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Host responses of different Triticeae to species of the cereal cyst nematode complex in relation to breeding resistant durum wheat

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Summary – Twenty eight lines or cultivars of diploid (genomes A, D, S^I, U), tetraploid (genomes AB, D^vM^v, UM, US^v), and hexaploid (genome ABD) wheat were studied for their capacity to sustain the development of nine populations of *Heterodera avenae* originating from six countries (Algeria, France, Spain, Australia, India, and Israel), two populations of *Heterodera filipjevi* from Russia and Bulgaria, and one population of *Heterodera latipons* from Israel. Screenings were performed in artificial conditions using miniaturized tests. High resistance against populations of *H. avenae sensu stricto* occurred in the three levels of ploidy and in several genomes: S^I (*T. longissimum*), D^vM^v (*T. ventricosum*), UM (*T. ovatum*), US^v (*T. variabile*), and ABD (*T. aestivum* AUS 4930). Total or intermediate resistance was found in genome D (*T. tauschii* CPI 110813 or AUS 18913) but their expression in synthetic hexaploid wheat was incomplete resistance. It was confirmed that the *Cre1* gene from wheat cv. Loros is ineffective against *H. avenae* populations from Australia, India, and Israel but also against *H. filipjevi*. Inter- and intraspecific differentiation within the cereal cyst nematode complex, based on (a)virulence to Triticeae and fitness, and the use of total and intermediate resistance in breeding programmes are discussed. © Orstom/Elsevier, Paris

Résumé – ***Réaction de différentes Triticeae à un complexe de nématodes à kystes des céréales, en vue de la sélection du blé dur résistant*** – Vingt-huit lignées ou cultivars de *Triticum* diploïdes (génomes A, D, S^I, U), tétraploïdes (génomes AB, D^vM^v, UM, US^v) et hexaploïdes (génome ABD) ont été étudiés pour leur capacité à permettre le développement de neuf populations d'*Heterodera avenae* originaires de six pays (Algérie, France, Espagne, Australie, Israël et Inde), deux populations d'*Heterodera filipjevi* provenant de Russie et de Bulgarie et une population d'*Heterodera latipons* provenant d'Israël. Les tests ont été conduits dans des conditions artificielles selon une technique miniaturisée. Les résultats ont montré une résistance élevée à l'encontre des populations d'*H. avenae sensu stricto* au sein des trois niveaux de ploïdie et dans les différents génomes S^I (*T. longissimum*), D^vM^v (*T. ventricosum*), UM (*T. ovatum*), US^v (*T. variabile*) et ABD (*T. aestivum* AUS 4930). Des sources de résistance complète ou partielle ont été trouvées dans le génome D (*T. tauschii* CPI 110813 ou AUS 18913), mais leur expression dans les blés hexaploïdes synthétiques est incomplète. Il a été confirmé que le gène *Cre1* du blé cv. Loros est inefficace contre les populations d'*H. avenae* d'Australie, d'Inde et d'Israël, ainsi que contre les populations d'*H. filipjevi*. La différenciation inter- et intraspécifique dans ce complexe de nématodes à kystes des céréales pour leur (a)virulence vis-à-vis de Triticeae et leur capacité reproductive intrinsèque sont discutées, ainsi que l'utilisation de résistances complète et partielle dans les programmes de sélection. © Orstom/Elsevier, Paris

Keywords: cereal cyst nematodes, fitness, *Heterodera*, pathotype, resistance, Triticeae, virulence, wheat.

The cereal cyst nematode complex *Heterodera avenae* Wollenweber, *H. latipons* Franklin, and *H. filipjevi* Madzhidov, to which several 'Gotland-type' populations have recently been attached (Rumpenhorst *et al.*, 1996; Bekal, 1997; Bekal *et al.*, 1997), affects the yield of cereals (Rivoal & Cook, 1993). Damage from these nematodes occurs mostly in Mediterranean regions where agroclimatological conditions (heat, drought) worsen the moisture stress caused by the parasites, as demonstrated for *H. avenae* (Lili *et al.*, 1991). In these regions, widespread cereal monocropping and insufficient or absent weed control provide many potential hosts for a large increase in populations of parasitic nematodes, often including several species (Bekal *et al.*, 1997).

H. avenae is the best known species: it is widely distributed and damage has been assessed in many countries (Rivoal & Cook, 1993). Moreover, this species is polymorphous with many pathotypes (Andersen & Andersen, 1982; Cook & Rivoal, 1998) and at least two ecotypes, indicating an adaptation of its life cycle to the thermal hatching conditions in a Mediterranean climate or in a somewhat temperate oceanic climate (Banyer & Fischer, 1971; Rivoal, 1982).

Economic and environmental constraints make it necessary to develop integrated control systems to ensure a reasonable management of parasite populations, which must remain below their damage thresholds (Roberts, 1993). Resistant varieties are a necessary part of this type of plant protection system.

However, most of the resistances used are based on oligogenous systems that often target a single species, or even a single pathotype (Cook & Rivoal, 1998). Field use of this type of genetic system may create a selective pressure that will break the resistance. Also, the development of secondary species, not targeted by the resistance genes involved, may result in an unbalanced biocenosis (Rivoal *et al.*, 1995).

Surveys for resistance to several populations attributed (or presumed to belong) to the species *H. avenae* yielded interesting sources of resistance in wheat and related species (Sikora *et al.*, 1972; O'Brien & Fischer, 1974; Dosba & Rivoal, 1981; Balakhnina *et al.*, 1986; Rivoal *et al.*, 1986; Eastwood *et al.*, 1991; Singh *et al.*, 1991). Further studies identified several genes, such as *Cre1* in *Triticum aestivum* cv. Loros and AUS 10894 (Slootmaker *et al.*, 1974; Rivoal & Cook, 1993), *Cre2* and *Crex* in *T. ventricosum* 11 (Delibes *et al.*, 1993; Jahier *et al.*, 1996), *Cre3* and *Cre4* in *T. tauschii* (Eastwood *et al.*, 1994), and *Rkn-Mn1* in *T. variabile* 1, a gene active against both *Meloidogyne naasi* Franklin and *H. avenae* (Barloy *et al.*, 1996). So far, the major gene *Cre1* is the most used and contributed to the selection of bread wheat with high potential yield and with intermediate or total resistance, depending on the virulence of the pathotype involved, in Australia (Brown, 1982; Martin, 1994) and France (Rivoal *et al.*, 1990), respectively.

In its zone of cultivation, durum wheat is subject to the attacks of the various species in the nematode complex listed above (Sikora, 1987; Rumpenhorst *et al.*, 1996). However, few studies have been specifically made on resistance, except investigations in Russia (Balakhnina, 1989) concerning *H. filipjevi*, which was previously attributed to *H. avenae* (Subbotin *et al.*, 1996). Because of the low variability for resistance in bread and durum wheats, we decided to conduct a wide survey of cultivated and wild tetraploids and to include in the survey some diploids (*T. tauschii*, *T. monococcum*, etc.) that had proved to be resistant to *H. avenae* in Australia, or differentiated some pathotypes of this nematode in France (Rivoal *et al.*, 1986; Eastwood *et al.*, 1991). The survey also included other diploids (*T. longissimum*, *T. umbellulatum*) and tetraploids (*T. ovatum*) selected for their resistance to drought conditions due to a better ability for osmotic adjustment (Zaharieva, 1996; Rekika *et al.*, 1997).

We tested these Triticeae against the widest possible range of species and pathotypes of these cyst nematodes (*H. avenae*, *H. filipjevi*, and *H. latipons*) to determine, in identical experimental conditions, the resistance levels that would be acceptable for as many of these parasites as possible. Moreover, this comparison of populations originating from Mediterranean regions, India, Russia, and Australia provided the opportunity to improve our knowledge on the variability of virulence of these nematodes to Triticeae, which had been little studied so far (Cook & Rivoal, 1998).

Materials and methods

Biological material

Twenty eight lines or cultivars of *Triticum* including representatives of the three ploidy levels in Triticeae were tested against twelve populations of cereal cyst nematodes, including five different pathotypes of the species *H. avenae* (Tables 1, 2). The virulence phenotypes (pathotypes) were provided from literature data or from additional tests, using the European host differentials (Andersen & Andersen, 1982; Bekal, 1997).

Methods

The resistance to nematodes of the lines or cultivars tested was assessed by miniature tests according to a slightly modified method of Caubel and Chaubet (1988). The nematode inoculum consisted of second stage juveniles (J2s) hatched from cysts placed on small 250 µm-mesh sieves in watch glasses filled with water. Hatching of J2s occurs at 7 ± 1°C. The J2s exited progressively from the cysts and were periodically harvested and stocked at 3 ± 1°C until used. J2s older than 2 months were not used to avoid any reduction of viability.

Caryopses sprouted after 2 days at 20°C and one was planted into each 20 ml plastic tube. The tubes were filled with a mixture of 80% Fontainebleau sand and 20% kaolin. A solution of 100 ml mineral fertilizer (Hakaphos bleu 15-10-15, Compagnie Française BASF, Levallois-Perret, France) at 4 g/l concentration was added per kg of mixture. Two days after planting, about 90 J2s in 0.5 ml of water were injected into the sand by the base of each plant, for each of the tested populations. The plants were then grown in constant temperature chambers at 16 ± 1°C or 18 ± 1°C, for populations from temperate oceanic climate and Mediterranean climates, respectively. The chambers were illuminated at a 16 h photoperiod. The plastic tubes were positioned and supported by a metal mesh on a layer of Fontainebleau sand in trays. Correct humidity was maintained by an additional watering each week. There were ten replications per line or cultivar for each nematode population.

The host capacity of the plants was assessed after they were grown for 2 months by counting the number of white females or cysts formed. These were extracted by washing the roots with a strong stream of water. The nematodes were retained on a 250 µm-mesh screen. Mean and standard deviation of the numbers of nematodes per line or cultivar were calculated for each nematode population.

Table 1. *Origins of Triticum lines arranged by their ploidy level and type of genome.*

Lines	Origins
Diploids (2n=14)	
Genome A	
T. monococcum 157	J. Jahier, INRA, Le Rheu, France
T. monococcum 830	J. Jahier
Genome D	
T. tauschii ssp. *eusquarrosa* var. *meyeri* AUS 18913	R.F. Eastwood, Horsham, Australia
T. tauschii ssp. *eusquarrosa* var. *meyeri/typica* CPI 110813	R.F. Eastwood
Genome S^I	
T. longissimum 18	J. Valkoun, ICARDA, Alep, Syria.
Genome U	
T. umbellulatum 88	M. Zaharieva, IIPGR, Sadovo, Bulgaria
Tetraploids (2n=28)	
Genome AB	
T. durum 7655	J. Jahier
T. dicoccoides 829	J. Jahier
T. dicoccoides 4	J. Jahier
T. turgidum	
226	J. Jahier
cv. Kabir	M. Nachit, ICARDA, Alep, Syria
cv. Cham1	M. Nachit
cv. Oued Zenati	M. Nachit
cv. Korifla	M. Nachit
cv. Jennah Khotifa	M. Nachit
cv. Om Rabi	M. Nachit
cv. Bidi 17	J.C. Dussautoir, INRA, Montpellier, France
cv. Agathé	J.C. Dussautoir
cv. Capdur	J.C. Dussautoir
cv. Huguenot	J.C. Dussautoir
Genome D^vM^v	
T. ventricosum 11	J. Jahier
Genome UM	
T. ovatum 79	P. Monneveux, ENSA, Montpellier, France
Genome US^v	
T. variabile 1	J. Jahier
Hexaploids	
Genome ABD	
T. turgidum (Langdon)x *T. tauschii* AUS 18913	R.F. Eastwood
T. turgidum (Langdon)x *T. tauschii* CPI 110813	R.F. Eastwood
T. aestivum	
cv. Loros	J. MacKey, University of Uppsala, Sweden
cv. Arminda	J. Jahier
AUS 4930	F. Green, Field Crop Pathology, Plant Research Center, Urbvae, South Australia

Table 2. Origins of the cereal cyst nematode populations tested.

Population	Country	Code	Pathotype*	Source
Heterodera avenae				
Sidi Hosni	Algeria	E43	Ha41	F. Labdelli, INA, El Harrach, Algeria
Dahmouni	Algeria	E42	Ha41	F. Labdelli
Villasavary	France	Fr1	Ha41	R. Rivoal, INRA, Le Rheu, France
St Georges du Bois	France	Fr2	Ha11	R. Rivoal
Nuisement/Coole	France	Fr4	Ha12	R. Rivoal
Santa Olalla	Spain	E48	Ha71	M. Romero, CSIC, Madrid, Spain
Nir Oz	Israel	E57	Ha41	Y. Spiegel, The Volcani Center, Bet Dagan, Israel
South Australia	Australia	E50	Ha13	J.M. Fischer, University of Adelaide, Australia
Najafgarh	India	E83	Ha71	K.K. Kaushal, I.A.R.I, New Dehli, India
Heterodera filipjevi				
Puschkin	Russia	E88	ND	S.A. Subbotin, Institute of Parasitology of Russian Academy of Sciences, Moscow, Russia
Karnobat**	Bulgaria	A26	ND	D. Stoyanov, Plant Protection Institute, Kostinbrod, Bulgaria
Heterodera latipons				
Gilat	Israel	E69	ND	Y. Spiegel

* Pathotype designation according to the international test (Andersen & Andersen, 1982); ND: not determined.
** This 'Gotland-type' population was attributed to *H. filipjevi* based on recent morpho-biometric, virulence, and genetic polymorphism data (Bekal, 1997; Bekal *et al.*, 1997).

Three levels were defined for the host ability of the plants tested: total resistance (level 1) to the parasite development when the number of nematodes per plant was less than 1. Intermediate resistance (level 2), when there were up to three females or cysts per plant, which corresponds to the resistance threshold used by Ireholm (1994). For more than three females or cysts, the host ability (level 3) varies depending on both the plant genotype and the fitness, which is the intrinsic reproductive ability of the nematode populations. This has been previously described for *H. avenae* pathotypes in France (Rivoal & Person-Dedryver, 1982).

STATISTICAL ANALYSES

The numbers of white females and cysts recorded on each plant were subjected to a two-way analysis of variance after *log(x+1)* transformation of the data for adjustment of normality. Both the nematode populations and the plant lines were classified according to a Newman-Keuls test ($P \leq 0.05$). A correspondence factor analysis highlighted the major differences within the two factors, plants and nematodes. These analyses were made using the SAS package (Anon., 1988).

Results

The analysis of variance on the numbers of white females and cysts showed highly significant ($P \leq 0.001$) effects of both factors, plants and nematodes. Two rankings were made. The first compared the resistance levels of the various plant genotypes to the different nematode species and populations tested (columns). The second compared each plant genotype to the others, at any ploidy levels, according to the average numbers of females and cysts produced for all of the nematode populations (discriminating letters on the first line of Tables 3, 4, and 5). Moreover, the highly significant ($P \leq 0.001$) nematode-plant interaction was highlighted by a correspondence factor analysis, which showed the potential for inter- and intraspecific differentiation of these nematodes using the host reactions of these Triticeae.

DIPLOID *TRITICUM*

The plants with genome D (*T. tauschii* CPI 110813) and genome S^l (*T. longissimum* 18) were those with the most frequent total (level 1) or intermediate (level 2) resistance, since level 3 (more than three females or cysts per plant) was observed only with Fr1 (*H. avenae)* and A26 and E88 (*H. filipjevi)* on CPI 110813 and with E43 (*H. avenae)* on *T. longissimum* 18 (Table 3). These two genotypes also showed intermediate resistance and total resistance, respectively, against *H. latipons*. Relative to all nematode populations tested, *T. tauschii* AUS 18913 was statistically ranked at the same level (letter *h* on the first line of the table) as CPI 110913, but its level 1 resistance was

Table 3. *Host responses of diploid* Triticum *species to populations of* Heterodera avenae, H. filipjevi, *and* H. latipons. *For each population, the table gives the mean and standard deviation of the numbers of white females or cysts per plant.*

Nematode populations	*T. monococcum* 157 *fg*	*T. monococcum* 830 *f*	*T. tauschii* AUS 18913 *h*	*T. tauschii* CPI 110813 *h*	*T. longissimum* 18 *j*	*T. umbellulatum* 88 *j*
H. avenae						
E43	12.3 ± 3.83 *abc*	12.2 ± 4.40 *ab*	***2.2*** ± 1.65 *def*	***1.0*** ± 1.10 *c*	4.2 ± 1.04 *a*	4.3 ± 1.67 *ab*
E42	7.2 ± 3.28 *bc*	7.5 ± 2.70 *b*	***1.7*** ± 0.89 *def*	**0.5** ± 0.70 *c*	**0.7** ± 0.75 *c*	***2.3*** ± 1.47 *bc*
Fr1	6.2 ± 3.19 *cd*	9.6 ± 3.21 *ab*	3.2 ± 1.08 *bcd*	3.5 ± 1.40 *b*	***1.7*** ± 1.45 *bc*	8.5 ± 3.20 *a*
Fr2	***1.5*** ± 1.20 *ef*	***1.1*** ± 1.44 *d*	**0.8** ± 0.73 *ef*	***1.4*** ± 1.13 *c*	**0.1** ± 0.28 *c*	3.4 ± 1.56 *abc*
Fr4	7.6 ± 5.86 *cd*	***2.8*** ± 1.67 *c*	***2.7*** ± 1.33 *cde*	***1.5*** ± 1.10 *c*	**0.6** ± 0.89 *c*	9.3 ± 2.61 *a*
E48	***2.6*** ± 0.97 *de*	***2.1*** ± 1.72 *cd*	***2.1*** ± 1.34 *def*	**0.6** ± 0.72 *c*	**0.6** ± 0.60 *c*	***1.7*** ± 1.31 *bcd*
E57	17.2 ± 5.44 *a*	16.2 ± 1.75 *a*	7.3 ± 3.78 *ab*	***1.3*** ± 1.00 *c*	**0.6** ± 0.74 *c*	9.1 ± 2.22 *a*
E50	13.8 ± 4.10 *ab*	13.1 ± 3.90 *ab*	**0.4** ± 0.61 *f*	**0.8** ± 0.73 *c*	**0.3** ± 0.50 *c*	8.8 ± 2.24 *a*
E83	5.4 ± 0.44 *cd*	7.6 ± 2.30 *b*	**0.4** ± 0.56 *f*	**0.9** ± 0.60 *c*	**0.6** ± 0.89 *c*	9.7 ± 4.90 *a*
H. filipjevi						
E88	**0.2** ± 2.37 *f*	***1.2*** ± 0.81 *cd*	8.2 ± 2.25 *a*	10.3 ± 2.97 *a*	***2.0*** ± 1.43 *bc*	**0.7** ± 0.56 *cd*
A26	**0.6** ± 0.78 *f*	**0.7** ± 0.94 *d*	***2.6*** ±c 1.44 *cde*	4.0 ± 1.30 *b*	***2.5*** ± 1.38 *ab*	**0.1** ± 0.20 *d*
H. latipons						
E69	3.8 ± 2.90 *de*	7.9 ± 1.44 *b*	5.4 ± 2.63 *abc*	***1.0*** ± 1.00 *c*	**0.1** ± 0.28 *c*	5.2 ± 4.80 *abc*

The classification of the log (x+1) *transformed data, according to the Newman-Keuls test ($P \leq 0.05$), concerns both the nematode populations (letters placed under the mean data) and the plants (letters placed under the name of each line or cultivar). Means followed by the same letter are not significantly different. Means with bold or bold italic numbers indicate total (level 1) or intermediate (level 2) resistance, respectively.*

only to three *H. avenae* populations (Fr2, E50, E83). *T. umbellulatum* 88 (genome U) had total resistance to the two *H. filipjevi* populations (A26 and E88) and interme-diate resistance to the *H. avenae* populations (E42 and E48).

Lines 157 and 830 of *T. monococcum* (genome A) prevented the development of populations A26 and E88 of *H. filipjevi* via total resistance, or even intermediate resistance. They also showed intermediate resistance to populations Fr2 and E48 of *H. avenae*. However, only *T. monococcum* 830 had a level 2 resistance to Fr4.

TETRAPLOID *TRITICUM*

T. variabile 1 (genome US^v) was intermediately, or sometimes totally resistant, to all of the tested nematode populations (Table 4, cont. 2). Total resistance with a spectrum of activity almost as wide was observed in *T. ovatum* 79 (genome UM) and *T. ventricosum* 11 (genome $D^v M^v$). Only *H. avenae* (E57) and *H. latipons* were able to develop on *T. ovatum* 79 and *T. ventricosum* 11, respectively. Development of nematode populations was different on each of the four AB tetraploid wheats (*T. dicoccoides* 4 and 829, *T. durum*

Table 4. *Host responses of tetraploid* Triticum *species to populations of* Heterodera avenae, H. filipjevi, *and* H. latipons. *For each population, the table gives the mean and standard deviation of the numbers of white females or cysts per plant.*

Nematode populations	*T. durum*	*T. dicoccoides*	*T. dicoccoides*	*T. turgidum*		
	7655	829	4	226	cv. Kabir	cv. Cham1
	e	*d*	*e*	*e*	*e*	*b*
H. avenae						
E43	10.7 ± 3.70 *b*	15.5 ± 3.60 *a*	8.1 ± 2.70 *abc*	8.2 ± 2.50 *bc*	6.3 ± 2.50 *b*	21.8 ± 7.00 *ab*
E42	4.7 ± 1.30 *c*	8.2 ± 3.60 *ab*	5.8 ± 1.80 *bc*	8.5 ± 1.60 *bc*	7.4 ± 1.90 *b*	10.7 ± 4.00 *cd*
Fr1	8.5 ± 3.20 *bc*	16.3 ± 2.30 *a*	10.0 ± 2.80 *ab*	8.5 ± 2.30 *bc*	6.8 ± 1.60 *b*	24.6 ± 4.00 *a*
Fr2	5.0 ± 1.50 *c*	5.7 ± 2.04 *b*	5.3 ± 1.10 *bc*	5.6 ± 1.30 *bc*	6.1 ± 1.50 *b*	13.6 ± 3.00 *bcd*
Fr4	***1.0*** ± 0.79 *d*	10.2 ± 2.80 *ab*	4.5 ± 1.20 *bc*	4.5 ± 1.80 *c*	5.8 ± 3.40 *b*	9.4 ± 2.70 *d*
E48	5.2 ± 2.00 *c*	5.1 ± 1.56 *b*	3.6 ± 1.20 *bc*	6.3 ± 2.10 *bc*	10.4 ± 2.50 *b*	16.0 ± 3.70 *abc*
E57	22.4 ± 6.40 *a*	9.8 ± 3.31 *ab*	8.6 ± 2.30 *ab*	10.5 ± 2.00 *b*	20.2 ± 5.70 *a*	19.6 ± 3.80 *ab*
E50	11.8 ± 5.00 *ab*	10.1 ± 5.00 *ab*	9.4 ± 3.60 *ab*	9.0 ± 5.30 *bc*	8.4 ± 2.80 *b*	19.2 ± 3.80 *ab*
E83	19.3 ± 8.90 *a*	15.1 ± 3.90 *a*	5.8 ± 2.40 *bc*	19.4 ± 4.00 *a*	11.7 ± 4.20 *b*	17.4 ± 3.70 *ab*
H. filipjevi						
E88	7.5 ± 2.80 *bc*	7.7 ± 2.70 *ab*	6.0 ± 1.20 *bc*	7.2 ± 2.50 *bc*	6.6 ± 2.60 *b*	8.6 ± 1.00 *d*
A26	5.6 ± 3.10 *c*	6.0 ± 2.60 *b*	5.5 ± 1.50 *bc*	8.2 ± 2.40 *bc*	6.6 ± 2.30 *b*	10.5 ± 1.50 *cd*
H. latipons						
E69	6.4 ± 1.70 *bc*	7.2 ± 2.40 *ab*	17.0 ± 8.20 *a*	5.5 ± 4.00 *bc*	***3.0*** ± 2.00 *c*	4.6 ± 1.80 *e*

Nematode populations	*T. turgidum*				
	cv. Oued Zenati	cv. Korifla	cv. Jennah *Khotifa*	cv. Om Rabi	cv. Bidi 17
	b	*cd*	*e*	*b*	*bc*
H. avenae					
E43	19.1 ± 8.43 *ab*	18.1 ± 6.60 *ab*	17.7 ± 5.29 *ab*	9.5 ± 2.72 *c*	10.2 ± 2.74 *ab*
E42	11.1 ± 3.31 *cd*	10.1 ± 3.50 *ab*	8.0 ± 2.40 *c*	10.3 ± 1.67 *c*	11.5 ± 2.80 *ab*
Fr1	28.2 ± 4.89 *a*	10.8 ± 3.27 *ab*	19.5 ± 3.51 *a*	14.1 ± 3.48 *bc*	14.7 ± 3.76 *a*
Fr2	5.4 ± 1.53 *c*	15.3 ± 0.60 *ab*	7.4 ± 3.70 *c*	13.1 ± 4.88 *bc*	10.2 ± 2.56 *ab*
Fr4	12.0 ± 6.59 *bc*	9.3 ± 4.40 *ab*	5.4 ± 3.50 *c*	9.6 ± 2.70 *c*	9.2 ± 2.00 *ab*
E48	16.6 ± 3.13 *ab*	11.7 ± 2.80 *ab*	11.0 ± 3.70 *abc*	17.7 ± 3.25 *ab*	11.3 ± 3.04 *ab*
E57	26.7 ± 5.81 *a*	20.3 ± 7.10 *a*	8.0 ± 2.00 *c*	19.3 ± 3.76 *ab*	15.6 ± 5.38 *a*
E50	15.2 ± 2.64 *ab*	11.2 ± 1.80 *ab*	7.7 ± 2.61 *c*	18.7 ± 5.11 *ab*	11.8 ± 4.88 *ab*
E83	16.4 ± 4.72 *ab*	13.0 ± 4.00 *ab*	4.3 ± 1.72 *c*	22.1 ± 2.88 *a*	15.6 ± 4.28 *a*
H. filipjevi					
E88	21.6 ± 6.78 *ab*	11.1 ± 4.78 *ab*	9.6 ± 2.56 *bc*	14.9 ± 4.88 *abc*	11.2 ± 2.25 *ab*
A26	7.1 ± 1.59 *c*	6.8 ± 1.50 *b*	6.5 ± 1.79 *c*	10.6 ± 2.13 *c*	7.2 ± 2.17 *b*
H. latipons					
E69	7.5 ± 3.30 *c*	3.9 ± 2.12 *c*	***1.7*** ± 1.70 *d*	9.6 ± 3.00 *c*	7.2 ± 2.47 *b*

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Table 4. (End).

Nematode populations	*T. turgidum*			*T. ventricosum*	*T. ovatum*	*T. variabile*
	cv. Agathé *cd*	cv. Capdur *e*	cv. Huguenot *bc*	11 *k*	79 *k*	1 *k*
H. avenae						
E43	11.6 ± 1.88 *abc*	7.8 ± 2.50 *bc*	25.5 ± 4.50 *a*	**0.6** ± 0.63 *b*	**0** *b*	**0** *c*
E42	8.0 ± 2.60 *bcd*	8.4 ± 2.20 *bc*	7.3 ± 2.30 *c*	**0** *c*	**0.1** ± 0.22 *b*	**0.2** ± 0.32 *c*
Fr1	16.8 ± 5.76 *a*	9.4 ± 3.48 *bc*	26.7 ± 8.75 *a*	**0** *c*	**0.8** ± 1.01 *b*	**0.7** ± 0.86 *bc*
Fr2	9.7 ± 2.53 *abc*	7.0 ± 1.20 *bc*	11.2 ± 1.84 *b*	**0.1** ± 0.22 *c*	**0** *b*	**0.1** ± 0.22 *c*
Fr4	6.3 ± 2.16 *cd*	***2.0*** ± 1.60 *d*	11.6 ± 2.28 *b*	**0** *c*	**0** *b*	**0** *c*
E48	10.1 ± 3.68 *abc*	5.1 ± 2.37 *c*	6.0 ± 2.00 *c*	**0** *c*	**0** *b*	**0.5** ± 0.62 *bc*
E57	15.0 ± 4.18 *ab*	12.5 ± 2.37 *b*	14.6 ± 5.06 *b*	**0.1** ± 0.22 *c*	6.0 ± 1.68 *a*	**0** *c*
E50	10.1 ± 3.63 *abc*	7.7 ± 1.75 *bc*	*	**0** *c*	**0.1** ± 0.17 *b*	*
E83	17.5 ± 5.63 *a*	26.4 ± 5.22 *a*	22.7 ± 3.31 *a*	**0.8** ± 0.69 *b*	**0.2** ± 0.28 *b*	**0.6** ± 0.82 *bc*
H. filipjevi						
E88	5.2 ± 2.75 *d*	5.3 ± 4.56 *c*	13.8 ± 3.27 *b*	**0** *c*	**0.6** ± 0.72 *b*	***1.8*** ± 1.22 *ab*
A26	7.2 ± 2.50 *cd*	4.5 ± 1.50 *c*	4.2 ± 1.44 *c*	**0.1** ± 0.22 *c*	**0** *b*	***1.9*** ± 0.63 *a*
H. latipons						
E69	8.7 ± 3.80 *bcd*	7.2 ± 1.56 *bc*	4.6 ± 1.13 *c*	8.4 ± 2.08 *a*	**0.1** ± 0.20 *b*	***1.1*** ± 1.28 *abc*

The classification of the log (x+1) *transformed data, according to the Newman-Keuls test ($P \leq 0.05$), concerns both the nematode populations (letters placed under the mean data) and the plants (letters placed under the name of each line or cultivar). Means followed by the same letter are not significantly different. Means with bold or bold italic numbers indicate total (level 1) or intermediate (level 2) resistance, respectively.*

7655, and *T. turgidum* 226) and an intermediate resistance to Fr4 was observed in *T. durum* 7655 (Table 4). Notable differences were seen among the durum wheat cultivars in the development of the various members of this cyst nematode complex. The means for all of the nematode populations tested showed that Capdur, Jennah Khotifa, and Kabir were the least suited for the development of these nematodes (letter *e*). Some of these durum wheats (Jennah Khotifa, Kabir) even showed an intermediate (level 2) resistance against *H. latipons* (E69).

The durum wheats Cham 1, Oued Zenati, Jennah Khotifa, and Huguenot, and possibly Agathé, revealed significant differences in the intrinsic reproduction capacity of *H. avenae* in France. These differences were seen between Fr1 on the one hand and the more northerly distributed Fr2 and Fr4 on the other. Two *H. avenae* populations, E57 from Israel and E83 from India, had the highest reproduction potential on those tetraploids with the AB genome, and particularly *T. durum* 7655, *T. turgidum* 226, Bidi 17, and Capdur.

HEXAPLOID *TRITICUM*

The wheat cultivar Arminda, used as a host control, showed its characteristically high host ability for the three species of nematodes (the only genotype mean with the letter *a*), although this cultivar exhibited significant differences in its capacity to reproduce some of the nematode populations (Table 5). In contrast, the total resistance of cv. Loros was seen only against the *H. avenae* populations from France, Spain, and Algeria. This cultivar differentiated the two populations of *H. filipjevi* (A26 et E88) based on its significantly higher reproduction capacity for the Russian population (E88). The same was true of the line AUS 4930, although there was no information on *H. avenae* populations E57, E50, and E83. AUS 4930 also showed total resistance to *H. latipons*.

The resistance of *T. tauschii* AUS 18913 and CPI 110813 was seen also in their respective synthetic hexaploids, but a general loss of efficacy was observed against all nematode populations, as seen in the mean ranking of the lines (letters *e*, *g*, and *h* in Tables 3 and 5). On average, the expression of resistance was significantly higher with CPI 110813 (letter *g*). However, both synthetic wheats had a very interesting intermediate resistance to Fr4 (*H. avenae*).

INTER- AND INTRASPECIFIC DIFFERENTIATION OF THE NEMATODES

The host responses of the various lines and cultivars tested made it possible to globally differentiate some

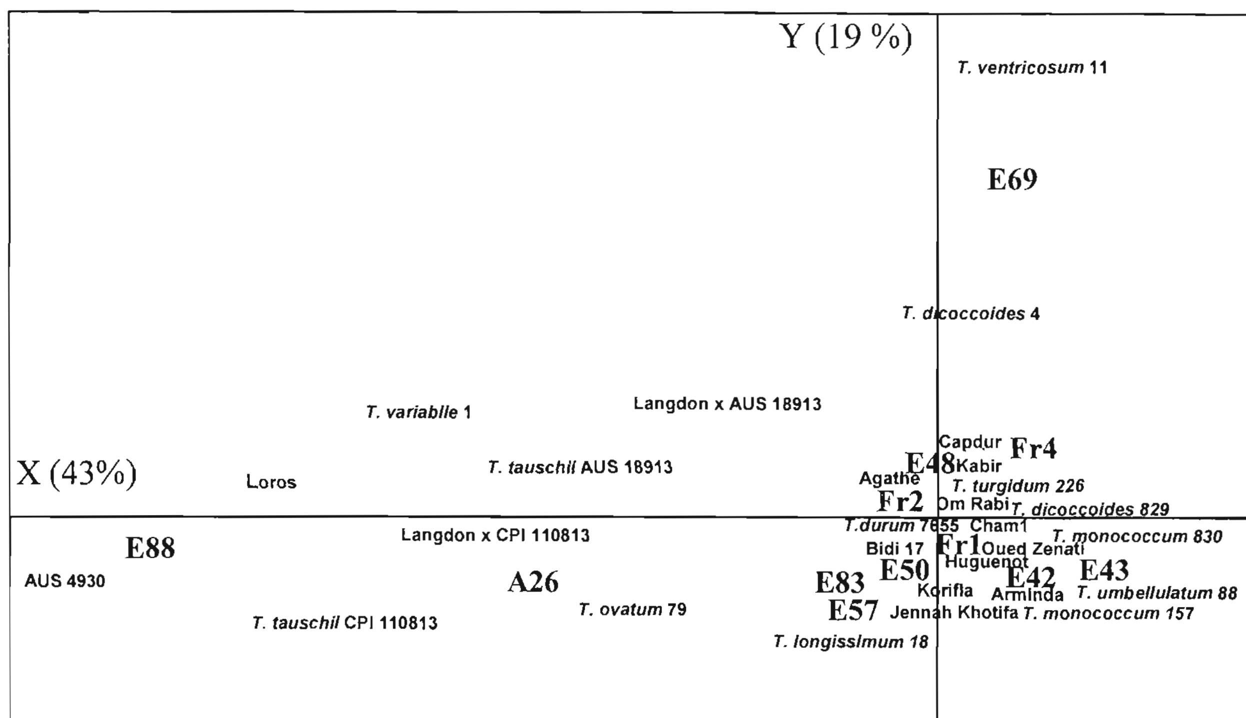

Fig. 1. *Correspondence factor analysis of host response (mean numbers of cysts or females formed per plant) of 28* Triticum *lines or cultivars toward populations of* Heterodera avenae *(E43, E42, Fr1, Fr2, Fr4, E48, E50, E57, and E83),* H. filipjevi *and related populations (E88 and A26), and* H. latipons *(E69). (Refer to Table 1 for the identify of the lines and cultivars of bread and durum wheats tested; the percentages indicated on the axes X and Y give the variability observed.)*

nematode populations using a correspondence analysis. Thus, on axis X that accounts for 43% of variation, populations E88 and A26 attributed to the species *H. filipjevi* were separated from all *H. avenae* populations by their reproduction capacity on the *T. ovatum* 79 and *T. variabile* 1 diploids, on *T. tauschii* AUS 18913 and CPI 110813 tetraploids and their respective synthetic hexaploids, and on cultivars Loros and AUS 4930 of *T. aestivum* (Fig. 1). In *H. filipjevi*, the clear separation between the population from Russia (E88) and the population from Bulgaria (A26) was caused by both their (a)virulence against the line AUS 4930 and significant differences in their intrinsic reproduction capacity on lines AUS 18913 and CPI 110813 of *T. tauschii* and on cv. Loros of *T. aestivum* (Tables 3, 5).

Axis Y, which accounts for 19% of the variation, clearly differentiated *H. latipons* (E69) from all *H. avenae*, mostly because of its high reproduction on both tetraploid lines, *T. ventricosum* 11 and *T. dicoccoides* 4.

Discussion and conclusion

Counting females and cysts that developed on plants cultivated on a sand/kaolin medium and inoculated with J2s provided a reliable assessment of the host responses of various Triticeae to a complex of species and populations of cereal cyst nematodes. This test proved easier than previous techniques based on soils naturally or artificially infested with cysts (Rivoal *et al.*, 1978). However, the test resulted in a relatively low maximum number of nematodes per plant. The 5% rule, commonly used to characterize the resistance of cereals to *H. avenae* (Nielsen, 1972), was difficult to apply in the present conditions. Reproduction capacity (fitness) between nematode populations can vary by up to a factor of three, *e.g.*, with cv. Arminda, which prohibited an objective definition of reference hosts. Consequently, we used the three ranking levels of plant genotypes. In fact, in the case of the host control Arminda, level 1 corresponded to Nielsen's rule when the number of females is lower than twenty. For higher numbers, the classification proposed here was more accurate than the previously defined standard.

The low standard deviations of the distributions of each nematode population were proof of the genetic homogeneity of the plant material used. Intrinsic differences in root development among the various lines

Table 5. *Host responses of hexaploid* Triticum *species to populations of* Heterodera avenae, H. filipjevi, *and* H. latipons. *For each population, the table gives the mean and standard deviation of the numbers of white females or cysts per plant..*

Nematode populations	Langdon × AUS 18913 *e*	Langdon × CPI 110813 *g*	*T. aestivum* cv. Loros *i*	*T. aestivum* cv. Arminda *a*	*T. aestivum* AUS 4930 *j*
H. avenae					
E43	4.8 ± 2.16 *cd*	***2.4*** ± 1.35 *cd*	**0.2** ± 0.35 *e*	23.3 ± 6.84 *a*	**0.2** ± 0.28 *c*
E42	4.1 ± 1.74 *d*	***2.6*** ± 1.38 *cd*	**0.1** ± 0.15 *e*	17.3 ± 5.37 *abcd*	**0.2** ± 0.32 *c*
Fr1	6.4 ± 1.88 *bcd*	4.9 ± 2.35 *abcd*	**0.2** ± 0.36 *e*	21.0 ± 6.82 *ab*	**0.3** ± 0.48 *c*
Fr2	5.5 ± 1.30 *cd*	6.6 ± 1.78 *abc*	**0** *e*	12.4 ± 2.80 *cd*	**0** *c*
Fr4	***2.0*** ± 1.56 *e*	***1.7*** ± 1.53 *d*	**0.2** ± 0.32 *e*	21.0 ± 4.80 *ab*	**0** *c*
E48	11.6 ± 3.07 *b*	***2.5*** ± 1.73 *cd*	**0** *e*	11.1 ± 1.93 *de*	**0.1** ± 0.20 *c*
E57	11.5 ± 3.92 *b*	3.8 ± 1.59 *abcd*	6.4 ± 2.22 *bc*	21.0 ± 4.33 *ab*	*
E50	5.2 ± 1.36 *cd*	3.8 ± 1.84 *bcd*	4.2 ± 1.00 *cd*	17.7 ± 2.74 *abc*	*
E83	22.2 ± 3.56 *a*	4.1 ± 1.91 *abcd*	6.2 ± 1.50 *bc*	19.2 ± 5.12 *ab*	*
H. filipjevi					
E88	10.8 ± 3.84 *b*	13.5 ± 5.18 *a*	17.2 ± 7.75 *a*	14.0 ± 3.00 *bcd*	24.4 ± 5.97 *a*
A26	8.0 ± 1.90 *bc*	8.0 ± 1.17 *ab*	6.5 ± 1.38 *b*	11.0 ± 1.71 *de*	***1.3*** ± 1.00 *b*
H. latipons					
E69	11.5 ± 5.51 *b*	3.1 ± 1.66 *bcd*	3.2 ± 0.96 *d*	8.1 ± 1.63 *e*	**0.4** ± 0.49 *c*

The classification of the log (x+1) *transformed data, according to the Newman-Keuls test ($P \leq 0.05$), concerns both the nematode populations (letters placed under the mean data) and the plants (letters placed under the name of each line or cultivar). Means followed by the same letter are not significantly different. Means with bold or bold italic numbers indicate total (level 1) or intermediate (level 2) resistance, respectively. * Tests not carried out.*

of Triticeae tested also could have added a bias to the assessment of their respective resistance level. However, the virulence (seven females per plant on average) of the *H. avenae* population E57 from Israel on *T. tauschii* AUS 18913, a line that, like other diploids, is noted for its low root production, did not support this hypothesis or the reservations made by Eastwood *et al.* (1991) concerning the comparison of host responses of Triticeae with different ploidy levels.

Total resistance implies the presence of genes having a major effect on plant-nematode relationships and nematode populations that are homogeneous for virulence (Cook & Rivoal, 1998). This qualitative resistance was easily demonstrated for *T. ovatum* 79, *T. variabile* 1, and *T. ventricosum* 11, for most of the populations tested. Depending on populations, total and intermediate resistances were observed with *T. monococcum* 157 and 830, *T. tauschii* AUS 18913 and CPI 110813, *T. longissimum* 18, and *T. umbellulatum* 88. Resistance of the bread wheat cv. Loros was not universal with *H. avenae* and did not apply to *H. filipjevi* and *H. latipons*. The data on the resistance of AUS 4930 need to be completed.

The host responses of Triticeae to cyst nematodes were assessed from a small number of cases, considering the richness of this botanical family and the complexity and wide distribution of this group of nematodes (Ritter, 1982; Zaharieva, 1996). However, this evaluation did increase our knowledge on the potential virulence of the nematodes and defined host differentials at both inter- and intraspecific levels. If a mixture of species were suspected, it would be easy to extract *H. latipons* (E69) by culture on *T. ventricosum* 11. Similarly, the two populations A26 and E88 attributed to *H. filipjevi* would be isolated by culture on *T. aestivum* cv. Loros or AUS 4930, or even on *T. variabile* 1, as long as the identity of the nematode species is verified by RFLP on ribosomal DNA (Bekal *et al.*, 1997). Within *H. avenae*, population E57 from Israel is easily differentiated by its almost exclusive virulence to *T. ovatum* 79. The avirulence of both populations of *H. filipjevi* to *T. monococcum* 157 is noticeable. Differences in host responses of *T. monococcum* 830 differentiate pathotypes Fr1 and Fr4 in France, as already mentioned by Rivoal *et al.* (1986).

The tests, made under standard conditions and always with the same inoculum, confirmed that, for both *H. avenae* and *H. filipjevi*, populations can be differentiated by their (a)virulence, which defines distinct pathotypes, and by their reproduction capacity or 'fitness' (Rivoal & Person-Dedryver, 1982). Analysis of variance and/or correspondence factor analysis

Table 6. *Major sources of resistance to cereal cyst nematodes (*Heterodera*) in various* Triticum *lines or cultivars.*

Genotypes	Species and populations*		
	H. avenae	*H. filipjevi* E88, A26	*H. latipons* E69
Diploids			
T. monococcum 157	(-)** Fr2, E48	-	
T. monococcum 830	(-) Fr2, Fr4, E48	- A26 (-) E88	
T. tauschii AUS 18913	- Fr2, E50, E83 (-) E43, E42, Fr4, E48	(-) A26	
T. tauschii CPI 110813	- E42, E48, E50, E83 (-) E43, Fr2, Fr4, E57		(-)
T. longissimum 18	- E42, Fr2, Fr4, E48, E57, E50, E83 (-) Fr1	(-)	-
T. umbellulatum 88	(-) E42, E48	-	
Tetraploids			
T. ventricosum 11	- E43, E42, Fr1, Fr2, Fr4, E48, E57, E50, E83	-	
T. ovatum 79	- E43, E42, Fr1, Fr2, Fr4, E48, E50, E83	-	-
T. variabile 1	- E43, E42, Fr1, Fr2, Fr4, E48, E57, E83	(-)	(-)
Hexaploids			
T. aestivum cv. Loros	- E43, E42, Fr1, Fr2, Fr4, E48		
T. aestivum AUS 4930	- E43, E42, Fr1, Fr2, Fr4, E48	(-) A26	-

**Refer to Table 2 for the origin of the populations.*
***Resistance level: -, total; (-), intermediate.*

revealed marked differences between the Fr1 and Fr4 populations or between the E57 and E83 populations, depending on their development on various durum wheats such as Oued Zenati, Jennah Khotifa, or *T. turgidum* 226. Populations A26 and E88 of *H. filipjevi* were differentiated by their (a)virulence to AUS 4930 and by a difference in reproduction capacity on *T. tauschii* CPI 110813, the durum wheat cultivars Oued Zenati and Huguenot, and the bread wheat cultivar Loros.

As happened with oats and barley, the populations of *H. avenae* had different virulences toward the different Triticeae, which indicates a very high genetic variability in this species (Rivoal *et al.*, 1995; Lasserre *et al.*, 1996). This variability in virulence was well shown by the *Cre1* gene of cv. Loros, the efficacy levels of which clearly differentiated *H. avenae* populations from Europe and North Africa from those from Israel, India, and Australia. However, Fr1 from France and E57 from Israel were attributed to the same pathotype –Ha41– because of their identical (a)virulence characteristics toward oats or barley (Mor *et al.*, 1992; Cook & Rivoal, 1998). In *T. ovatum* 79, the addition of genome M, which includes the *Cre2* gene in *T. ventricosum 11* (Rivoal *et al.*, 1986; Delibes *et al.*, 1993; Jahier *et al.*, 1996), to the genome U cancelled the virulence of all *H. avenae* populations tested, except E57 from Israel. Two accessions with the two genomes UM also proved resistant to a population from Punjab, India (Singh *et al.*, 1991). Testing these genotypes with a larger sample of *H. avenae* populations would increase our knowledge of genetic relationships between this species and Triticeae, which would ease the choice of genotypes in resistance breeding programmes. The same situation was found in the species *H. filipjevi* and the related

Gotland-type populations, where differences of virulence toward oats and barley had already been observed (Ireholm, 1994; Subbotin, pers. comm.), and in *H. latipons*.

Germplasms that can be used for a plant breeding programme for durum wheats resistant to Mediterranean populations of cereal cyst nematodes have been identified. Some of the genes involved have been identified or are being identified, *e.g.*, in *T. tauschii*, *T. variabile*, and *T. ventricosum* (Delibes *et al.*, 1993; Eastwood *et al.*, 1994; Jahier *et al.*, 1996; Barloy *et al.*, 1996). The absence of variability in the resistance of durum wheats was confirmed and should lead to the use of resistance genes from the bread wheat cultivar Loros and the line AUS 4930, which is also resistant to *Pratylenchus thornei* (Nicol, 1996), or resistance genes from wild species. Total or intermediate resistance of the *T. ovatum* 79, *T. variabile* 1, and *T. ventricosum* 11 tetraploids clearly presents a potential for introgression. Table 6 summarizes the major genotypes that included total or intermediate resistance to the various nematode populations and species tested. Plant breeders still have to solve the problems related to genetic incompatibility and to the expression of resistance at different ploidy levels (Auriau *et al.*, 1992). Synthetic hexaploid wheats created by crossing *T. turgidum* Langdon with *T. tauschii* AUS 18913 or CPI 110813 expressed an intermediate resistance that is acceptable for practical use. The creation of cultivars with total or intermediate resistances should ensure a reasonable management of the parasite populations by avoiding in part the problems raised by resistance breaking from selection pressure and by biocenotic imbalance in the species targeted or not by the genes involved (Lasserre *et al.*, 1996).

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