceous plants. There is sexual dimorphism with the male remaining worm-like, whereas the female becomes lemon-shaped and spends its life inside or attached to the root. The adult white female is clearly visible on roots with the swollen body, about 1 mm across, protruding from the root surface. Eggs are retained within the female's body, and after the female has died, the body wall hardens to a resistant brown cyst, which protects the eggs and juveniles. The eggs within the cyst remain viable for several years (Kort, 1972). *Heterodera avenae* has only one generation per year, with the hatch of eggs determined largely by temperature (Rivoal and Cook, 1993).

The symptoms produced on the roots are different dependent on the host. Wheat attacked by *H. avenae* shows increased root production such that the roots have a 'bushy knotted' appearance usually with several females visible at each knot (Rivoal and Cook, 1993) as illustrated in Plate 55. Oat roots are shortened and thickened, while barley roots appear less affected. Other species of *Heterodera* also appear to produce host-specific symptoms on the roots of cereals. For example, in Israel *H. latipons* did not produce knotted roots as *H. avenae* (Mor *et al.*, 1992). Above-ground symptoms of *H. avenae* appear early in the season as pale green patches of plants with fewer tillers. Patches may vary in size from 1 m^2 to 100 m^2 or more. In France, successful detection of *H. avenae* in wheat fields was achieved with the use of radiothermometry (Nicolas *et al.*, 1991; Lili *et al.*, 1991). It is possible that this technique could be extended to thermography, which could improve the detection of cereal cyst nematode attacks in large areas.

Heterodera avenae is the best known species, but is polymorphous with many pathotypes (Andersen and Andersen, 1982; Cook and Rivoal, 1998). The induction or suppression of dormancy (diapause) by different temperatures regulates the hatching of *H. avenae* juveniles. In Mediterranean climates, the diapause is obligate and durable, acting when the climate is hot and dry and being suppressed when the soil temperature falls and moisture rises (Rivoal and Cook, 1993). The diapause requirements in other climates with *Heterodera* species are less well understood but they are essential to understanding the biology and control of those species.

To date, the pathotypes of *H. avenae* have been recognized with the test developed by Andersen and Andersen (1982) designated The International Cereal Test Assortment for Defining Cereal Cyst Nematode Pathotypes,

Pathotypes of cer

Pathotype	Heterode	
	Ha11	Ha2
Differential		
Barley		
Emir [*Rha*?[c]]	S[d]	S
Ortolan [*Rha1*[c]]	R	R
Siri [*Rha2*[c]]	R	R
Morocco [*Rha3*[c]]	R	R
Varde	S	-
KVL191	R	R
Bajo Aragon	R	-
Herta	S	S
Martin 403-2	R	-
Dalmastische	(R)	-
La Estanzuela	-	-
Harlan 43	R	-
Oats		
SunII	S	R
Nidar	S	-
Pusa Hybrid BS1	R	R
Silva	(R)	-
Avena sterilis	R	R
IGV.H 76-646	R	-
Wheat		
Capa	S	S
Loros	R	R
Iskamish K-2-light	S	-
AUS 10894	R	-
Psathias	-	-

[a]*H. hordecalis.*
[b]*H. bifenestra.*
[c]Resistance genes 1 to 3 in barley de
[d]S = susceptible; R = resistant; (S) o
Source: From Rivoal and Cook, 199

which has been modified by
(1993) and is presented in Ta
tests, it is quite difficult to
distinctions between resista
bility based on the numbe
Further, pathotypes may al
tures, which complicates d
pathotype in a particular sam
Sosa-Moss, 1990).

TABLE 22.1
Pathotypes of cereal cyst nematodes defined by an International Test Assortment of cereal cultivars

Pathotype	*Heterodera avenae* group Ha1 pathotypes							Ha2	Ha3			*H.h.*[a]	*H.b.*[b]
	Ha11	Ha21	Ha31	Ha41	Ha51	Ha61	Ha71	Ha12	Ha13	Ha23	Ha33	Hh1	Hb1
Differential													
Barley													
Emir [*Rha?*[c]]	S[d]	S	-	S	-	R	S	S	S	S	S	S	S
Ortolan [*Rha1*[c]]	R	R	R	R	R	R	R	S	S	S	S	S	S
Siri [*Rha2*[c]]	R	R	R	S	S	S	R	R	S	S	S	S	S
Morocco [*Rha3*[c]]	R	R	R	R	R	R	R	R	R	R	R	R	S
Varde	S	-	-	S	-	S	S	S	S	S	S	S	S
KVL191	R	R	R	-	S	S	S	R	-	-	-	-	-
Bajo Aragon	R	-	-	R	-	R	R	R	S	S	R	S	R
Herta	S	S	R	-	R	-	R	S	S	-	-	-	-
Martin 403-2	R	-	-	R	-	R	R	R	R	S	S	S	S
Dalmastische	(R)	-	-	S	-	R	(S)	S	S	(R)	S	(R)	S
La Estanzuela	-	-	-	-	-	-	S	-	-	(R)	-	(R)	S
Harlan 43	R	-	-	-	-	-	R	R	-	R	S	-	-
Oats													
SunII	S	R	R	R	R	S	R	S	S	S	S	R	S
Nidar	S	-	-	S	-	S	R	S	S	S	S	R	S
Pusa Hybrid BS1	R	R	-	R	R	R	R	R	S	R	S	R	S
Silva	(R)	-	-	R	-	(R)	R	(R)	(R)	(R)	S	R	S
Avena sterilis	R	R	-	R	R	R	R	R	R	R	R	R	S
IGV.H 76-646	R	-	-	R	-	R	R	R	S	S	S	-	S
Wheat													
Capa	S	S	-	S	-	S	S	S	S	S	S	R	S
Loros	R	R	-	R	-	(R)	R	R	(R)	S	S	R	R
Iskamish K-2-light	S	-	-	R	-	(R)	-	S	S	S	S	R	R
AUS 10894	R	-	-	R	-	R	S	R	(R)	S	S	R	R
Psathias	-	-	-	S	-	-	-	S	S	S	R	R	S

[a]*H. hordecalis.*
[b]*H. bifenestra.*
[c]Resistance genes 1 to 3 in barley defining 3 pathotype groups.
[d]S = susceptible; R = resistant; (S) or (R) = intermediate; - = no observation.
Source: From Rivoal and Cook, 1993; and previously modified from Andersen and Andersen, 1982.

which has been modified by Rivoal and Cook (1993) and is presented in Table 22.1. In these tests, it is quite difficult to make clear-cut distinctions between resistance and susceptibility based on the number of cysts alone. Further, pathotypes may also occur in mixtures, which complicates delineation of the pathotype in a particular sample (Swarup and Sosa-Moss, 1990).

Economic importance

Heterodera avenae has been associated with economic levels of damage exclusively in light soils. However, it can cause economic damage irrespective of soil type when the intensity of cereal cropping exceeds a certain limit (Kort, 1972). Yield losses due to this nematode are: 15 to 20 percent on wheat in Pakistan (Maqbool, 1988); 40 to 92 percent on wheat and 17 to 77 percent on barley in Saudi Arabia (Ibrahim *et al.*, 1999); and 20 percent on barley and 23 to 50 percent on wheat in Australia (Meagher, 1972).

Recent studies by Scholz (2001) implicate yield loss with both barley and durum wheat with *H. latipons*. Also *H. avenae* and *H. zeae* are major pests of wheat and barley in Pakistan (Maqbool, 1988). In India, *H. zeae* is considered to be one of the most economically important nematodes attacking cereals (Sharma and Swarup, 1984). *Heterodera avenae* has been associated with severe diseases present in India known as *molya*, but it only occurs on temperate cereals, such as barley and wheat, while tropical cereals, such as sorghum and maize, are non-hosts (Gill and Swarup, 1971; Sharma and Swarup, 1984). In the northwestern part of India, between four- and sixteen-fold increases in yield of wheat and barley have been obtained after nematicide treatments (Swarup *et al.*, 1976).

Staggering annual yield losses of 3 million pounds sterling in Europe, 72 million Australian dollars in Australia and 9 million US dollars in India have been calculated as being caused by *H. avenae* (Wallace, 1965; Brown, 1981; Van Berkum and Seshadri, 1970). The losses in Australia are now greatly reduced due to control of the disease with resistant and tolerant cultivars.

Little is known about the economic importance of the species *H. latipons*, even though it was first described in 1969 (Sikora, 1988). Field studies in Cyprus indicated a 50 percent yield loss on barley (Philis, 1988). Because the cysts are similar in size and shape, it is possible that previous findings of this recently described nematode species have erroneously been attributed to the economically important *H. avenae* (Kort, 1972). In West Asia and North Africa, *H. latipons* has been found on wheat and barley in four countries (Sikora, 1988). It has also recently been confirmed in Turkey (Nicol *et al.*, unpublished data). It has also been reported from several Mediterranean countries associated with the poor growth of wheat (Kort, 1972). Unfortunately, this nematode has not been studied in detail, and information on its host range, biology and pathogenicity is scarce; nonetheless, it is suspected to be an important constraint on barley and durum wheat production in temperate semi-arid regions (Sikora, 1988; Scholz, 2001). Other cyst nematodes, such as *P. punctata* and *H. hordecalis,* have been described from roots of cereals in several countries, but their distribution and economic importance is unknown.

Control

One of the most efficient methods of controlling *H. avenae* is with grass-free rotations using non-host crops. In long-term experiments, non-host or resistant cereal frequencies of 50 percent (80 percent in lighter soils) keep populations below damaging thresholds (Rivoal and Besse, 1982; Fisher and Hancock, 1991). Clean fallow and/or deep summer ploughing reduce the population density of the nematode but are not always environmentally sound.

Cultivar resistance is considered one of the best methods for nematode control and has been found to be successful in several countries such as Australia, Sweden and France on a farm scale (R. Rivoal, personal communication, 2000). However, it has also been observed that the use of resistance, especially derived from single dominant genes, may cause a disequilibrium in the biological communities and possibly ecological replacement with other nematodes, such as *Pratylenchus* (Lasserre *et al.*, 1994). Another potential concern is the breakdown of resistance sources with repeated use. This has occurred in France with the resistant oat cultivar Panema and the appearance of a new *H. avenae* pathotype (Lasserre *et al.*, 1996).

In order for cultivar resistance to be effective and durable, a sufficient understanding of the number of species and pathotypes within species is essential. The International Cereal Test Assortment for Defining Cereal Cyst Nematode Pathotypes (Andersen and Andersen, 1982) offers classification of pathotype variation; pathotypes from Australia and India are often distinct from those in Europe (Sikora, 1988). Although useful, a pathotype scheme for a species complex based on interaction with three cereal genera will not easily describe extensive variation in virulence (Rivoal and Cook, 1993). Furthermore, to date there are few molecular or other diagnostic methods that can provide consistent and reliable pathotype and pathogenicity differentiation.

The extensive review by Rivoal and Cook (1993), revised in Table 22.2, gives some indication of the worldwide accessions of germplasm within oats, barley, triticale, rye, wheat and wild grass relatives that offer control of some of the species and pathotypes described in Table 22.1 and, where known, the genetic control and chromosome location. Some resistant cultivars simultaneously reduce populations of several European pathotypes (Williams and Siddiqi, 1972). Since this review, developments have found additional *Triticum* accessions that appear to possess high degrees of resistance to a broad array of *Heterodera* species and pathotypes.

Molecular technology has also been applied to identify markers for various cereal cyst nematode resistance genes using techniques such as RFLP and polymerase chain reaction (PCR) in both barley (Kretschmer *et al.*, 1997; Barr *et al.*, 1998) and wheat (Williams *et al.*, 1994; Eastwood *et al.*, 1994a; Ogbonnaya *et al.*, 1996; Lagudah *et al.*, 1998; Paull *et al.*, 1998). Furthermore, many of the wild grass relatives have been introgressed into a hexaploid wheat background for breeding purposes. Many of these have had molecular work applied to identify the location and the possibility to produce markers to the known gene(s). More details about introgressions, substitutions and molecular characterization of these materials can be found in McIntosh *et al.* (2001). Some of these markers are actively being implemented in marker-assisted selection and pyramiding of gene resistance in Australian cereal breeding programmes against *H. avenae*, pathotype Ha13 (Jefferies *et al.*, 1997; Ogbonnaya *et al.*, 1998). This is an example where there is sufficient understanding of the biology of the pathogen and genetic control of the resistance so that both conventional breeding and the modern tools of molecular biology can be combined to the advancement of controlling this disease. Such potential exists for other nematodes, but will require a similar understanding and combining of related skill base.

The utilization of these identified sources, and possibly of other as yet unidentified sources of resistance, is country-specific and dependent on the number and types of *Heterodera* species and pathotypes that need to be controlled. Many developing countries unfortunately have limited resources and/or expertise to establish this information, and current control methods are based on understanding the response of local cultivars to the pathogen(s). For example, in Israel all locally grown wheat and barley cultivars tested against *H. avenae* and *H. latipons* are excellent hosts. However, the oat cultivars tested were extremely poor hosts to *H. avenae* but good hosts to *H. latipons* (Mor *et al.*, 1992). In Mediterranean countries, such as Algeria, Spain, Israel and southern France, oats appeared generally to be a poor host for *H. avenae*, in comparison to northern Europe where they are considered to be a good host, suggesting the possibility that the nematode has developed host race types (R. Rivoal, personal communication, 2000). In order to make the best use of existing research findings, greater collaboration between research institutions and countries where the nematode is considered important is essential. An excellent example of this is the most recent report by Rivoal *et al.* (2001), which offers a great start to unravelling the

TABLE 22.2

Principal sources of genes[a] used for breeding resistance to *Heterodera avenae* in cereals[b]

Cereal species	Cultivar or line	Origin	Genetic information	Remarks[c]	Used	References[d]
Oats						
Avena sterilis	I376	-	1,2 or 3 dominant genes	R, worldwide	UK, Belgium, Australia	1
A. sativa	Panema	UK	1 dominant gene from I376	S, Australia	UK	1
	Nelson	Sweden	1 dominant gene from C.I. 3444, allelic to Panema, 2 dominant genes	-	NW. Europe, France	1
A. byzantina	NZ Cape	New Zealand	?	S, UK	Australia	1
	Mortgage Lifter	Australia	2 recessive genes	-	-	1
	TAMO 301, 302	Texas, USA	?	-	Australia	1
	No. 11527	-	?	R, Siberia	-	1
Barley						
Hordeum spp.	many cvs e.g. Emir	N. Europe	?	R, to some pathotypes in many cvs	-	1
	Drost	Sweden	1 dominant gene (*Rha1*)	R, to some pathotypes in many cvs	N. Europe	1
	Ortolan	Germany	1 or 2 dominant genes, allelic to *Rha1*	R, to some pathotypes in many cvs	-	1
	ex. L.P. 191	?N. Africa	1 dominant gene (*Rha2*), not linked to *Rha1*	many bred cvs; pR, Australia	N. Europe	1
	ex. Morocco	N. Africa	1 dominant gene (*Rha3*), allelic to *Rha2*	-	Australia	1
	L.P. 191	-	1or 2 dominant genes	-	-	1
	Morocco	-	?	-	-	1
	Athenais	Greece	1 dominant gene, not *Rha1*	-	Australia	1
	Nile, C.I. 3576	Egypt	1 dominant gene, similar to *Rha2*	-	Australia	1
	C.I. 8147	Turkey	1 dominant gene, not *Rha1*	-	Australia	1
	Martin	Algeria	2 dominant genes, ?similar to *Rha3*	-	Australia	1
	C164, RD2052	India	1 dominant gene	R, pathotype-1 (Delhi population)	India	6
Wheat						
Triticum aestivum	Loros, AUS 10894	-, Australia	1 dominant gene, *Cre1* (formerly *Ccn1*) on chromosome 2BL	S, India; pR to several pathotypes	NW. Europe, Australia	1, 4
	Katyil	Australia	*Ccn1*	S, India	Australia	1
	Festiguay	Australia	*CreF* on chromosome 7L?	pR in cv Molineux	Australia	1, 14
	AUS4930 = 'Iraq 48'	Iraq	?	R, to several cereal cyst pathotypes and species and *Pratylenchus thornei*	Australia, France, CIMMYT (under evaluation)	4, 8, 11, 12
T. durum	Psathias	-	?	S, to some pathotypes also pR	-	1
	7654, 7655, Sansome, Khapli	-	?	S, to some pathotypes also pR	France	1

TABLE 22.2
(Continued)

Cereal species	Cultivar or line	Origin	Genetic information	Remarks[c]	Used	References[d]
Triticale						
Triticosecale	T701-4-6	Australia	1 dominant gene, chromosome 6RL, *CreR*	also used in wheat breeding	Australia	1
	Driva	Australia	?	= Ningadhu in cv Tabara	Australia	1
	Salvo	Poland	?	-	UK	1
Rye						
Secale cereale	R173 Family	-	On chromosome 6RL, *CreR*	R, Australia (Ha13)	Australia (under investigation)	17

	Festiguay	Australia	*CreF* on chromosome 7L?	pR in cv Molineux	Australia	1, 14
	AUS4930 = 'Iraq 48'	Iraq	?	R, to several cereal cyst pathotypes and species and *Pratylenchus thornei*	Australia, France, CIMMYT (under evaluation)	4, 8, 11, 12
T. durum	Psathias	-	?	S, to some pathotypes also pR	-	1
	7654, 7655, Sansome, Khapli	-	?	S, to some pathotypes also pR	France	1

TABLE 22.2
(Continued)

Cereal species	Cultivar or line	Origin	Genetic information	Remarks[c]	Used	References[d]
Triticale						
Triticosecale	T701-4-6	Australia	1 dominant gene, chromosome 6RL, *CreR*	also used in wheat breeding	Australia	1
	Driva	Australia	?	= Ningadhu in cv Tabara	Australia	1
	Salvo	Poland	?	-	UK	1
Rye						
Secale cereale	R173 Family	-	On chromosome 6RL, *CreR*	R, Australia (Ha13)	Australia (under investigation)	17
Wild grass relatives						
Aegilops tauschii (*T. tauschii*)	CPI 110813	Central Asia	On chromosome 2DL, *Cre4*	R, Australia (Ha13) and several other countries	Australia synthetic hexaploid lines	7, 15
Ae. tauschii (*T. tauschii*)	AUS 18913	-	1 dominant gene on chromosome 2DL, *Cre3*	R, Australia (Ha13) and several other countries	Australia advanced breeding lines	7, 15
T. variabilie	1	West Asia	Gene *Rkn-mn1* on chromosome 3U or 3S[v]	R, to various pathotypes and *Meloidogyne naasi* and *H. latipons*	France, Algeria, Spain, India, Syria	1, 3, 9, 15
T. longissimum	18	-	?	R and pR to several pathotypes	France (under evaluation)	4
T. ovatum	79	Mediterranean basin	?	R and pR to several pathotypes	France (under evaluation)	4
T. triunciale (*Ae. triuncialis*)	TR-353	Spain	1 dominant gene, *Cre7* (formerly *CreAet*)	R, to several pathotypes (French, Swedish, Spanish)	Spain (under evaluation)	16
T. geniculata (*Ae. geniculata*)	?	Spain, Bulgaria, Jordan, Tunisia	?	R, to several *H. avenae* populations and *H. latipons*	France, CIMMYT (under evaluation)	18
T. ventricosum (*Ae. ventricosa*)	VPM 1	-	On chromosome 2AS, *Cre5* (formerly *CreX*)	R, to French pathotype (Ha12)	France, Australia (under evaluation)	10, 13
T. ventricosum (*Ae. ventricosa*)	11, AP-1, H-93-8	Mediterranean basin	On genome N[v], *Cre2*	R, to Spanish, French and UK (Ha11) pathotypes	Spain (under evaluation)	1, 5, 2, 15
T. ventricosum (*Ae. ventricosa*)	11, AP-1, H-93-8, H-93-35	Mediterranean basin	1 dominant gene on chromosome 5N[v], *Cre6*	R, to Australian pathotype (Ha13), not effective against Spanish (Ha71)	Spain, Australia (under evaluation)	13, 15

[a]See also differentials listed in Table 22.1.
[b]Information unavailable from reference = -; no published scientific studies conducted = ?
[c]R = resistant; pR = partially resistant; S = susceptible.
[d]1 = Rivoal and Cook, 1993; 2 = Andres *et al.*, 2001; 3 = Barloy *et al.*, 1996; 4 = Bekal *et al.*, 1998; 5 = Delibes *et al.*, 1993; 6 = Dhawan and Gulati, 1995; 7 = Eastwood *et al.*, 1994a; 8 = F. Green, personal communication, 1998; 9 = Jahier *et al.*, 1998; 10 = Jahier *et al.*, 2001; 11 = Nicol *et al.*, 1998; 12 = Nicol *et al.*, 2001; 13 = Ogbonnaya *et al.*, 2001; 14 = Paull *et al.*, 1998; 15 = Rivoal *et al.*, 2001; 16 = Romero *et al.*, 1998; 17 = Taylor *et al.*, 1998; 18 = Zaharieva *et al.*, 2000.

complexity of *Heterodera* populations and the existing knowledge of resistant sources and their possible uses in controlling the cereal cyst nematode in different regions of the world.

The use of chemical fumigants and nematicides, although proven effective in experimental fields in many countries, is not an economically feasible option for most farmers. Application of nematicides for the control of *H. avenae* on wheat has resulted in 50 to 75 percent yield increases in Pakistan, but their use is not feasible on a commercial scale (Maqbool, 1988).

The deployment of biological control agents is not yet an option, but natural biological control has been found to operate in some circumstances. The fungi *Nematophora gynophila* and *Verticillium chlamydosporium* have been associated with reduction and suppression of *H. avenae* populations under intensive cereals in the United Kingdom (Kerry and Andersson, 1983; Kerry, 1987; Kerry and Crump, 1998), and similar suppression may occur in other regions with similar climates.

ROOT LESION NEMATODES

Distribution

The genus *Pratylenchus* is a large group with many species affecting both monocots and dicots. Many of the species are morphologically similar, which makes them difficult to identify. At least eight species of lesion nematodes have been recorded for small grains (Rivoal and Cook, 1993). Of these, four species (*P. thornei*, *P. crenatus*, *P. neglectus* and *P. penetrans*) have a worldwide distribution, especially in the temperate zones (Kort, 1972). *Pratylenchus crenatus* is more common in light soils, *P. neglectus* in loamy soils and *P. thornei* in heavier soil types (Kort, 1972). However, the work of Nicol (1996) suggests that both *P. thornei* and *P. neglectus* can occur in a range of soil types, and mixtures of the two species are not uncommon in southern Australia.

Pratylenchus thornei is the most studied species on wheat and is a known parasite of cereals worldwide, being found in Syria (Saxena *et al.*, 1988; Greco *et al.*, 1984), former Yugoslavia, Mexico and Australia (Fortuner, 1977), Canada (Yu, 1997), Israel (Orion *et al.*, 1982), Morocco (Ammati, 1987), Pakistan and India (Maqbool, 1988), Algeria (Troccoli *et al.*, 1992) and Italy (Lamberti, 1981). Unfortunately, very little is known about the economic importance and distribution of the other species on cereals.

Biology

Pratylenchus species are polycyclic, polyphagous migratory root endoparasites that are not confined to fixed places for their development and reproduction. Eggs are laid in the soil or inside plant roots. The nematode invades the tissues of the plant root, migrating and feeding inside the root causing characteristic dark brown or black lesions on the root surface, hence its common name. Extensive lesioning, cortical degradation and reduction in both seminal and lateral root systems is seen with increasing nematode density, as illustrated in Plate 56. Secondary attack by fungi frequently occurs at these lesions. The life cycle is variable between species and environment and ranges from 45 to 65 days (Agrios, 1988). Above-ground symptoms of *Pratylenchus* on cereals, as with other cereal root nematodes, is non-specific where infected plants appear stunted and unthrifty, sometimes with reduced numbers of tillers and yellowed lower leaves (Plate 57).

Economic importance

As previously mentioned, the most studied of these species on wheat is *P. thornei* and, somewhat less so, *P. neglectus* and *P. penetrans*. *Pratylenchus thornei* is considered the most economically important species in at least three countries; yield losses on wheat have been reported between 38 and 85 percent in Australia (Thompson and Clewett, 1986; Doyle *et al.*, 1987; Taylor and

McKay, 1993; Eastwood *et al.*, 1994b; Nicol, 1996; Taylor *et al.*, 1999), 32 percent in Mexico (Van Gundy *et al.*, 1974) and 70 percent in Israel (Orion *et al.*, 1984). *Pratylenchus thornei* appears to be associated with regions experiencing a Mediterranean climate. It is highly probable, given the distribution of this nematode, that similar losses may also be occurring in many other countries, however this has not been studied.

The other species of lesion nematodes where yield loss studies have been conducted (*P. neglectus* and *P. penetrans*) are not recognized as having a global distribution on cereals, and the current yield loss studies would suggest that the damage potential of these nematodes is not as great as that of *P. thornei*. In Australia, losses on wheat with *P. neglectus* ranged from 16 to 23 percent (Vanstone *et al.*, 1995; Taylor *et al.*, 1998), while in Canada *P. penetrans* losses were 10 to 19 percent (Kimpinski *et al.*, 1989). Yield loss work by Vanstone *et al.* (1998) in the field where both *P. thornei* and *P. neglectus* were present indicates losses between 56 and 74 percent on wheat. Recent studies by Sikora (1988) have identified *P. neglectus* and *P. penetrans* in addition to *P. thornei* on wheat and barley in North Africa and all of these plus *P. zeae* in West Asia. Further work is necessary to determine the significance of these species in these regions.

Control

Unlike cereal cyst nematode, no commercially available sources of cereal resistance to *P. thornei* are available, although sources of tolerance have been used by cereal farmers in northern Australia for several years (Thompson *et al.*, 1997). Work by Thompson and Clewett (1986) and Nicol *et al.* (1996, 1998, 2001) identified wheat lines that have proven field resistance, and work is continuing to breed this resistance into suitable backgrounds. Recent work by Thompson and Haak (1997) identified 29 accessions from the D-genome donor to wheat, *Aegilops tauschii*, suggesting there is future potential for gene introgression. Some of this material also contained the *Cre3* and other different unidentified sources of cereal cyst nematode resistance genes conferring resistance to some cereal cyst nematode pathotypes. As with cereal cyst nematode, molecular biology is also being used to investigate genetic control and location, followed by the identification of markers for resistance to both *P. thornei* and *P. neglectus*. Recent work with Australian germplasm referred to by McIntosh *et al.* (2001) reports the gene *Rlnn1* on chromosome 7AL effective against *P. neglectus*, and two quantitative trait loci on chromosomes 2BS and 6DS have been found for *P. thornei*. No commercial sources of resistance are currently available for other species of *Pratylenchus* that attack cereals.

The use of crop rotation is a limited option for root lesion nematodes due to the polyphagous nature of the nematode. Little is understood about the potential role of crop rotation in controlling these nematodes, although some field and laboratory work has been undertaken to better understand the ability of both *P. thornei* (O'Brien, 1983; Clewett *et al.*, 1993; Van Gundy *et al.*, 1974; Nicol, 1996; Hollaway *et al.*, 2000) and *P. neglectus* (Vanstone *et al.*, 1993; Lasserre *et al.*, 1994; Taylor *et al.*, 1998, 2000) to utilize cereals and leguminous crops as hosts. It is possible, depending on crop rotation patterns and the population dynamics of the nematodes, that resistant cultivars of cereals alone may not be sufficient to maintain the nematode below economic levels of damage.

As with other nematodes, chemical control, although in most cases effective against root lesion nematodes, is not economically viable with cereal crops. Cultural methods offer some control options, but are of limited effectiveness; in order to be of major significance, they need to be integrated with other control measures. Di Vito *et al.* (1991) found that mulching fields with polyethylene film for six to eight weeks suppressed *P. thornei* populations by 50 percent. Van Gundy *et al.* (1974) found that delaying the sowing of winter irrigated wheat by one month in Mexico gave maximum yields. In Australia, cultivation reduced populations of *P. thornei* (Thompson *et al.*, 1983; Klein *et al.*, 1987).

ROOT KNOT NEMATODES

Distribution

Several *Meloidogyne* spp. are known to attack cereals and tend to favour light soils and warm temperatures. Several species attack Poaceae in cool climates, including *M. artiellia*, *M. chitwoodi*, *M. naasi*, *M. microtyla* and *M. ottersoni* (Sikora, 1988). In warm climates, *M. graminicola*, *M. graminis*, *M. kikuyensis* and *M. spartinae* are important (Taylor and Sasser, 1978). In tropical and subtropical areas, *M. incognita*, *M. javanica* and *M. arenaria* are all known to attack cereal crops (Swarup and Sosa-Moss, 1990).

To date, only *M. naasi* and *M. artiellia* have been shown to cause significant damage to wheat and barley in the winter growing season (Sikora, 1988). The most important and most studied species of the root knot nematodes on cereals worldwide are described below. There is little information on most other species, many of which are of unknown importance.

Meloidogyne naasi is reported from the United Kingdom, Belgium, the Netherlands, France, Germany, former Yugoslavia, Iran, the United States and the former Soviet Union, occurring mostly in temperate climates (Kort, 1972). However, it has also been found in Mediterranean areas on barley in the Maltese islands (Inserra *et al.*, 1975) and in New Zealand and Chile on small grains (Jepson, 1987). It is probably the most important root knot nematode affecting grain in most European countries in contrast to the United States (Kort, 1972). *Meloidogyne naasi* does not appear to be widespread in temperate semi-arid regions, such as West Asia and North Africa (Sikora, 1988).

Meloidogyne naasi is a polyphagous nematode, reproducing on at least 100 species of plants (Gooris and D'Herde, 1977) including barley, wheat, rye, sugar beet, onion and several broadleaf and monocot weeds (Kort, 1972). However, Poaceae are considered to be better hosts (Gooris, 1968). In Europe, oats are a poor host compared with other cereals, whereas in the United States, oats are an excellent host of *M. naasi* (Kort, 1972). Host races of *M. naasi* have been identified in the United States by using differential hosts (Michel *et al.*, 1973), which makes controlling this nematode more difficult.

Another species of root knot nematode that attacks cereals is *M. artiellia*, which has a wide host range including crucifers, cereals and legumes (Ritter, 1972; Di Vito *et al.*, 1985). It is known to reproduce well on cereals and severely damage legumes (Sikora, 1988). This nematode is chiefly known from Mediterranean Europe in Italy, France, Greece and Spain (Di Vito and Zacheo, 1987), but also in West Asia (Sikora, 1988), Syria (Mamluk *et al.*, 1983), Israel (Mor and Cohn, 1989) and western Siberia (Shiabova, 1981).

Meloidogyne chitwoodi is a pest on cereals in the Pacific Northwest of the United States and is also found in Mexico, South Africa and Australia (Eisenback and Triantaphyllou, 1991). Many cereals, including wheat, oats, barley and maize, and a number of dicots are known to be hosts (Santo and O'Bannon, 1981). *Meloidogyne graminis* is not known to be widely distributed, being limited to the southern United States where it is associated with cereals and more often turf grasses (Eriksson, 1972).

Biology

The young juveniles of *M. naasi* invade the roots of cereals within one to one and one-half months of germination, after which small galls on the root tips can be observed. *Meloidogyne naasi* generally has one generation per season (Rivoal and Cook, 1993). The juveniles develop, and the females become almost spherical in shape. Females deposit eggs in an egg sac. They usually appear eight to ten weeks after sowing and are found embedded in the gall tissue (Kort, 1972). Large galls may contain 100 or more egg-laying females (Rivoal and Cook, 1993). Later in the season, galling of the roots, especially the root tips, is common. Galls are typically curved, horseshoe or spiral-shaped (Kort, 1972). The egg masses in galls survive in the soil. Eggs have a diapause, broken by increasing temperature after a cool period (Antoniou, 1989). In warmer regions on perennial or volunteer grass hosts, more than one generation per season is possible (Kort, 1972; R. Rivoal, personal communication, 2000).

Symptoms of *M. naasi* attack closely resemble those caused by *H. avenae*, with patches of poorly growing, yellowing plants that may vary in size from a few square metres to larger areas. Other root knot nematodes attacking cereals are suspected to produce similar symptoms, but most are much less studied than *M. naasi*.

Economic importance

Information on the economic importance of root knot nematodes on cereals is limited to a few studied species. *Meloidogyne naasi* can seriously affect wheat yield in Chile (Kilpatrick *et al.*, 1976) and Europe (Person-Dedryver, 1986). On barley, it has been known to cause up to 75 percent yield loss in California, United States (Allen *et al.*, 1970). It is also associated with yield loss on barley in France (Caubel *et al.*, 1972), Belgium (Gooris and D'Herde, 1977) and the United Kingdom (York, 1980). Severe losses can occur with entire crops of spring barley lost in the Netherlands and France (Schneider, 1967). *Meloidogyne naasi* damage is not known to be widespread in temperate, semi-arid regions (Sikora, 1988), but rather has been associated with wet and/or over-compacted soils (Franklin, 1973).

Damage to wheat by *M. artiellia* is known from Greece, southern Israel and Italy (Kyrou, 1969; Mor and Cohn, 1989). In Italy, 90 percent yield losses on wheat have been recorded (Di Vito and Greco, 1988). *Meloidogyne chitwoodi*, an important pathogen of potatoes, also damages cereals in Utah, United States (Inserra *et al.*, 1985), and Mexico (Cuevas and Sosa-Moss, 1990). In controlled laboratory studies, *M. incognita* and *M. javanica* have been shown to reduce plant growth of wheat (Roberto *et al.*, 1981; Sharma, 1981; Abdel Hamid *et al.*, 1981), and *M. incognita* is a known field problem on wheat in northwestern India (Swarup and Sosa-Moss, 1990).

Control

Control methods for root knot nematodes have only been investigated in detail for the known economically important species *M. naasi*. Partial resistance was found in barley and also in *Ae. tauschii* and *T. monococcum*, while full resistance was identified with *H. chilense*, *H. jabatum*, *Ae. umbellulatum* and *Ae. variabile* (Cook and York, 1982b; Roberts *et al.*, 1982; Person-Dedryver and Jahier, 1985; Person-Dedryver *et al.*, 1990; Yu *et al.*, 1990).

Cultural management options for *M. naasi* include rotations using poor or non-host crops (Cook *et al.*, 1986) and the use of fallow during the hatching period (Allen *et al.*, 1970; Gooris and D'Herde, 1972).

SEED GALL NEMATODES

Distribution

Seed gall nematode (*Anguina tritici*), commonly known as ear cockle, is frequently found on small grain cereals where farm-saved seed is sown without the use of modern cleaning systems. Cereals are infected throughout West Asia and North Africa (Sikora, 1988), the Indian subcontinent, China, parts of Eastern Europe (Tesic, 1969; Swarup and Sosa-Moss, 1990), Iraq (Stephan, 1988) and Pakistan (Maqbool, 1988). It has also been reported from most European countries, the Russian Federation, Australia, New Zealand, Egypt, Brazil and several areas in the United States (Swarup and Sosa-Moss, 1990).

Biology

The nematode is spread in galled or 'cockled' seeds when infected seed is sown. A single gall may contain over 10 000 dormant juveniles. Once sown, the galls take up water, and the juveniles emerge and remain between the leaves of the growing plant. The primary leaves become twisted and distorted, and the plant may die from a heavy attack (Kort, 1972). In growing seedlings, the juveniles are carried upward towards the growing point of the plant, and when the ear is formed, the flower head is invaded by the juveniles. As a result, the ovules and other flowering parts of the plant are transmuted into galls or cockles. Inside the galls, the nematodes mature, and the females lay thousands of eggs from which the juveniles hatch and remain dormant in the seed. The nematode is favoured by wet and cool weather (Kort, 1972).

Symptoms of *A. tritici* attack may be indicated by small and dying plants with the leaves generally twisted due to nematode infection (Swarup and Sosa-Moss, 1990). The attacked ears are easily recognized by their smaller size and darkened colour compared with normal seeds, but the infected seeds may be easily confused with common bunt (*Tilletia tritici*). Under dry conditions, the juveniles may survive for decades (Kort, 1972).

The nematode is also associated with a bacterium, *Corynebacterium michiganense* pv. *tritici*, which causes yellow ear rot. The economic loss associated with this combination is increased because of the lower price for infected grain (Rivoal and Cook, 1993).

Economic importance

Worldwide, wheat, barley and rye are commonly attacked, but barley is less attacked in India (Paruthi and Gupta, 1987). In Iraq, seed gall is an important pest on wheat with infection ranging from 0.03 to 22.9 percent and causing yield losses up to 30 percent (Stephan, 1988). Barley is also attacked in Iraq but with an isolate that does not affect wheat (Al-Tabib *et al.*, 1986).

In Pakistan, seed gall is a known pest on wheat and barley and is found in nearly all parts of the country, causing yield losses of 2 to 3 percent; association with the bacterium produces serious yield losses on wheat (Maqbool, 1988). In China, Chu (1945) found yield losses between 10 and 30 percent on wheat.

Control

Seed gall can easily be controlled through seed hygiene: sowing clean, non-infected seed obtained by using certified seed or by cleaning infected seed either with modern seed cleaning techniques or by sieving and fresh-water flotation (Singh and Agrawal, 1987). Although seed gall has been eradicated from the Western Hemisphere through the adoption of this approach, it remains a problem on the Indian subcontinent, in West Asia and to some extent in China (Swarup and Sosa-Moss, 1990).

For countries where hygiene practices are difficult to implement, host resistance and crop rotation offer some control of seed gall. Resistance to *A. tritici* has been identified in Iraq in both wheat and barley (Saleh and Fattah, 1990) and in Pakistan (Shahina *et al.*, 1989) and is currently being sought in India (Swarup and Sosa-Moss, 1990). In Iraq, laboratory screening has identified sources of resistance in both wheat and barley (Stephan, 1988). Oat, maize and sorghum are considered to be non-hosts (Limber, 1976; Paruthi and Gupta, 1987), and while they may offer some option for reducing populations by rotation, the disease is not completely controlled.

STEM NEMATODES

Distribution

Ditylenchus dipsaci is by far the most common and important species of stem

nematode on cereals,
throughout western and
United States, Canada
Argentina and North
although it is of greatest e
in temperate zones (Ko
damage is rarely associa
soils with a clay base a
associated with damage
Another species, *D. r*
buted throughout the Sca
the United Kingdom,
Germany, Poland, the fo
the United States and C
tode also occurs on many
importance.

Biology

Ditylenchus dispaci is a n
site that invades the foli
the stem of cereals, where
tissues and feeds on adjac
tion continues inside th
year-round but is minim
tures. When an infected pl
return to the soil and fro
neighbouring plants. Ty
stem nematode attack incl
dwarfing and twisting of
shortening of internodes
of axillary buds, produ
number of tillers to give
appearance. Heavily infe
at the seedling stage resul
in the field, while other
to produce flower spikes
The nematodes are high
and can cover a distance o
hours (Kort, 1972), hen
spread from one plant to
There are a number of b
strains of *D. dipsaci*, whi
cally indistinguishable
range. Kort (1972) stated
is more common in Euro
strain is more commo
Kingdom. Rye strains att

nematode on cereals, being widespread throughout western and central Europe, the United States, Canada, Australia, Brazil, Argentina and North and South Africa, although it is of greatest economic importance in temperate zones (Kort, 1972). Economic damage is rarely associated with sandy soils; soils with a clay base are more likely to be associated with damage (Kort, 1972).

Another species, *D. radicicola*, is distributed throughout the Scandinavian countries, the United Kingdom, the Netherlands, Germany, Poland, the former Soviet Union, the United States and Canada. This nematode also occurs on many grasses of economic importance.

Biology

Ditylenchus dispaci is a migratory endoparasite that invades the foliage and the base of the stem of cereals, where it migrates through tissues and feeds on adjacent cells. Reproduction continues inside the plant almost all year-round but is minimal at low temperatures. When an infected plant dies, nematodes return tó the soil and from there they infect neighbouring plants. Typical symptoms of stem nematode attack include basal swellings, dwarfing and twisting of stalks and leaves, shortening of internodes and an abundance of axillary buds, producing an abnormal number of tillers to give the plant a bushy appearance. Heavily infected plants may die at the seedling stage resulting in bare patches in the field, while other attacked plants fail to produce flower spikes (Kort, 1972).

The nematodes are highly motile in the soil and can cover a distance of 10 cm within two hours (Kort, 1972), hence their ability to spread from one plant to another is rapid. There are a number of biological races or strains of *D. dipsaci*, which are morphologically indistinguishable but differ in host range. Kort (1972) stated that the rye strain is more common in Europe and that the oat strain is more common in the United Kingdom. Rye strains attack rye and oats as well as several other crops, including bean, corn, onion, tobacco and clover, and a number of weed species commonly associated with the growth of cereals in many countries (Kort, 1972). The oat strain attacks oats, onion, pea, bean and several weed species but not rye (Kort, 1972). Wheat is also attacked by *D. dipsaci* in central and eastern Europe (Rivoal and Cook, 1993).

The species *D. radicicola* invades root tips of plants to form local swellings, which are characteristically spiral-shaped and easily confused with the galled root symptoms caused by *M. naasi*.

Economic importance

Economic damage by *D. dipsaci* depends on a combination of factors, such as host plant susceptibility, infection level of the soil, soil type and weather conditions. The longer the soil moisture content in the surface layer of soils is optimum for nematode activity, the greater the chance of a heavy attack. This is a problem with cereal crops growing on heavy soils in high-rainfall areas (Griffin, 1984). The nematode is economically important on rye and oats, but not on wheat and barley (Sikora, 1988). Although few studies have examined the economic importance of this nematode, work on oats in the United Kingdom attributed a 37 percent yield loss to *D. dipsaci* (Whitehead *et al.*, 1983).

Little is known about the economic importance of *D. radicicola*; however, under field conditions in Scandinavia it caused poor growth of barley and is known locally as *krok*. S'Jacob (1962) suggested that biological races of this species occur.

Control

The occurrence of different biological races or strains of *D. dipsaci* makes it a difficult nematode to control. The only economic and highly effective method is the use of host resistance, which has been summarized in table form by Rivoal and Cook (1993). In the United Kingdom, the most successful oat crop has resistance derived from the landrace cultivar Grey Winter, which has also proven to be effective in Belgium (Rivoal and Cook, 1993).

Rotational combinations of non-hosts, including barley and wheat, offer some control method for the rye and oat races of *D. dipsaci*. However, once susceptible oat crops have been damaged, rotations are largely ineffective (Rivoal and Cook, 1993).

OTHER NEMATODES

There are other plant-parasitic nematodes that have been found or are implicated potentially to cause yield loss on cereals, although their global distribution and economic importance to date has not been clearly defined. These nematodes or nematode combinations can be found in reviews by Kort (1972), Griffin (1984), Swarup and Sosa-Moss (1990) and Rivoal and Cook (1993).

FUTURE DIRECTIONS

There are several genera and species of nematodes that are of economic importance to small grain cereals. The current understanding of some nematodes, such as the cereal cyst nematode, *H. avenae*, is much more extensive than others with respect to both biology and control measures, mainly in the form of host resistance. Others, such as seed gall nematode, *A. tritici*, are relatively easily controlled with the adoption of seed hygiene. Unfortunately, knowledge is limited with respect to the basic biology and control options for most of the other important nematodes described.

In the future, the ability to reduce yield losses caused by nematodes will require a greater understanding of many basic questions about pathogen biology and the application of appropriate control measures. The use of chemicals is an unrealistic commercial option for most cereal growers, and to date many of the cultural methods fail to offer complete control. As a consequence, it is inevitable that breeding for resistance and perhaps tolerance is the major strategy for long-term and environmentally sound control of these pathogens. As stressed in this chapter, in order to accomplish this, a sufficient understanding of pathogen biology and plant reactions is necessary. To capitalize on this information, it is necessary to combine research efforts, particularly for some of the more complex nematodes with race and pathotype differences; hence there is a great need for global collaborative research programmes. Furthermore, the adoption of molecular tools to assist both in pathogen identification and plant breeding will become an integral part of future research developments and ultimate control of these important pathogens.

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