Review

The importance, biology and management of cereal cyst nematodes (*Heterodera spp.*)

F. MOKRINI[1] N. VIAENE[2,3] L. WAEYENBERGE[2] M. AFECHTAL[5] A. ESSARIOUI[6], M. MOENS[2,4]

(Reçu le 30/03/2017; Accepté le 15/06/2017)

Abstract

Cereals are exposed to biotic and abiotic stresses. Among the biotic stresses, plant-parasitic nematodes play an important role in decreasing crop yield. Cereal cyst nematodes (CCNs) are known to be a major constraint to wheat production in several parts of the world. Significant economic losses due to CCNs have been reported. Recognition and identification of CCNs are the first steps in nematode management. This paper reviews the current distribution of CCNs in different parts of the world and the recent advances in nematode identification. The different approaches for managing CCNs are also discussed.

Keywords: Cereals, cyst nematodes, identification, management, control

L'importance, la biologie et la gestion des nématodes à kyste des céréales (*Heterodera spp.*)

Résumé

Les céréales sont exposées à des stress biotiques et abiotiques. Parmi les stress biotiques, les nématodes parasites des plantes jouent un rôle important dans la diminution du rendement des cultures. Les nématodes à kystes des céréales (CCNs) sont connus pour être une contrainte majeure à la production de blé dans plusieurs parties du monde. Des pertes économiques considérables dues aux CCNs ont été signalées. La reconnaissance et l'identification des CCNs sont un élément important dans la gestion des nématodes. Cet article passe en revue la répartition actuelle des CCNs dans différentes parties du monde et les progrès récents dans l'identification des nématodes. Les différentes approches de gestion des CCNs sont également discutées.

Mots clés: Céréales, gestion, identification, nématodes à kystes

INTRODUCTION

Among the cereals, wheat (*Triticum aestivum* and *T. durum*) and barley (*Hordeum vulgare*) occupy the most prominent position in terms of production, acreage and source of nutrition, particularly in developing countries (Nicol et *al*., 2011). By 2030, the world production of cereals is expected to increase to 8 billion tonnes; that of *T. aestivum* is estimated to increase from 584 million tonnes (average 1995-1999) to 860 million tonnes (Hossain et Teixeira Da Silva, 2012). In Morocco, cereals occupy 75% of the cultivated area and account for 10–20% of the agricultural gross domestic product (Benabdelouahab et *al*., 2016). Cereal production of the season 2013-2014 was estimated at 6.8 million tonnes and includes 4.42 million tonnes of common wheat, 0.5 million tonnes of durum wheat and 0.4 million tonnes of barley, ranking 15th among the cereal producing countries (Anonymous, 2014). Productivity of soft wheat (*T. aestivum*), durum wheat and barley is low, due to biotic and abiotic stresses. Consequently, Morocco is not self sufficient in wheat production most of the years and imports bread wheat for its domestic consumption (Balaghi et *al*., 2013). Cereal production occurs in most parts of the country but is mainly concentrated in 6 regions, each contributing differently to a certain type of cereal (Table 1).

Table 1: Contribution (%) of the main cereal producing regions of Morocco to the national production of soft wheat (*T. aestivum*), durum wheat and barley (average of 1990-2011) (Balaghi et al., 2013)

Region	Soft wheat	Durum wheat	Barley
Tadla	11.4	5.1	4.5
Gharb	25.6	4.4	-
Chaouia	10.7	22.4	15.6
Saïss	14.6	16.4	4.4
Haouz	6.1	12.2	22.4
Oriental	-	-	11.0
Total	86.4	60.5	57.9

THE CEREAL CYST NEMATODES (CCNS)

Heterodera is a very important genus of the family Heteroderidae (Nematoda). Members of this genus are obligate parasites and different species attack different crops, often causing great economic damage. The genus is particular among nematode genera because of the ability of the female to transform into a tough brown cyst, which protects the eggs formed within her body.

[1] National Institute for Agricultural Research (INRA), Agadir, Morocco. Email: fmokrini.inra@gmail.com
[2] Institute for Agricultural and Fisheries Research, Plant, Crop Protection, Burg. Van Gansberghelaan 96, B-9820 Merelbeke, Belgium
[3] Department of Biology, Ghent University, K.L. Ledeganckstraat 35, B-9000 Ghent, Belgium
[4] Faculty of Bio-science engineering, Ghent University, Coupure links 653, B-9000 Ghent, Belgium
[5] National Institute for Agricultural Research (INRA), Km 9, 14000, Kénitra, Morocco
[6] National Institute for Agricultural Research (INRA), Errachidia, Morocco

DISTRIBUTION AND IMPORTANCE

Cereal cyst nematodes form a group of several closely related species that have been documented as causing economic yield losses in wheat production systems in several parts of the world, including West Asia, North Africa, Europe, Australia and the United States of America (Rivoal et Cook, 1993; Nicol et Rivoal, 2008; Sahin et *al*., 2009; Yan et Smiley, 2009). Twelve species affect roots of cereals and grasses (Nicol et Rivoal, 2008; Subbotin et *al*., 2010), among which three species, *viz. H. avenae*, *H. latipons* and *H. filipjevi*, are considered the most economically important, and sometimes coexist (Rivoal et Cook, 1993; Abidou et *al*., 2005; Mc Donald et Nicol, 2005).

Out of these three species, *H. avenae* is the most widely distributed and damaging species in temperate wheat producing regions throughout the world (Rivoal et Cook, 1993). It is known as a major production constraint of cereals in Europe (Rivoal et Cook, 1993), Australia (Brown, 1984), India (Khan *et al*., 1990; Singh et *al*., 2009), North America (Miller, 1986), and in several countries of North Africa and West Asia (Sikora, 1988; Al-Yahya et *al*., 1998; Nicol et *al*., 2011). *Heterodera latipons* has been found in the Mediterranean region (Greco, 1994), but has also been detected in the temperate continental climates of Southern Russia, Ukraine, Central Asian Republics (Subbotin et *al*., 1996), Iran (Talatschian et *al*., 1976), Europe (Sabova et *al*., 1988), and Canada (Sewell, 1973). *Heterodera filipjevi* has been found in more continental climates such as Russia, Tadzhikistan (Subbotin et *al*., 1999), but also in Pakistan, Turkey (Rumpenhorst *et al*., 1996), Norway (Holgado et *al*., 2004), and USA (Smiley et *al*., 2008). Several other species of *Heterodera* (*e.g.*, *H. hordecalis*, *H. zeae* and *H. bifenestra*) are reported on wheat but are not considered to be of major economic importance (Smiley et Nicol, 2009; Lambardo et *al*., 2009; Sharma et *al*., 2009).

In Morocco, *H. avenae* was reported for the first time in an irrigated wheat field in 1951 (Ritter, 1982). It has been increasingly detected over the last few years and is recognized as a damaging pathogen of wheat and barley in most cereal growing areas, especially in Zaer, Saiss, Chaouia and Doukkala (Meskine et *al*., 1984; Znasni, 2003; Mokrini et *al*., 2009, 2012a). Recently, *H. latipons* was found for the first time in the wheat growing area of Saiss region (Ain Jmaa) (Mokrini et *al*., 2012b). However, *H. filipjevi* has never been reported in Moroccan cereal fields.

Cereal cyst nematodes can cause considerable yield reduction, especially in temperate climates and semi-arid regions where they can aggravate drought stress (Rivoal et Cook, 1993). Yield losses caused by CCNs can be up to 90% in severely infested fields (Rivoal et Cook, 1993; Riley et *al*., 2009). Several authors have reported that water stress is one of the key environmental conditions that can exacerbate damage caused by CCNs (*e.g.,* Nicol et *al*., 2011). Yield losses due to *H. avenae* on wheat are reported to be 40-92% in Saudi Arabia (Ibrahimi et *al*., 1999), 10% in China (Peng et *al*., 2009), 40-50% in Morocco (Rammah, 1994), and 23-50% in Australia (Meagher, 1972). It has been calculated that *H. avenae* is responsible for annual yield losses of 72 million Australian dollars in Australia (Brown, 1981). Several studies have shown the economic importance of *H. latipons* and *H. filipjevi* (Nicol et *al*., 2006; Hajihasani et *al*., 2010). Nicol et *al*. (2006) showed that *H. filipjevi* infestation can be highly destructive to *Triticum* spp. Hajihasani et *al*. (2010) performed a study on the effects of *H. filipjevi* on the yield and growth parameters of *T. aestivum* cv. Sardari (bread wheat). The authors concluded that a population density of 20 eggs or second-stage juveniles (J2) per g of soil reduced grain yield up to 55%, root dry weight up to 70%, aerial shoot dry weight up to 48%, spike height up to 36%, and plant height up to 32%. In addition to yield loss of wheat, Philis (1988) reported up to 50% yield loss of barley in fields infested with *H. latipons* in Cyprus. In Turkey, *H. filipjevi* was found in all wheat growing areas in the East Anatolia Region, the Central Anatolian Plateau (CAP) and transition zone (Sahin et *al*., 2009, Toktay et *al*., 2015) with an estimate of yield loss up to 50% in several rain-fed winter locations (Nicol et *al*., 2006).

IDENTIFICATION OF *HETERODERA* SPECIES

In the *H. avenae* group, as in each *Heterodera* group, only minor morphological and morphometrical differences distinguish species from each other. The structures of the cone top of the cyst, including fenestra, bullae and underbridge are used to separate the species. However, the increasing number of species in this group makes reliable morphological identification more difficult and time consuming (Subbotin et *al*., 2003). Molecular identification can confirm traditional identification, especially for morphologically closely related species. Several molecular techniques can be used for the separation of species and populations of the *H. avenae* group, including species-specific primer sets for differentiating *H. avenae*, *H. filipjevi*, and *H. latipons* (Toumi et *al*., 2013a, Toumi *et al*., 2013b; Yan *et al*., 2013; Waeyenberge et Viaene, 2015), sequences of ITS-rDNA (Ferris et *al*., 1994; Bekal et *al*., 1997; Subbotin *et al*., 2003) and restriction fragment length polymorphism (RFLP) (Subbotin et *al*., 1999).

CEREAL CYST NEMATODE PATHOTYPES

The term "pathotype" refers to a biological entity (nematode population) that is distinguished by its inherent capacity (or inability) to multiply on a given host genotype with one or more genes for resistance (Trudgill, 1986). Numerous schemes have been developed to classify nematodes according to their parasitic capabilities (Triantaphyllou, 1987).The pathotype scheme for CCNs is based on their multiplication on host differentials of barley, oats and wheat cultivars in the *International Cereal Test Assortment* developed by Andersen and Andersen (1982). The test uses 12 barley (*Hordeum vulgare*), six oat (*Avena sativa*), and six wheat differential cultivars to define pathotypes of *H. avenae*. This scheme distinguishes three primary groups, based on host resistance reactions of barley cultivars carrying the resistance genes Rha1, Rha2, and Rha3. In Europe, North Africa, and Asia, most populations of *H. avenae* belong to groups 1 (Ha1) and 2 (Ha2) (Al-Hazmi et *al*., 2001; Cook et Noel, 2002; Znasni, 2003). Pathotypes of group 3 are mostly found in Australia, Europe, and North Africa (Rivoal et Cook, 1993). In

Morocco, Znasni (2003) reported the presence of two pathotype groups (Ha1 and Ha2). The characterization of the CCNs species and pathotype is essential for developing resistance in breeding and applying appropriate cultivars in nematode management programs.

BIOLOGY

The life cycle of members of the *H. avenae* group involves various stages, including the egg, four juvenile stages, and the adult nematode (Subbotin et *al*., 2010). The species completes one generation per growing season (Rivoal et Cook, 1993); to complete its life cycle, the nematode requires between three and four months under low soil temperature (5-15°C) and high soil moisture (Smiley et Nicol, 2009). Cyst nematodes are characterized by the developing female swelling and becoming a cyst, which contains several hundred eggs. Within the cyst, eggs may remain dormant in soil for several years. Each egg contains a single first-stage juvenile (J1), which moults inside the egg to become a second-stage juvenile (J2) (Figure 1). Emergence of J2 from eggs enclosed in brown cysts requires a period of dormancy (diapause) that differs among species and climatic region (Smiley et Nicol, 2009). The induction or suppression of dormancy by different temperatures regulates the hatching of juveniles. For *H. avenae*, two ecotypes appeared to differ in the induction or suppression of dormancy (diapause) by different thermal conditions (Rivoal, 1986). In Mediterranean climates, the diapause is acting when the climate is hot and dry; diapause is suppressed when the soil temperature falls and moisture rises (Rivoal et Cook, 1993).

Further research with North African populations (Algeria, Morocco and Tunisia) demonstrated hatching schemes relevant to the Mediterranean ecotype, with a higher optimum of hatching temperatures, which could express adaptation of populations to warmer climatic conditions (Rivoal et Nicol, 2009). Scholzand Sikora (2004) demonstrated that the hatch of *H. latipons* in Syria was similar to the Mediterranean ecotype of *H. avenae* from France and southwest Spain. By contrast, *H. filipjevi* originating from Turkey does not show any diapause as the juveniles hatch immediately at the beginning of the winter wheat growing period (Sahin et *al*., 2009).

Second-stage juveniles of CCNs invade just behind the growing apex of the root tip (Von Mende et *al*., 1998) and then pass through cells towards the stele where they initiate the development of a cluster of multinucleate feeding cells called a syncytium (Baldwin et Mundo-Ocampo, 1991). The J2 then go through a moult to the third-stage (J3). The syncytium provides food for the development and maturation of the juveniles to adult stage. The strong sexual dimorphism develops after the fourth-stage (J4). The adult males become vermiform and leave the root (Sijmons et *al*., 1994), whereas the females swell into a white lemon-shaped body that protrudes out of the surface of the root. After mating, the females produce eggs that are kept within their bodies. When all eggs have formed, the female dies and becomes a cyst, detached from the root (Smiley et Nicol 2009).

SYMPTOMS

Aboveground symptoms caused by members of the *H. avenae* group include yellowing, poor tillering, stunting and patchy growth of the host plants. There may be a burning of the leaves, similar to that caused by drought conditions. This is due to the nematode interfering with the

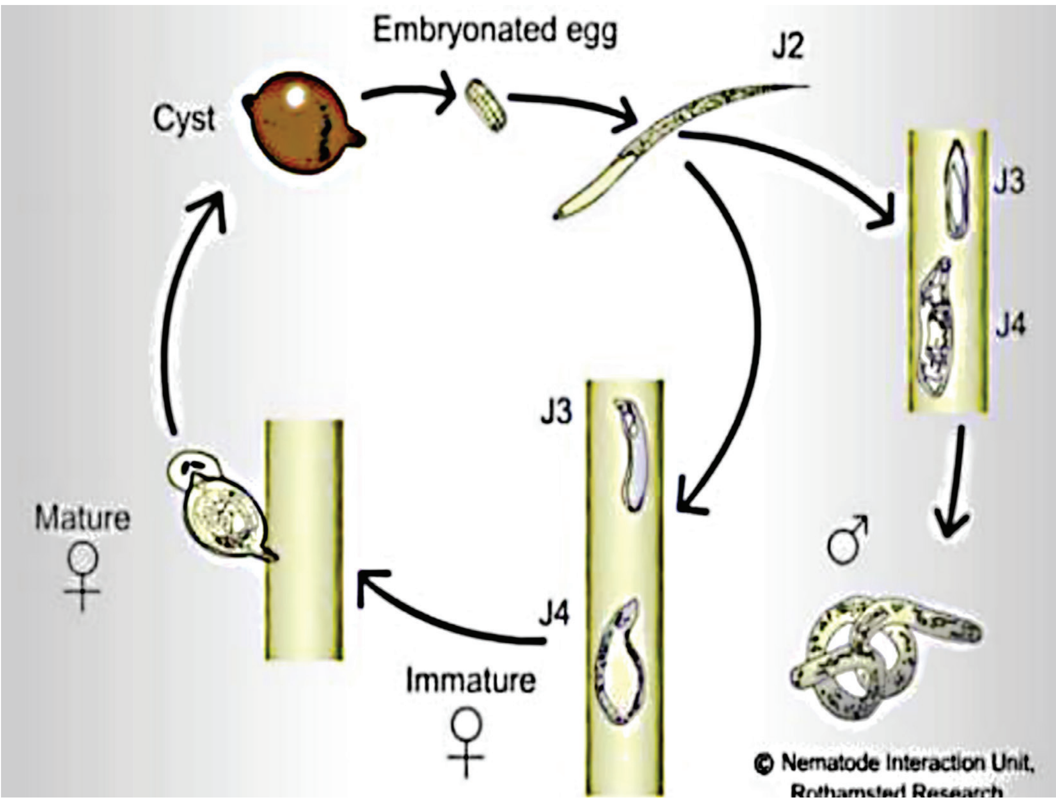

Figure 1: The life cycle of cereal cyst nematodes (Heterodera spp.) illustrating infective second-stage juveniles (J2) infecting roots and further stages of juveniles (J3 and J4) developing into adult females or males (Rothamsted Research)

metabolic balance of the plant and inhibiting hydrostatic water pressure, which results in wilting (Griffin, 1988). The symptoms caused by members of the *H. avenae* group on the roots are different depending 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 et Cook, 1993). While *H. avenae* is far more common than *H. filipjevi*, these two species have similar host ranges and cause similar symptoms and economic losses (Smiley, 2009). Root symptoms often do not become recognizable until one to three months after planting, depending on climatic conditions and spring or winter wheat growth habits (Smiley et Nicol, 2009). Root systems of wheat and barley plants infested with *H. avenae* include elongation of the main root, bunched tips of rootlets and a knotted appearance due to cysts. Infected oat roots appear 'ropery' and swollen (Smiley et Yan, 2010). Root symptoms of *H. latipons* are different from those seen with *H. avenae*, with no characteristic "knotting" caused by excessive production of lateral roots at the site of infection (Mor et *al*., 1992).

MAJOR METHODS OF CONTROL

Reducing yield loss caused by cereal cyst nematodes requires control of CCNs below the damage threshold or growing non-susceptible crops. This requires observations of population dynamics and yield losses on representative local cultivars under natural field conditions (Smiley et Nicol, 2009). Cultural practices based on rotations of non-hosts (non-cereals) and clean fallow can effectively control CCNs (Dababat et *al*., 2015). Singh et *al*. (2009) showed that *H. avenae* population densities decreased by 70% after rotation with non-host crops like carrot (*Daucus carota*), fenugreek (*Trigonella foenum-graecum*), and onion (*Allium cepa*), or by fallow and summer ploughing. Nematicides can be applied, but are not preferred by the farmers because of the high cost per unit area in wheat (Dababat et *al*., 2015). However, when the nematode population in the soil is high, and other management approaches are inadequate, chemical control can bring the *H. avenae* population below damage threshold levels (Hague et Gowen, 1987).

Chemical control of nematodes is often considered economically and environmentally unacceptable (Viaene et *al*., 2013), so development of microbial antagonists for CCNs might be one of the few remaining alternatives (Riley et *al*. 2010). A range of microorganisms has been investigated as potential biocontrol agents for CCNs including, *Pochonium chlamydosporium*, *Trichoderma longibrachiatum* and *Purpureocillium lilacinus* (Kerry et *al*., 1984; Zhang et *al*., 2014). Likewise, some bacteria have been shown to offer potential as biocontrol agents. A bacterium similar to *Pasteuria* spp. was able to parasitise*H. avenae* and was shown to prevent 38 to 56 % of the juveniles from invading roots (Davies et *al*., 1990). Bansal et *al*. (1999) showed that *Azotobacter chroococcum* reduced cyst formation by 48%. However, little information has been gathered on biological control of CCNs in recent years.

Soil solarization offers an alternative management method to control nematodes (Viaene et *al*., 2013). Al-Rehiayani and Belal (2009) showed that soil solarization using polyethylene sheets during hot summer months in Al-Qassim (Saudi Arabia) was effective in reducing populations of *H. avenae* in wheat.

The potential use of biofuigation derived from plants or organisms is an alternative non-chemical for controlling many plant-parasitic nematodes. For CCNs, there is no information about their control by this approach. Haroon et *al*. (2009) used some medicinal plants (root extracts) for controlling *Heterodera zeae* and they concluded that *Calendula officinalis, Ambrosia maritima* and *Origanum vulgare* significantly reduced the hatching of eggs and mortality of *H. zeae* compared to the control. In addition, several studies have demonstrated the potential of brassicaceous crops to control the potato cyst nematode *Globodera pallida* in potato production (Ngala et *al*., 2015).

One of the most economic, environmental and promising methods of managing CCNs is the use of resistant wheat germplasm (Dababat et *al*., 2015). Many sources of resistance in wheat germplasm have been reported (Smiley et Nicol, 2009). Resistance sources around the world were obtained from wild wheat relatives through breeding programme (Ogbonnaya *et al*., 2001). At least nine single dominant resistance genes (*Cre* genes) have been found, many of which derive from wild relatives of wheat (Dababat et *al*., 2015). Six *Cre* genes (*Cre*2 to *Cr*7) were derived from *Aegilops* spp. (Jahier et *al*., 2001); other resistance genes were derived from *T. aestivum* (*Cr1* and *Cr8*) and rye (*Secale cereale*) lines (*CreR*) (Barloy et *al*., 1996). Sources of resistance to *H. avenae* have been collated and reviewed and, where possible, have had their genetic location and gene designation reported (Table 2) (Rivoal et *al*., 2001; Nicol et *al*., 2003; Mc Donald et Nicol, 2005; Nicol et Rivoal, 2008; Vanstone et *al*., 2008).

Some sources of resistance currently used to control *H. avenae* in wheat and barley in Australia have been found to be effective against *H. latipons*. The Iraqi landrace AUS4930 is resistant to both *H. australis* (= Australian pathotype Ha13) and the Turkish *H. filipjevi* (pathotype HF1) (Nicol et Rivoal, 2000). However, the use of resistance requires a sound knowledge of the virulence spectrum of the targeted species. Several studies showed that the wheat cultivars resistant to populations of *H. avenae* in one region were fully susceptible to populations of the same species in other regions (Bonfil et *al*., 2004; Smiley et Nicol, 2009).

CONCLUSION

Accurate identification of the nematode species present in the field and knowledge of their population density are essential when designing effective control measures. As is common for other nematode species, CCNs are traditionally identified on the basis of their morphology and morphometrics. Unfortunately, this is time-consuming and hardly applicable when species-mixtures need to be identified and quantified. However, it was shown that DNA-based methods can be excellent tools complementing the traditional identification. Genetic resistance, biological agents, cultural practices, and chemical strategies can all be part of a management strategy, but each of them has its limitations. However, the use of resistant cereal lines or cultivars is considered the most economically feasible and environmentally sustainable method. Advances in research on CCNs in cereals are exchanged and discussed regularly during the meetings of the International Cereal Nematode Initiative (ICNI). The 6th ICNI meeting will take place in September 2017, Agadir, Morocco.

REFERENCES

Abidou H., Valette S., Gauthier G.P., Rivoal R., El-Ahmed A.,Yahyaoui, A. (2005). Molecular polymorphism and morphometrics of species of the *Heterodera avenae* group in Syria and Turkey. *J. Nematol.* 37: 146–154.

Al-Rehiayani S.M., Bellal, M. (2009). Effect of solarization on *Heterodera avenae* and wheat yield in Al-Qassim, Saudi Arabia. *Proceedings of the first Workshop of the International Cereal Cyst Nematode Initiative*, 21-23 October 2009, Antalya, Turkey, pp. 233–236.

Al-Yahya F.A., Alderfasi A.A., Al-Hazmi A.S., Ibrahim A.A.M, Abdul-Razig A.T. (1998). Effects of cereal cyst nematode on growth and physiological aspects of wheat and barley under field conditions. *Pak. J. Nematol.* 16: 55–62.

Andersen S., Andersen K. (1982). Suggestions for determination and terminology of pathotypes and genes for resistance in cyst-forming nematodes, especially *Heterodera avenae*. *EPPO Bulletin* 12: 379–386.

Table 2: Main sources of genes used in bread wheat (*Triticum aestivum*) for resistance to the cereal cyst nematode *Heterodera avenae* (after Smiley et Nicol, 2009)

Cereal species	Genotype	Resistance gene and location	Use in cultivars
T. aestivum	Loros, AUS10894	*Cre*1 (formerly Ccn1) on chromosome 2BL	NW Europe, Australia, NW USA
	Katyil	Con	Australia
	Festiguay	*Cre*8 (formerly CreF) on chromosome 7L or 6B	Australia
	AUS4930 = Iraq48	Possible identical genetic location as Cre1: also resistant to *P. thornei*	Under evaluation in Australia, France and CIMMYT
	Molineux	Chromosome 1B	Australia
	Raj MR1	One dominant gene	Released cv. in India
T. durum	Psathias 7654, 7655	Not known	Not known
Triticosecale	T701-4-6	*Cre*R on chromosome 6RL	Australia
	Drira	Not known	Australia
	Ningadhu		
	Tahara	Not known	Not known
	Salvo	Not known	UK
Secale cereale	R173 family	*Cre*R on chromosome 6RL	Australia
Aegilops tauschii	CPI 110813	*Cre*4 on chromosome 2DL	Australian synthetic hexaploid lines
	AUS 18913	*Cre*3 on chromosome 2DL	Australian advanced breeding lines
A. peregrine	1	*Cre* (3S) with Rkn2 on chromosome 3S, CRX not yet located	Not known
A. longissima	18	Not known	France
A. geniculate	79, MZ1, MZ61, MZ77, MZ124	Not known	France
A. triuancialis	TR-353	*Cre*7 (formerly *Cre*A et)	France
A. ventricosa	VPM 1	*Cre*5 (formerly *Cre*X) on chromosome 2AS	Spain
		*Cre*2 (formerly *Cre*X) on genome N	

Anonymous (2014). Ofice National Interprofessionnel des Céréales et des Légumineuses (www.onicl.org.ma).

Balaghi R., Jliben, M., Tychron B., Eerecus H. (2013). *Agro-meteorological yield forecasting in Morocco*. Rabat, Morocco, INRA, pp. 132.Publisher: Institut National de la Recherche Agronomique du Maroc, Editor: Institut National de la Recherche Agronomique du Maroc, ISBN: 978 - 9954 - 0 - 6683 – 6.

Baldwin J.G., Mundo-Ocampo M. (1991). Heteroderinae, cyst and non-cyst-forming nematodes.In W.R. Nickle (Ed.) *Manual of agricultural nematology*. New York: Marcel Dekker.pp. 275–362.

Bansal R.K., Dahiya R.S., Lakshminarayana K., Suneja S., Anand R.C., Narula N. (1999). Effect of rhizospheric bacteria on plant growth of wheat infected with *Heterodera avenae*. *Nematologia Mediterranea* 27: 311–314

Barloy D., Martin J., Rivoal R., Jahier J. (1996). Genetic and molecular characterization of lines of wheat resistant to cereal cyst nematode *Heterodera avenae*. *Nematropica* 26: 240.

Benabdelouahab T., Balaghi R., Hadria R., Lionboui H., Djaby B., Tychon B. (2016). Testing aquacrop to stimulate durum wheat yield and schedule irrigation in a semi-arid irrigated perimeter in Morocco. *Irrigation and Drainage* 65: 631–643.

Bonfil D.J., Dolgin B., Mufradi I., Asido S. (2004). Bioassay to forecast cereal cyst nematode damage to wheat in fields.*Precis Agriculture* 5: 329–344.

Brown R.A. (1981). Nematode diseases. In: *Economic importance and biology of cereal root diseases in Australia*. Report to Plant Pathology Subcommittee of Standing Committee on Agriculture.

Brown R.H. (1984). Ecology and control of cereal cyst nematode (*Heterodera avenae*) in Southern Australia.*J. Nematol.*16: 216–222.

Cook R., Noel G.R. (2002). Cyst nematodes: *Globodera* and *Heterodera* species. In: Starr, J.L., Cook, R. et Bridge, J. (Eds). *Plant resistance to parasitic nematodes*. Wallingford, UK, CABI Publishing, pp. 71–105.

Dababat AA, Imren M, Gul Erginbas O, Ashrafi S, Yavuzaslanoglu E, Toktay T, Pariyar SH, Elekcioglu H, Morgounov A, Mekete T. (2015). The importance and management strategies of cereal cyst nematodes, *Heterodera* spp., in Turkey. *Euphytica.* 202: 173–188.

Davies K.G., Flynn C.A., Laird V., Kerry B.R. (1990). The life-cycle, population dynamics and host specificity of a parasite of *Heterodera avenae*, similar to *Pasteuria penetrans*. *Revue Nématologie* 13: 303–309.

Ferris V.R., Ferris J.M., Faghini J., Ireholm A. (1994). Comparisons of isolates of *Heterodera avenae* using 2-D PAGE protein patterns and ribosomal DNA. *J.Nematol.* 26: 144–151.

Greco N. (1994). Survey on nematodes of barley in Syria, *Preliminary research report submitted to ICARDA*, Aleppo, Syria.

Griffin G.D. (1982). Differences in the response of certain weed host populations to *Heterodera schachtii*. *J. Nematol.* 14: 174–182.

Hague N.G.M., Gowen S.R. (1987). Chemical control of nematodes. In: Brown, R.H. et Kerry, B.R. (Eds). *Principles and Practice of Nematode Control in Crops*. Academic Press, Australia, pp. 131–178.

Hajihasani A., Tanha Maafi Z., Hajihasani M. (2010). The life cycle of *Heterodera filipjevi* in winter wheat under microplot conditions in Iran.*Nematologica Mediterranea* 38: 53–57.

Holgado R., Skau K.A.O., Magnusson C. (2009). Field damage in potato by lesion nematode *Pratylenchus penetrans,* its association with tuber symptoms and its survival in storage.*Nematologia Mediterranea* 37: 25–29.

Haroon S.A., Ezzat O., Reham M. (2009). The effect of root exudates from certain Egyptian medicinal plants on the cyst nematode, *Heterodera zeae. Proceedings of the first Workshop of the International Cereal Cyst Nematode Initiative*, 21-23 October 2009, Antalya, Turkey, pp. 227–232.

Hossain A., Teixeira Da Silva J.A. (2012).Phenology, growth and yield of three wheat (*Triticum aestivum* L.) varieties as affected by high temperature stress. *Not.Sci. Biol.* 4: 97–109.

Ibrahimi A.A., Al-Hazmi A.S., Al-Yahya F.A, Alderfasi A.A. (1999). Damage potential and reproduction of *Heterodera avenae* on wheat and barley under Saudi field conditions. *Nematology* 6: 625–630.

Kerry B.R., Simon A., Rovira A.D. (1984). Observations on the introduction of *Verticillium chlamydosporium* and other parasitic fungi into soil for control of the cereal cyst nematode *Heterodera avenae.Ann. Appl. Biol.* 105: 509–516.

Khan R., Agarwal V., Mathur B.N. (1990). Chemical control of simultaneous cereal cyst nematode and termite infestations in wheat in Rajasthan, India, *RACHIS (ICARDA) Barley and Wheat Newsletter* 9: 9–11.

Lambardo S., Handoo Z., Rapisarda C., Colombo A. (2009). Occurrence and distribution of cyst nematodes infecting cereals in Sicily, Italy. *Proceedings of the first Workshop of the International Cereal Cyst Nematode Initiative*, 21-23 October 2009, Antalya, Turkey, pp. 61–65.

McDonald, A.H., Nicol, J.M. (2005).Nematode parasites of cereals. In: Luc, M, Sikora, RAet Bridge, J. (Eds). *Plant parasitic nematodes in subtropical and tropical agriculture*. CABI Publishing, Wallingford, pp. 131–191.

Meagher J.W. (1972). Cereal cyst nematode (*Heterodera avenae* Woll.).Studies on ecology and control in Victoria.*Technical Bulletin* 24, Dep. Agric. Vict. 50 pp.

Meskine M., Janati A., Abbad Andaloussi F. (1984). Résultats préliminaires de l'étude sur les nématodes phytophages associés aux cultures de blé et orge. *Journées nationales de phytiatrie. Rabat*, 28–30.

Miller L.I. (1986). Economic importance of cyst nematodes in North America. In: Lamberti, F. et Taylor, C.E. (Eds). *Cyst nematodes*. New York, USA, Plenum Press.pp. 373–385.

Mokrini F., Abbad Andaloussi F., Alaoui Y., Troccoli A. (2009). Importance and distribution of the main cereal nematodes in Morocco. *Proceedings of the first Workshop of the International Cereal Cyst Nematode Initiative*, 21-23 October 2009, Antalya, Turkey, pp. 45–50.

Mokrini F., Waeyenberge L., Viaene N., Moens, M. (2012). Occurrence of nematodes of the *Heterodera avenae* group and *Pratylenchus* spp. on wheat and barley in Morocco. *31st International Symposium of the European Society of Nematologists*, 23-27 September 2012, Adana, Turkey, 107 [Abstr.].

Mor M., Cohn E., Spiegel Y. (1992). Phenology, pathogenicity and pathotypes of cereal cyst nematodes, *Heterodera avenae* and *H. latipons* (Nematoda: Heteroderidae) in Israel. *Nematologica* 38: 494–501.

Ngala B.M., Haydock P.P.J., Woods S., Back, M.A. (2015). Biofumigation with *Brassica juncea, Raphanus sativus* and *Eruca sativa* for the management of field populations of the potato cyst nematode *Globodera pallida*. *Pest ManagSci.* 71: 759–769.

Nicol J., Rivoal R., Taylor S., Zaharieva M. (2003). Global importance of cyst (*Heterodera* spp.) and lesion nematodes (*Pratylenchus* spp.) on cereals: Distribution, yield loss, use of host resistance and integration of molecular tools. In: Cook, R.et Hunt, D.J. (Eds). *Proceedings of the Fourth International Congress of Nematology,* 8-13 June 2002, Tenerife, Spain.*Nematology Monographs and Perspectives 2*. Leiden, The Netherlands, Brill, pp. 1–19.

Nicol J.M, Bolat N., Sahin E., Tülek A., Yıldırım A.F., Yorgancılar A., Kaplan A., Braun H.J. (2006) The cereal cyst nematode is causing economic damage on rainfed wheat production systems of Turkey. *Phytopathology* 96: 169 (Supplement).

Nicol J.M, Rivoal R. (2000). Development of AUS4930 - A source of resistance against root lesion nematode and the cereal cyst nematode (CCN) complex for global breeding. In: *Proceedings of the Second Australasian Soilborne Diseases Symposium, Lorne, Victoria, 5-8 March, 2001.* Victoria, Australia.pp. 67–68.

Nicol J.M., Rivoal R. (2008). Global knowledge and its application for the integrated control and management of nematodes on wheat. In: Ciancio, A. et Mukerji, K.G. (Eds). *Integrated management and biocontrol of vegetable and grain crops nematodes, Vol. 2.* Dordrecht, The Netherlands, Springer, pp. 243–287.

Nicol J.M., Turner S.J., Coyne D.L., Nijs L.D., Hockland S., Maafi Z.T. (2011). Current nematode threats to world agriculture. In: Jones, J., Gheysen, G. et Fennol, C. (Eds). *Genomics and molecular genetics of plant-nematode interactions.* Dordrecht, The Netherlands, Springer, pp. 21–43.

Ogbonnaya F.C., Seah S., Delibes A., Jahier J., Lopez-Brana I., Eastwood R.F. et Lagudah E.S. (2001). Molecular-genetic characterisation of a new nematode resistance gene in wheat. *Theor. Appl.Genet.* 102: 623–629.

Peng D.L., Nicol J., Li H.M., Hou S.G., Li H.X., Chen S.L., Ma P., Li H.L., Riley I.T. (2009). Current knowledge of cereal cyst nematode (*Heterodera avenae*) on wheat in China. In: Riley, I.T., Nicol, J.M. et Dababat,A.A.(Eds). *Cereal Cyst Nematodes: Status, Research and Outlook*. Ankara, Turkey, CIMMYT. pp. 29-34.

Philis I. (1988). Occurrence of *Heterodera latipons* on barley in Cyprus. *Nematologia Mediterranea* 16: 223.

Rammah A. (1994). Cereal cyst nematode (*Heterodera avenae*) in Morocco. Fifth Arab Congress of Plant Protection, Fez, Morocco, 27th Novembre- 2nd December. pp.199.

Riley I.T., McKay A.C. (2009). Cereal cyst nematode in Australia: biography of a biological invader. In: Riley, I.T., Nicol, J.M. et Dababat, A.A. (Eds.). *Cereal cyst nematodes: status, research and outlook*. CIMMYT, Ankara, Turkey. pp. 23–28.

Riley I.T., Hou S.Y., Chen S.L. (2010). Crop rotational and spatial determinants of variation in *Heterodera avenae* (cereal cyst nematode) population density at village scale in spring cereals grown at high altitude on the Tibetan plateau, Qinghai, China. *Australas. Plant Pathol.* 39: 424–430.

Rivoal R., Cook R. (1993). Nematode pests of cereals. In: Evans, K., Trudgill, D.L. et Webster, J.M. (Eds). *Plant parasitic nematodes in temperate agriculture*. Wallingford, UK, CABI Publishing, pp. 259–303.

Rivoal R. (1986). Biology of *Heterodera avenae* Wollenweber in France. IV. Comparative study of the hatching cycles of two ecotypes after their transfer to different climatic conditions. *Revue de Nématologie* 9: 405–410.

Rivoal R., Bekal S., Valette S., Gauthier J.P., BelHadjFradj M., Mokabli A., Jahier J., Nicol J.M.,Yahyaoui A. (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.

Rumpenhorst H.J., Elekçioğlu I.H., Sturhan D., Öztürk G., Eneli S. (1996).The cereal cyst nematode *Heterodera filipjevi* (Madzhidov) in Turkey. *Nematologia Mediterranea* 24:135–138.

Sahin E., Nicol J.M., Elekcioglu H., Rivoal R. (2009). Hatching of *Heterodera filipjevi* in controlled and natural temperature conditions in Turkey. *Nematology* 12: 277–287.

Saxena M.C. Sikora R.A., Srivastava J.P. (1988). *Nematodes parasitic to cereals and legumes in temperate semi-arid regions*. *Proceedings of a workshop held at Larnaca, Cyprus, 1-5 March 1987. pp. 217. ICARDA, Aleppo, Syria.*

Sewell R., (1973). Plant-parasitic nematodes from Canada and abroad, 1971. *Can. Plant Dis. Surv.* 53: 34–35.

Sharma S.K., Siddiqui A.U., Parihar A. (2009). Studies on morphometric variation within the population of *Heterodera Zeae* on cereals in India.*Proceedings of the first Workshop of the International Cereal Cyst Nematode Initiative*, 21-23 October 2009, Antalya, Turkey, pp. 73-78.

Sijmons P.C., Atkinson H.J., Wyss U. (1994). Parasitic strategies of root nematodes and associated host cell responses. *Annu. Rev. Phytopathol.* 32: 235–259.

Singh A.K., Sharma A.K., Shoran J. (2009). *Heterodera avenae* and its management on wheat in India. In: Riley, I.T., Nicol, J.M. et Dadabat,A.A. (Eds).*Cereal cyst nematodes: status, research and outlook,*CIMMYT: Ankara, Turkey. pp 149–153.

Sikora R.A. (1988). Plant parasitic nematodes of wheat and barley in temperate and temperate semi-arid regions - a comparative analysis. In:Saxena, M.C., Sikora, R.A. et Srivastava, J.P. (Eds). *Nematodes parasitic to cereals and legumes in temperate semi-arid regions*. Aleppo, Syria, ICARDA.pp. 46-48.

Smiley R.W., Yan G.P., Handoo Z.A. (2008). First record of the cereal cyst nematode *Heterodera filipjevi* in Oregon. *Plant Dis.* 92: 1136.

Smiley R.W, Nicol J.N. (2009). Nematodes which challenge global wheat production. In: Carver, B.F. (Ed.) *Wheat Science and Trade*. Ames, IA, WileyBlackwell. pp. 171–187.

Smiley R.W., Yan G.P. (2010).Cereal cyst nemaotdes. Biology and management in Pacific Northwest wheat, barley, and oat crops. Pacific Northwest Extension Bulletin 620.

Subbotin S.A. Rumpenhorst H.J., Sturhan D. (1996). Morphological and electrophoretic studies on populations of the *Heterodera avenae* complex from the former USSR. *Russ. J. Nematol.* 4: 29-39.

Subbotin S.A., Waeyenberge L., Molokanova I.A., Moens M. (1999). Identification of *Heterodera avenae* group species by morphometrics and rDNA-RFLPs. *Nematology* 1: 195–207.

Subbotin S.A., Sturhan D., Rumpenhorst H.J,Moens M. (2003). Molecular and morphological characterization of the *Heterodera avenae* species complex (Tylenchida: Heteroderidae). *Nematology* 5: 515–538.

Subbotin S.A., Mundo-Ocampo M., Baldwin J.G. (2010). Systematics of cyst nematodes (Nematode: Heteroderinae). In: Hunt, D.J. et Perry, R.N. (Eds). *Nematology monographs and Perspectives* 8A. Leiden, The Netherlands, Brill.

Talatchian P., Akhiani A., Grayeli Z., Shah-Mohammadi M.,Teimouri F. (1976). Survey on cyst forming nematodes in Iran in 1975 and their importance. *Iran. J. Plant Pathol*. 12: 42–43

Toktay H., İmren M., Öcal A., Waeyenberge L., Viaene N., Dababat A.A. (2015). Incidence of cereal cyst nematodes in the East Anatolia Region in Turkey.*Russ. J. Nematol.* 23: 29–40.

Toumi F., Waeyenberge L., Viaene N., Dababat A., Nicol J.N., Ogbonnaya F., Moens M. (2013a). Development of two species-specific primer sets to detect the cereal cyst nematodes *Heterodera avenae* and *H. filipjevi*. *Eur. J. Plant. Pathol.* 136: 613–624.

Toumi F, Waeyenberge L, Viaene N, Dababat A, Nicol JN, Ogbonnaya F, Moens M. (2013b).Development of a species-specific PCR to detect the cereal cyst nematode, *Heterodera latipons*. *Nematology.*15: 709–717.

Triantaphyllou A.C. (1987). Genetics of nematode parasitism of plants. In: Veech, A. et Dickson, D.W. (Eds). *Vistas on nematology*. Hyattsville, MD, USA, Society of Nematologists, pp. 354–371.

Trudgill D.L. (1986). Yield losses caused by potato cyst nematodes: A review of the current position in Britain and prospects for improvements. *Ann. Appl. Biol.* 108: 181–198.

Vanstone V.A., Hollaway G.J., Stirling G.R. (2008) Managing nematode pests in the southern and western regions of the Australian cereal industry: continuing progress in a challenging environment. *Australas. Plant Pathol.* 37: 220-234.

Viaene N., Coyne, D. L., Davies K. G. (2013). Biological and cultural management. In: Perry, R.N. et Moens, M. (Eds.). *Plant Nematology*, 2nd ed. Wallingford, CABI Publishing, pp. 383 – 410.

Von Mende N., GravotoNobre M.J., Perry R.N. (1998). Host finding invasion and feeding In:Sharma, S.B. (Ed.). *The cyst nematodes* London, UK, Kluwer Academic Publishers. pp .1–30.

Waeyenberge L., Viaene N. (2015). Molecular identification of cereal cyst nematodes: status, prospects and recommendations. In:Dababat, A.A., Muminjanov, H et Smiley, R.W. (Eds). *Nematodes of Small Grain Cereals: current status and research.* FAO, Ankara, Turkey. pp. 239–250.

Yan G.P., Smiley R.W. (2010). Distinguishing *Heterodera filipjevi* and *H. avenae* using polymerase chain reaction-restriction fragment length polymorphism and cyst morphology, *Nematology* 100: 216–224.

Yan G.P., Smiley R.W., Okubara P.A., Skantar A.M. (2013). Species-specific PCR assays for differentiating *H. filipjevi* and *H. avenae*. *Plant Dis.* 97: 1611–1619.

Zhang S.W., Gan Y.T., Xu B.L. (2014). Efficacy of *Trichoderma longibrachiatum* in the control of *Heterodera avenae.BioControl* 59: 319–333.

Znasni Y. (2003). Caractérisation de certaines populations marocaines des nématodes à kystes des céréales *Heterodera avenae.* Mémoire de fin d'étude à l'Institut Agronomique et Vétérinaire, Hassan II de Rabat, pp. 25–31.