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REVIEW

The importance and management strategies of cereal cyst nematodes, *Heterodera* spp., in Turkey

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Abstract Cereal cyst nematodes (CCNs) can cause significant economic yield losses alone or in combination with other biotic and abiotic factors. The damage caused by these nematodes can be enormous when they occur in a disease complex, particularly in areas subject to water stress. Of the 12 valid CCN species, *Heterodera avenae*, *H. filipjevi,* and *H. latipons* are considered the most economically important in different parts of the world. This paper reviews current approaches to managing CCNs via genetic resistance, biological agents, cultural practices, and chemical strategies. Recent research within the soil borne pathogen program of the International Maize and Wheat Improvement Center has focused on germplasm screening, the potential of this germplasm as sources of resistance, and how to incorporate new sources of resistance into breeding programs. Breeding for resistance is particularly complicated and difficult when different species and pathotypes coexist in nature. A lack of expertise and recognition of CCNs as a factor limiting wheat production potential, combined with inappropriate breeding strategies and slow screening processes limit genetic gains for resistance to CCNs.

Keywords Cereal cyst nematodes · *Cre* genes · Integrated pest management · Resistance · Wheat

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The importance of wheat and associated cereal cyst nematodes in Turkey

Wheat (*Triticum aestivum* L.) is the staple diet for approximately two billion people worldwide and provides almost 55 % of the carbohydrates and 20 % of the food calories consumed globally (Breiman and Graur 1995). It exceeds every other grain crop (including rice and maize) in terms of acreage and production and is therefore considered the world's most important cereal grain crop cultivated over a wide range of climatic conditions. According to genetic and archaeological studies, the origins of modern day wheat were found in the Karacadag mountain region of what is today southeastern Turkey. There, some 12,000 years ago, both Einkorn and Emmer wheat were domesticated (Nesbit and Samuel 1998; Ozkan et al. 2005).

Turkey is currently the tenth largest wheat producer in the world with a gross production of 22.1 million tons over 7.77 million ha in 2013 (http://faostat.fao.org). Its primary wheat-producing areas are the Central Anatolian Plateau (CAP), Thrace region, and South East Anatolia (SEA). Of these, CAP is the main winter wheat production area with 10 million ha of cultivated land. In this region, wheat is produced under rainfed conditions with average yields of less than 2 t/ha (Benli et al. 2007). The Thrace region is the European part of Turkey and produces winter wheat under high rainfall conditions and intensive cropping systems in rotation with sunflower. SEA is the primary area for spring wheat cultivation with 3 million tons produced annually (Anonymous 2013).

Cereal cyst nematodes (*Heterodera avenae* complex, avenae group; CCNs) are found worldwide and cause significant economic yield losses in many countries, particularly in those where rainfed cereal systems predominate (Nicol et al. 2003). CCNs can have synergistic negative effects in combination with other biotic and abiotic factors, such as water stress and fungal pathogens (Nicol et al. 2004, 2006). Nicol (2002) reported yield losses of 15–20 % in Pakistan, 40–90 % in Saudi Arabia, 23–50 % in Australia, and 24 % in the USA due to CCNs, and Whitehead (1998) estimated that 10 % of cereal production worldwide is lost due to plant-feeding nematodes. Barker et al. (1998) reported that damage that caused by CCNs (mainly *H. avenae*) resulted in losses of about $78 billion around the globe. Based on their worldwide distribution, predominance in areas where cereal is grown, and their pathogenicity, CCNs are ranked as major pests affecting the world's food supply.

Species of CCN

The CCN group consists of 12 valid species, with *H. avenae*, *H. filipjevi,* and *H. latipons* considered the most economically important species in West Asia, North Africa, and the Mediterranean (Nicol et al. 2011). These three species also constitute a major limiting biotic factor to cereal production in temperate rainfed growing regions including China, India, Turkey, Australia, the United States, and many countries in Europe (Rivoal and Cook 1993; Dixon et al. 2009).

In Turkey, *H. avenae* was the first CCN reported from Erzurum, East Anatolia (Yüksel 1973). Later on, *H. avenae* was reported as widely distributed in the Eastern Mediterranean (Gözel 2001; Subbotin et al. 2003; Imren et al. 2012, 2013a) as well as in the Thrace and Aegean regions (Mısırlıoğlu and Pehlivan 2007). *H. filipjevi* and *H. latipons* are present in the CAP region; of these, *H. filipjevi* is the most dominant and was reported in 87 % of surveyed fields (Rumpenhorst et al. 1996; Oztürk et al. 1998; Abidou et al. 2005; Yavuzaslanoglu et al. 2012). Generally, *H. latipons* and *H. avenae* occur in mixed populations across most wheat growing areas of the SEA and Eastern Mediterranean regions (Kilic 2011; Kilic et al. 2012; Imren et al. 2012; Ocal 2012).

Imren and Elekcioglu (2014) conducted a study in the Turkey's Mediterranean region to estimate yield losses caused by *H. avenae* under naturally infested field conditions. Losses due to *H. avenae* reached up to 24 and 25.7 % in the 2011–2012 and 2012–2013 growing seasons, respectively (Table 1), and nematodes were present in 52 % of the survey samples.

A fundamental strategy in validating sources of resistance within wheat breeding programs is the identification of CCNs to the species level, combined with pathotype determination, as the resistant cultivar can react in various ways depending on the CCN species and/or pathotype. Identification of the CCN by morphological and morphometric methods is time consuming and inaccurate, especially when more than one species exist in the same field. More recent studies have therefore attempted to use molecular tools for developing species-specific primer sets to detect

Table 1 Yield losses caused by *Heterodera avenae* in spring wheat varieties cultivated in the Mediterranean Region of Turkey under field conditions in the 2011–2012 and 2012–2013 growing seasons (Imren and Elekcioglu 2014)

Wheat cultivar	2011–2012 growing season			2012–2013 growing season		
	Treated[a] (kg/ha)	Non-treated (kg/ha)	% yield loss	Treated (kg/ha)	Non-treated (kg/ha)	% yield loss
Silverstar	3,070 ± 8.1	2,640 ± 10.4	13.8*	5,900 ± 6.1	4,980 ± 4.2	15.5*
Seri-82	3,220 ± 9.4	2,440 ± 12.7	24.0*	4,410 ± 3.4	3,280 ± 8.6	25.7*
Ceyhan 99	3,340 ± 10.1	3,150 ± 9.7	5.8	5,330 ± 2	4,740 ± 6.3	11.0*
Osmaniyem	3,070 ± 7.30	2,530 ± 10.6	17.4*	4,840 ± 7.3	3,600 ± 7.6	25.6*
Karatopak	3,220 ± 9.0	2,520 ± 9.6	21.9*	3,630 ± 5.6	3,220 ± 6.1	11.3*
Adana 99	3,270 ± 9.9	3,120 ± 12.5	4.68	6,880 ± 5.2	6,240 ± 4.4	9.3*

* Means in treated and non-treated data are different from each other at ($P < 0.05$)

[a] Aldicarb (Temik 15 G) was applied as a nematicide with 4.2 kg a.i./ha dose mixed with wheat seeds just before sowing

Table 2 List of the most promising lines/varieties of winter wheat types screened against *Heterodera filipjevi* and distributed to international collaborators in 2012 (Soil Borne Pathogens Program-CIMMYT, unpublished data)

Cross name	TK ACC	CID	OC	*H. filipjevi*
ANARA			Kazakhstan	R
GA951079-3-5/Neuse	110502	ARS07-0419	USA-North Carolina	R
TARM (ANKARA-98)			Turkey	R
MV17/3/Azd/VEE//SERI82/RSH/4/FLN/ACC//ANA/3/PEW/5/RSK/CA8055//CHAM6	110457	1-C-17476	Iran-Karadj	R
MIRZABEY2000			Turkey	R
PATWIN	100893		USA	R
KERN(YR15;GPC;2NS)	100885		USA	R
SONMEZ			Turkey	R
CLEAR WHITE	100888		USA	R
KATYA	950590		Bulgaria	R
PFAU/MILAN//FUNG MAI 24	100981	CMSA01 M00330S	Mexico	R
AK702			Turkey	R
P8-6			Turkey	R
TOSUNBEY	040580		Turkey	R

TK ACC Turkish accession number, *CID* cross identification, *OC* Origin country

individual CCN species (Yan and Smiley 2010; Toumi et al. 2013a, b).

Since 2001, CIMMYT has collaborated with the Turkish Ministry of Food, Agriculture and Livestock to establish a soil borne pathogen program that tackles wheat root diseases caused by CCNs and the dry land root rot disease caused by *Fusarium culmorum*. The program aims to identify the predominant pathogens, as well as their distribution, economic importance, and sources of plant resistance. Based on studies conducted by the program, *H. filipjevi* was identified as a major pest for winter wheat in the CAP region, whereas *H. avenae* and *H. latipons* were identified as priorities in areas where spring wheat is dominant. The soil borne pathogen program thus worked to evaluate wheat resistance to *H. filipjevi*. The resistant germplasm resulting from this work is now distributed to breeding programs worldwide (Table 2, unpublished data).

Cereal cyst nematode management strategies

The challenges of reducing the damage caused by CCNs are compounded by the failure of experts to recognize CCNs as a major factor limiting cereal production. The effect of CCNs on wheat yield has not been well documented, especially in developing countries, thus contributing to a lack of specialists and understanding of the importance of CCNs (Smiley and Nicol 2009). Furthermore, the number of species and pathotype variations—combined with inappropriate breeding strategies and slow screening methods for genetic crop resistance (Rathjen et al. 1998)—create further challenges for effectively managing CCNs.

CCNs can be controlled by reducing the population below the economic threshold level for damage. This requires definitive studies of 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 CCNs. However, these management strategies each require a full understanding of the virulence and diapause characteristics for the local nematode population, and of the effectiveness and durability of the resistance gene(s) deployed against the given nematode population. The best way to control CCNs is via a concentrated and integrated approach, and there are many examples where the use of crop rotations, resistant cultivars, and chemical control measures have successfully managed CCNs. Integrated management—based primarily on genetic host resistance—seems to be most effective when two or more soil borne pathogens occur in the soil at same time (Nicol and Rivoal 2007).

Genetic resistance

Host-plant resistance, i.e. the ability of the host to inhibit nematode multiplication (Cook and Evans 1987), is one of the most effective methods of managing CCNs as it is environmentally sustainable and requires no additional equipment or cost. However, farmers will only use resistant cultivars if they are comparable to other commonly cultivated wheat cultivars in terms of yield performance. The continuous cultivation of wheat varieties with tolerance to CCNs can increase the nematode population and have adverse effects on the successive crop, particularly if it is a susceptible variety. Tolerance which is defined as the ability of a plant to yield well despite being attacked by nematodes (Rivoal and Nicol 2009), can be overcome with high initial nematode population (Rathjen et al. 1998). The use of host-plant resistance requires a sound knowledge of the virulence spectrum of the target species and pathotypes. Wheat cultivars resistant to *H. avenae* in one region may be fully susceptible in other regions, as demonstrated by Imren et al. (2013b) for landrace and national cultivars evaluated in Turkey. Furthermore, repeated plantings of wheat, barley, and oat cultivars with a single *H. avenae* resistance gene led to the emergence of new virulent pathotypes that have overcome the host-plant resistance (Lasserre et al. 1996; Cook and Noel 2002).

Sources of resistance to *H. avenae* populations worldwide have been collated, reviewed, and their gene designation reported (Rivoal et al. 2001; Nicol 2002; Nicol et al. 2003; McDonald and Nicol 2005; Nicol and Rivoal 2007; Table 3). To date, all these genes feature single-gene inheritance between the host plant resistance gene and the corresponding virulence genes in the pathogen and are used to successfully control *H. avenae* in countries such as Australia, France, India, and Sweden (Rathjen et al. 1998; Nicol et al. 2009). At least nine single dominant genes ("*Cre* genes") have been found, many of which derive from wild relatives of wheat. Six *Cre* genes (*Cre2* to *Cre7*) were derived from *Aegilops* spp. (Jahier et al. 2001); other resistance genes were derived from *Triticum aestivum* (*Cre1* and *Cre8*) and *Secale cereale* (*CreR*) (Slootmaker et al. 1974; Asiedu et al. 1990). Two other sources of resistance (*CreX* and *CreY*) have also been reported (Delibes et al. 1993) but their genetic control and gene designation are still unknown. Most of these resistance genes have been introgressed into hexaploid wheat.

The broad specificity of *Cre1* makes it the gene used most widely, and it has been bred into commercial cultivars grown in Australia and Europe. It is highly effective against populations of *H. avenae* from Europe, North Africa, and North America, but only moderately effective or ineffective against 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, as compared to *H. avenae* (Mokabli et al. 2002). In Turkey, the *Cre1* gene appears effective against *H. filipjevi*, but *Cre3* is not (Akar et al. 2009; Nicol et al. 2009; İmren et al. 2013b). The *Cre3* gene is effective against *H. avenae* in Australia (Vanstone et al. 2008), but not in Europe (Majnik et al. 2003;

Table 3 Principal sources of the genes used to breed wheat for resistance to cereal cyst nematodes

Genotype	Line	Gene	Literature
Triticum aestivum	Loros, AUS10894	*Cre1*	Slootmaker et al. (1974), Bekal et al. (1998)
	Festiguay	*Cre8*	Paull et al. (1998)
	AUS4930	*Cre1*	Bekal et al. (1998), Nicol et al. (2001)
T. durum	Psathias, 7654, 7655,	Unknown	Rivoal et al. (1986)
	Sansome, Khapli	Unknown	
Tritico secale	T701-4-6	*Cre R*	Dundas et al. (2001), Asiedu et al. (1990)
Secale cereale	R173 family	*Cre R*	Taylor et al. (1998)
Aegilops tauschii	CPI 110813	*Cre4*	Eastwood et al. (1994), Rivoal et al. (2001)
Aegilops variabilis		*Cre X, Cre Y*	Barloy et al. (2007)
Ae. Tauschii	AUS18913	*Cre3*	Eastwood et al. (1991, 1994), Rivoal et al. (2001)
Ae. Peregrine (Ae. variabilis)	1	*Cre (3S), Rkn2*	Barloy et al. (1996), Jahier et al. (1998), Rivoal et al. (2001)
Ae. Longissima	18	Unknown	Bekal et al. (1998)
Ae. Geniculata	79, MZ1, MZ61, MZ77, MZ124	Unknown	Bekal et al. (1998), Zaharieva et al. (2001)
Ae. Triuncialis	TR-353	*Cre7*	Romero et al. (1998)
Ae. Ventricosa	VPM1	*Cre5*	Jahier et al. (2001), Ogbonnaya et al. (2001)
	11, AP-1, H-93-8	*Cre2*	Delibes et al. (1993), Andres et al. (2001), Rivoal et al. (2001)
	11, AP-1, H-93-8, H-93-35	*Cre6*	Ogbonnaya et al. (2001), Rivoal et al. (2001)

Safari et al. 2005). The *Cre2* and *Cre4* resistance genes from *Aegilops*, and an unidentified resistance gene from wheat line AUS4930, offer promising sources of resistance against an array of CCN species and pathotypes (Nicol et al. 2001). Several lines containing *Cre5* were tested by Dababat et al. (2014a) and did not successfully confer resistance to CCNs. Imren et al. (2013b) used six *Cre* genes in international bread wheat germplasm to identify genetic resistance to *H. avenae*, *H. filipjevi,* and *H. latipons*. The results indicated that the resistant genes *Cre1*, *Cre3*, and *Cre7* provided resistance against both *H. avenae* and *H. latipons*. The other genes, *Cre8* and *CreR,* provided resistance against *H. filipjevi* only. None of the *Cre* genes studied provided complete resistance to the three CCN species.

Several CIMMYT synthetic wheat derivatives (e.g. CROC_1/AE. SQUARROSA (224)//OPATA) have been classified for their resistance to soil borne pathogens, including CCNs and the root lesion nematode *P. thornei* (Nicol et al. 2009; Mulki et al. 2013). In India, varieties Raj MR 1, CCNRV2, and CCNRV4 showed potential resistance to *H. avenae* (Bishnoi 2009), while in Australia, ten wheat cultivars including Meering, Festiguay, Molineux, Frame, Chara, and Annuello showed moderate resistance to *H. avenae* (Lewis et al. 2009). Sources of resistance to *H. filipjevi* have also recently been identified and preliminary research indicates heterogeneous responses between populations to different resistant genotypes (Nicol and Rivoal 2008).

The soil borne pathogen program annually screens about 1,000 accessions from the Turkey-CIMMYT-ICARDA International Winter Wheat Improvement Program (www.iwwip.org) under growth room, greenhouse, and field conditions at various locations in Turkey. Accessions with the most promising resistance are further tested for confirmation and validation. Cultivars are also individually screened for multiple disease resistance, such as root lesion nematodes (e.g. *Pratylenchus thornei, P. neglectus*) and the root rot fungus (*Fusarium culmorum*; CIMMYT, unpublished data; Table 4). To date, more than 100 genotypes with resistance to CCNs have been identified (Dababat et al. 2014a).

Of the wheat germplasm screened by the soil borne pathogens program, about 20 % are usually identified as having at least a moderate level of resistance. The most promising varieties with acceptable resistance levels (i.e. resistant or moderately resistant) are subsequently crossed with high yielding cultivars. Many locally adapted wheat varieties are susceptible

Table 4 The best performing CIMMYT-Mexico spring wheat germplasm resistant to the cereal cyst nematode *Heterodera avenae,* supported by data from other soil borne diseases

Cross name	GID	CID	SID	*Pt*	*Pn*	*Ha*	*Fc*
CHEN/AEGILOPS SQUARROSA (TAUS)//BCN/3/BAV92/4/BERKUT	5686537	462232	109	R	R	R	
KLDR/PEWIT1//MILAN/DUCULA	5686762	462712	61	R	R	R	R
D67.2/P66.270//AE.SQUARROSA (320)/3/CUNNINGHAM/4/PASTOR/SLVS	5895245	481431	274	R	R	R	R
VEE/MJI//2*TUI/3/2*PASTOR/4/BERKUT/5/PFAU/MILAN	5686412	480520	66	R	R	R	
SOKOLL//SW89-5124*2/FASAN	5894621	485799	45	R	R	R	
SOKOLL//SLVS/PASTOR/3/ATTILA*2//CHIL/BUC	5837084	481626	115	R	R	R	
SHI#4414/CROW/4/NIF/3/SOTY//NAD/CHR/5/FRAME	5423033	435167	50	R	R	R	
SOKOLL//W15.92/WBLL1	5435851	473237	30	R	R	R	R
MEX94.27.1.20/3/SOKOLL//ATTILA/3*BCN		473281	58	R	R	R	

GID, germplasm identification; CID, cross identification; SID, selection identification; Pt, *Pratylenchus thornei*; Pn, *Pratylenchus neglectus*; Ha, *Heterodera avenae*; Fc, *Fusarium culmorum*

to CCNs, thus having new available resistant wheat germplasm allows collaborators to create new crosses with local varieties and therefore improve genetic resistance to CCNs. Dababat et al. (2014a) recently evaluated 719 varieties and breeding lines from 25 countries and identified 114 resistant genotypes (15.8 %) and 90 moderately resistant genotypes (12.5 %) (Table 5). The highest frequency of resistant genotypes was observed in germplasm originating from Bulgaria (59.3 %), Russia (48.5 %), and South Africa (44.9 %).

Diverse collections of wheat germplasm are important for understanding the genetic basis for resistance and also for determining the gene(s) responsible for the resistance. The soil borne pathogens program recently phenotyped and genotyped two sets of winter and spring wheat to assess associations and resistance to CCNs; preliminary results indicated new promising source(s) of resistance to both *H. filipjevi* and *H. avenae* (unpublished data). Understanding the genetic background of these lines will help breeding programs pyramid the different sources of resistance in high yielding varieties. The breeding strategy of employing various *Cre* genes in Australia has been based on identifying their efficiency against a particular CCN pathotype (Ha13), where *Cre6* > *Cre1* > *CreF* ≥ *Cre5,* and then utilizing molecular markers for selection (Ogbonnoya et al. 2001). The effectiveness of *Cre1*, *Cre8,* and *Cre3* genes on CCNs was determined in South Australia; *Cre3* was determined as having the largest negative effect on CCNs, using a reliable marker (Safari et al. 2005), while the *Cre8* molecular marker was not reliable in the germplasm used. Barloy et al. (2007) also determined that pyramiding the *CreX* and *CreY* genes increased levels of resistance to *H. avenae* pathotype Ha12, compared to either gene separately. Furthermore, new sources and genes for CCN resistance have been identified in primary synthetic bread wheat, which is easily crossable with modern bread wheat and can be utilized in breeding (Mulki et al. 2013).

CCN pathotypes

The effectiveness of *Cre* genes in conferring total or partial resistance to CCNs depends on the pathotype of the specific CCN population. The *Cre2* gene exhibits a high level of resistance against *H. avenae* pathotypes Ha71 (Spanish), Ha12 and Ha41 (French), and Ha11 (British), but proved ineffective against HgI-HgIII (Swedish) and Ha13 (Australian) (Delibes et al. 1993; Ogbonnaya et al. 2001). *Cre3* and *Cre6* provide better resistance than *Cre1* against pathotype Ha13, but they are susceptible to Ha11 and Ha12 (Ogbonnaya et al. 2001). *Cre5* confers partial resistance to Ha12, Ha41, and Ha13 pathotypes of *H. avenae* (Rivoal et al. 1993; Jahier et al. 2001; Ogbonnaya et al. 2001). Wheat cultivars carrying *Cre8* exhibit partial resistance and tolerance to Ha13, but its effect on European pathotypes is unknown. Ogbonnaya et al. (2001) evaluated bread wheat lines introgressed with *Aegilops ventricosa* chromosomes for their resistance to *H. avenae* in Australia, and reported that the inhibition of Ha13 nematode reproduction ranked in the order *Cre6* > *Cre1* > *Cre5*. CIMMYT's International Root Disease

Table 5 Distribution of winter wheat germplasm accessions originating from different countries into three groups according to their resistance to *Heterodera filipjevi* (Dababat et al. 2014a)

Country	Total # of entries	Group 1 (Highly resistant)		Group 2 (Resistant)		Group 5 (Highly susceptible)	
		# of entries	%	# of entries	%	# of entries	%
Australia	7	1	14.3	2	28.6	2	28.6
Austria	5	0	0	0	0	3	60.0
Bulgaria	27	16	59.3	1	3.7	5	18.5
Canada	29	4	13.8	0	0	6	20.7
Georgia	4	0	0	1	25.0	0	0
Hungary	9	0	0	0	0	3	33.3
Iran	49	12	24.5	11	22.4	6	12.2
Kazakhstan	12	1	8.3	3	25.0	7	58.3
Mexico	12	0	0	2	16.7	4	33.3
Moldova	9	0	0	2	22.2	3	33.3
People's Republic of China	10	2	20.0	2	20.0	1	10.0
Romania	12	0	0	0	0	3	25.0
Russia	33	16	48.5	4	12.1	2	6.1
South Africa	49	22	44.9	3	6.1	2	4.1
Spain	3	0	0	2	66.7	0	0
Switzerland	5	0	0	0	0	2	40.0
Syria	14	0	0	0	0	11	78.6
Tajikistan	7	2	28.6	2	28.6	1	14.3
Turkey	82	17	20.7	9	11.0	15	18.3
IWWIP (Turkey-CIMMYT-ICARDA)	184	9	4.9	30	16.3	56	30.4
Ukraine	37	5	13.5	5	13.5	7	18.9
United Kingdom	6	0	0	0	0	2	33.3
USA	99	4	4.0	8	8.1	28	28.3
USA-IWWIP	10	3	30.0	3	30.0	2	20.0
Uzbekistan	5	0	0	0	0	0	0
Total	719	114	15.8	90	12.5	171	23.8

IWWIP International Winter Wheat Improvement Program, *CIMMYT* International Maize and Wheat Improvement Center, *ICARDA* International Center for Agricultural Research in the Dry Areas

Resistance Nursery, containing seven of the known *Cre* genes, has been distributed to collaborators around the world in order to establish the value of these genes in different regions.

Pathotypes are differentiated by testing unknown populations against a matrix of cereals in the *International Cereal Test Assortment* for defining CCN pathotypes, developed by Andersen and Andersen (1982). This test distinguishes three primary groups, based on host resistance reactions of barley cultivars carrying the resistance genes *Rha1*, *Rha2,* and *Rha3*. Additional barley, oat, and wheat differentials are used to further define pathotypes within each group (Tables 6, 7). Sub-specialized CCN species and pathotypes may develop in certain climatic conditions or geographical regions and each may respond differently to the source of resistance (Rathjen et al. 1998; Majnik et al. 2003; Barloy et al. 2007).

The most widely distributed populations of *H. avenae* in Europe, North Africa, and Asia belong to 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). In Turkey, a few studies have evaluated the CCN pathotypes of *H. filipjevi* and *H. avenae* (e.g. Ozarslandan et al. 2010; Imren et al. 2013c; Toktay et al. 2013). Imren et al. (2013c) studied the pathotypes of three *H. avenae* populations

Table 6 Pathotype tests of three *Heterodera avenae* cyst populations extracted from Imece, Karlık, and Basaslan in Turkey, based on the *International Test Assortment of Cereal Cultivars* and supported by data from Romero et al. (1996), Al-Hazmi et al. (2001), Subbotin et al. (2010), and Imren et al. (2013c)

Crop	Origin of cereal	Imren et al. (2013c)	Subbotin et al. (2010)	Al-Hazmi et al. (2001)	Romero et al. (1996)
Barley					
Varde	Norway	S	&	S	S
Emir (*Rha* "E")	Netherlands	S	S	S	S
Ortolan (*Rha* 1)	Germany	R	R	R	S
Morocco(*Rha* 3)	Denmark	R	R	R	R
Siri (*Rha* 2)	Denmark	R	R	R	R
Kvl 191 (*Rha* 2)	Denmark	R	R	R	R
Bajo Aragon	Denmark	R	&	R	R
Herta (*Rha* 2)	Sweden	S	S	S	S
Martin 403-2	Denmark	R	&	R	R
Dalmatische	–	S	&	&	R
La Enstuanzuela (*Rha* 2)	Denmark	S	&	S	S
Harlan 43	Denmark	S	&	&	R
Oat					
Sun II	Denmark	R	R	R	R
Pusa Hybrid Bsi	Denmark	R	R	R	R
Silva	Germany	R	&	R	R
Mk H. 72-646	Denmark	S	&	&	R
Wheat					
Capa	–	S	S	S	S
Aus 10894 (*Cre1*)	Denmark	S	&	S	S
Loro × Koga (*Cre1*)	Denmark	R	R	S	S
Psathias	Australia	R	&	S	S
Iskamish K-2 Light	Afghanistan	R	&	S	(S)

S, Susceptible; R, resistant; (), intermediate; &, no observations

from Karlik (Adana-Sarıcam), Imece (Hatay-Kırıkhan), and Besaslan (Hatay-Reyhanlı) in the Eastern Mediterranean region of Turkey. All populations demonstrated similar reactions to the *Test Assortment*, which were consistent with reactions for the Ha21 pathotype of the Ha1 group (Table 6). Toktay et al. (2013) reported that *H. filipjevi* populations found in Afsin, Elbistan, and Yozgat (Middle Anatolia and East Mediterranean regions) belonged to the Ha3 group and Ha33 pathotype. The Yozgat population seemed more virulent than the Elbistan or Afsin populations, though similar responses of the differentials indicated that all three *H. filipjevi* populations were the same pathotype (Table 7).

However, the concept of pathotype is incomplete as it was established to differentiate northern European populations of *H. avenae* and is increasingly incapable of clearly defining the resistance reactions achieved with populations in other regions. For example, 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 the polymorphism of *H. avenae, H. latipons,* and *H. filipjevi* (Cook and Noel 2002; McDonald and Nicol 2005).

Cultural practices

Crop rotation with non-cereals, or grass-free rotation, is very successful in reducing CCN populations below damaging thresholds. Organic amendments, such as manure, organic matter, or compost may also compensate for the negative effect of CCNs on wheat yields. In fallow, non-host, or resistant cultivars, populations of *H. avenae* can decline by 70–80 % annually through spontaneous hatching, resulting in juvenile mortality (Singh et al. 2009). For example, in northwestern USA, summer fallow is used to reduce

Table 7 Pathotype groups of three *Heterodera filipjevi* populations from Turkey, defined based on the *International Test Assortment of Cereal Cultivars* used to define pathotypes of *Heterodera filipjevi* Toktay et al. (2013)

Cereal type	Cultivar and resistance gene (if known)	Origin of cereal	*H. filipjevi* pathotype (Subbotin et al. 2010)		*H. filipjevi* population (Toktay et al. 2013)		
					Afsin	Elbistan	Yozgat
			Ha23	Ha33	Ha33	Ha33	Ha33
Barley	Varde	Norway	+	+	+	+	+
	Emir (*Rha"E"*)	Netherlands	(+)	+	+	+	+
	Ortolan (*Rha1*)	Germany	+	+	(+)	(–)	+
	Morocco (*Rha3*)	Denmark	–	–	–	–	–
	Siri (*Rha2*)	Denmark	+	+	+	+	+
	Kvl 191 (*Rha2*)	Denmark	"	"	+	+	–
	BajoAragon (*Rha2*)	Denmark	+	+	+	+	+
	Herta	Sweden	"	"	+	+	–
	Martin 403-2 (*Rha3*)	Denmark	+	+	–	–	–
	Dalmatische	–	(–)	+	+	+	+
	La Enstuanzuela	Denmark	(–)	"	+	+	+
	Harlan 43	Denmark	–	+	+	+	+
Oat	Sun II	Denmark	+	+	–	–	+
	Pusa Hybrid Bsi	Denmark	–	+	+	+	+
	Silva	Germany	(–)	+	–	–	–
	Mk H. 72-646	Denmark	+	+	+	+	–
Wheat	Capa		+	+	+	+	+
	Aus 10894 (*Cre1*)	Denmark	+	+	+	+	+
	Loro x Koga (*Cre1*)	Denmark	+	+	+	+	+
	Psathias	Australia	+	–	–	–	–
	Iskamish K-2 Light	Afghanistan	+	+	–	+	+

+, Susceptible; –, resistant; (), intermediate; ", no observations; (–), moderately resistant; (+), moderately susceptible

damage by *H. avenae*, and by fungal pathogens of non-irrigated wheat (Smiley et al. 1994). Irrigating fallow soils to stimulate larval activity, in combination with other cultural practices such as early crop destruction, can increase nematode starvation in the absence of a host (Barker et al. 1998).

Chemical control

Chemicals are used to control CCNs when other approaches are too costly, difficult to apply, or when a method such as rotation is inadequate (Hague and Gowen 1987). Treating the soil and seeds with a low rate of nematicides has been shown to efficiently manage CCNs in Australia, India, and Israel (Rivoal and Nicol 2009). Furthermore, applying an activator, such as phytoalexins or pathogenesis-related proteins, can induce the plant's resistance mechanism. Many studies have assessed the biochemical changes induced by chemical applications; for example, changes in enzyme patterns following a nematode invasion indicated that plant gene expression was altered in both susceptible and resistant wheat hosts. Resistance may partially result from the accumulation of compounds toxic to nematodes, which are produced during the oxidase-driven polymerization of lignin as nematodes start to feed, demonstrating that increased activity of specific peroxidases is associated with resistance (Andres et al. 2001). CCN infection enhances plant class III peroxidases, esterase, and superoxide dismutase activity in wheat roots carrying *Cre*2, *Cre*5, or *Cre*7 resistance genes (Andrés et al. 2001; Montes et al. 2004). Pokhare et al. (2012) reported that the application of three synthetic elicitor molecules—namely DL-*b*-amino-*n* butyric acid (BABA; at 2000, 4000, 6000, and 8,000 µg/ml), Jasmonic acid, and Salicylic acid (at 25, 50, 100, and 200 µg/ml)—induced resistance responses against *H. avenae*, with enzyme activity varying by 10–270 %. Foliar sprays of wheat with 8,000 mg/l

BABA reduced the number of *H. avenae* cysts by 90 %, whereas 2,000 mg/l BABA was enough to reduce the number of *H. latipons* cysts by 79 % (Oka and Cohen 2001).

Smiley et al. (2005) reported that the application of aldicarb (4.2 kg ai/ha) at the time of planting improved spring wheat yields by 24 % in moderately infested fields. In another study, Orion and Shleven (1989) reported that wheat seeds coated with furathiocarb (10 g ai/kg of seed), carbofuran (10 g ai/kg of seed), or oxamyl (3.6 g ai/kg of seed) for the management of CCNs and root lesion nematodes gave 38–48 % yield increases in the Northern Negev region of Israel, while Brown (1984) also reported that applying oxamyl (3–11 kg ai/ha) as a seed dressing was effective in reducing *H. avenae*. Kaushal et al. (2001) found that using carbofuranat (2 kg ai/ha) as a seed dressing in field trials gave economical yield increases and reduced levels of *H. avenae* in the soil. However, carbofuran cannot be recommended for soil application due to its toxic effects on non-target organisms (Khan 2006). Smiley et al. (2013) reported a significant reduction in white females in plots with nematicides application, compared to non-treated plots.

However, chemical management is generally considered inadequate due to high costs, environmental hazards, and health risks for farmers. Dababat et al. (2014b) studied three different concentrations of the fungicide thiabendazole on both susceptible and moderately resistant wheat germplasm, and reported that wheat genotypes treated with 50 g ai/100 kg of seed can protect the plant during the nematode infection (Fig. 1). This is important for locally-adapted susceptible varieties grown where CCNs exist. Fungicides with nematicidal or nematistatic activity could improve yields as a holistic approach until a better, genetically-based solution is available.

Biological control using fungal and bacterial microorganisms

As global awareness about environmental pollution increases, bio-management strategies are becoming popular methods for reducing chemical hazards and conserving the biodiversity of microbial communities. Bio-management is theoretically based on the antagonistic or parasitic abilities of living organisms against their hosts, thus bio-management strategies for CCNs

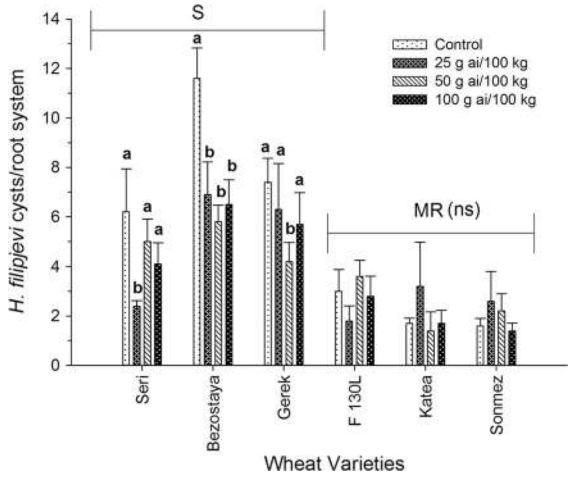

Fig. 1 Effect of thiabendazole on *Heterodera filipjevi* average cyst number on three moderately resistant (MR) and three susceptible (S) genotypes. Columns with *different letters* are significantly different based on Tukey's HSD test ($P \leq 0.05$; $n = 10$) (Dababat et al. 2014b)

include cultural methods and plant resistance (Sikora et al. 2005; Viaene et al. 2006).

Nematode bio-management strategies mainly focus on suppressing population densities of plant-parasitic nematodes in agro-ecosystems by employing natural enemies with different modes of action such as parasitizing, producing toxins, competing for nutrients, inducing systemic resistance, and promoting plant growth. Naturally occurring nematophagous bacteria and fungi can be classified into obligate parasites, facultative parasites, and endophytes, though the number of the organisms that can be used as biological control agents is limited (Stirling 1991; Trudgill et al. 1992; Davies 1998; Viaene et al. 2006).

Despite the fact that cysts are protective towards the eggs and their hardened wall is resistant to invasion by parasites, eggs inside the cyst appear to be susceptible to parasitism caused by fungi and bacteria (Riggs and Schuster 1998). Furthermore, the sedentary endoparasitic behavior of CCNs may make them an even better target for nematode parasitic microorganisms (Viaene et al. 2006).

Fungi associated with CCNs

Over the past 30 years, many investigations have attempted to study the role and use of various fungal species as biological control agents against CCNs.

Nematode population density can be affected by different types of fungi, such as obligate parasites, opportunistic parasites, trapping fungi, and endophytes. Kerry and Crump (1980) described how the nematophagous fungus *Nematophthora gynophila* can attack *H. avenae* by parasitizing the female nematode and preventing cyst formation. Kerry et al. (1982a, b, 1984, 1995) also discussed the biocontrol potential of *Nematophthora gynophila* and *Pochonia chlamydosporia* (syn. *Verticillium chlamydosporium*) against *H. avenae* on wheat and reported a reduction in nematode infection by 26–80 % when plants were treated with *P. chlamydosporia* isolates, the main parasite of "encysted eggs". These studies revealed that fungi that were capable of preventing cyst formation rate, reducing nematode fecundity, and parasitizing encysted eggs could be considered effective nematode biocontrol agents (Fig. 2).

Holgado and Crump (2003) reported the presence of nematophagous fungi on the eggs and juveniles of *H. avenae* and *H. filipjevi*. Similarly, Stein and Grabert (1992) evaluated fungi in the genera *Verticillium, Fusarium, Paecilomyces,* and *Pythium* isolated from the cysts and eggs of *H. avenae*. Their results confirmed that after the second cereal growing cycle, and depending on the fungus inoculated, the number of cysts was reduced by up to 98 %. Effective fungal species decreased nematode densities by reducing cyst formation.

Ismail et al. (2001) studied the diversity of egg parasitic fungi of *H. latipons* in soil samples collected from semiarid agricultural areas in Syria and samples from Germany that were infested with the sugar beet nematode *H. schachtii,* and found that *Fusarium* and *Acremonium* spp. were the most common isolates. By comparison, semiarid Syrian soils exhibited a higher level of antagonistic potential and a greater level of fungal egg pathogen biodiversity. This finding is important for bio-management in semiarid production areas in Syria, Turkey, and other similar regions where CCNs are widespread.

More recently, Mensi et al. (2011) reported the diversity of the microflora in four cereal regions in Tunisia and reported fungal species of *P. chlamydosporia*, *Alternaria* sp., *Aspergillus* sp., *Diplodia* sp., *Drechslera* sp., *Fusarium* sp., *Pithomyces* sp., *Pythium* sp., *Penicillium* sp., *Periconia* sp., *Trichothecium* sp., and bacterial species *Rhizopus* sp. These species were isolated from eggs, second stage juveniles, females, and cysts of *H. avenae*. Suppressive soils with high egg mortality rates were found to correlate with the highest frequency of *P. chlamydosporia* as the most distributed species associated with the nematode among all surveyed regions. This study also showed the association between *P. chlamydosporia* and the bacterium *Rhizobium radiobacter* that led to greatest nematode egg parasitism.

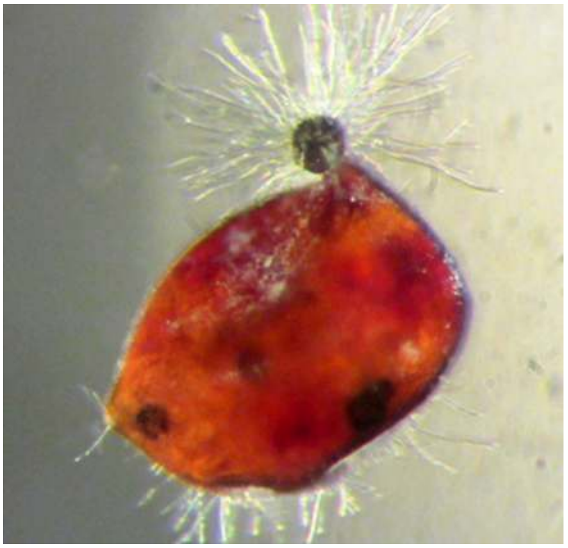

Fig. 2 Cyst of the cereal cyst nematode *Heterodera filipjevi,* extracted from a wheat field in Turkey, parasitized by a fungus. Courtesy of Mr. Samad Ashrafi and Dr. Abdelfattah A. Dababat, CIMMYT

Utilizing the biocontrol potential of different organisms may effectively reduce nematode densities when applied in combination. Research conducted by Khan et al. (2006) demonstrated that application of the nematophagous fungus *Paecilomyces lilacinus* and trapping fungus *Monacrosporium lysipagum* were most effective in controlling nematode populations and resulted in a reduction of 65 % of *H. avenae* cysts on barley. Yuan et al. (2011) screened different parasitic fungi isolated from cysts of *H. avenae* on 42 isolates and reported antagonistic properties on 11 of the tested isolates in pots (with average control efficacy >50 %), whereas in the field, five isolates (*Chaetomium* sp., *Fusarium solani*, *Penicillium oxalicum*, *Stemphylium solani,* and *F. proliferatum*) showed "good" control efficacy of more than 35 %. The initial success of biological control studies led to an expansion in the use of different natural enemies against nematodes, but fungi have yet to be exploited as biological control agents at a commercial scale for wheat.

Bacteria associated with CCNs

Several efforts have also been directed towards biological management of CCNs using bacteria, including obligate parasites (mainly *Pasteuria* spp.), opportunistic bacteria, plant growth promoting rhizobacteria, and endophytic bacteria (mainly *Bacillus* and *Pseudomonas* spp.) (Kloepper et al. 1992; Davies 1998; Hallmann et al. 1997, 2004). Sayer et al. (1991) reported that *Pasteuria nishizawae*, the *Pasteuria* species that infects *Heterodera* spp, has the potential to control CCNs. Rhizobacteria promote plant health and metabolite activity, which may lead to biocontrol potential against CCNs. Bansal et al. (1999) screened *Azotobacter chroococcum, Azospirillum lipoferum,* and *Pseudomonas* sp. on *H. avenae* infections in wheat and reported up to 60 % reductions in cyst formation.

Li et al. (2011) studied the biocontrol potential of more than 290 *Bacillus* strains isolated from wheat roots and reported a 100 % mortality of second stage CCN juveniles under in vitro conditions. Of the tested strains, *Bacillus pumilus* showed the greatest biological control in greenhouse pot trials. In Turkey, Yavuzaslanoglu et al. (2011) investigated the inhibition activity of 126 actinomycetes on second stage juveniles of *H. filipjevi* in wheat field soil samples under in vivo conditions. All active isolates belonged to the genus *Streptomyces* spp. and inhibited the motility of second stage juveniles by 60 %, thus demonstrating the potential of biocontrol agents in managing CCNs in these regions.

Conclusion

Eradicating CCNs is challenging, but nematode populations can be kept below economic thresholds by exploiting various bio-management strategies, especially the biocontrol methods described above in combination with other environmentally friendly control methods. The studies described here have demonstrated the successful and environmentally safe use of a number of microorganisms in biological control, and clearly show that their complicated biological relationships and mechanisms of action need to be studied in different approaches in order to develop our ability and tactics to maximize their potential in controlling CCNs.

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