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Spectrum of resistance to root-knot nematodes and inheritance of heat-stable resistance in in pepper (*Capsicum annuum* L.)

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Abstract *Capsicum annuum* L. has resistance to root-knot nematodes (RKN) (*Meloidogyne* spp.), severe polyphagous pests that occur world-wide. Several single dominant genes confer this resistance. Some are highly specific, whereas others are effective against a wide range of species. The spectrum of resistance to eight clonal RKN populations of the major *Meloidogyne* species, *M. arenaria* (2 populations), *M. incognita* (2 populations), *M. javanica* (1 population), and *M. hapla* (3 populations) was studied using eight lines of *Capsicum annuum*. Host susceptibility was determined by counting the egg masses (EM) on the roots. Plants were classified into resistant (R; EM ≤ 5) or susceptible (H; EM >5) classes. The french cultivar Doux Long des Landes was susceptible to all nematodes tested. The other seven pepper lines were highly resistant to *M. arenaria*, *M. javanica* and one population of *M. hapla*. Variability in resistance was observed for the other two populations of *M. hapla*. Only lines PM687, PM217, Criollo de Morelos 334 and Yolo NR were resistant to *M. incognita*. To investigate the genetic basis of resistance in the highly resistant line PM687, the resistance of two progenies was tested with the two populations of *M. incognita*: 118 doubled-haploid (DH) lines obtained by androgenesis from F_1 hybrids of the cross between PM687 and the susceptible cultivar Yolo Wonder, and 163 F_2 progenies. For both nematodes populations, the segregation patterns 69 R / 49 S for DH lines and 163 R / 45 S for F_2 progenies were obtained at 22°C and at high temperatures (32°C and 42°C). The presence of a single dominant gene that totally prevented multiplication of *M. incognita* was thus confirmed and its stability at high temperature was demonstrated. This study confirmed the value of *C. annuum* as a source of complete spectrum resistance to the major RKN.

Key words *Capsicum annuum* L. · Solanaceae · *Meloidogyne* spp. · Nematode resistance · Dominant *Me3* gene

Introduction

Plant parasitic nematodes are major pests world-wide causing crop losses of about 100 billion US dollars each year (Cai et al. 1997). This amounts to 10% of world crop production and one-third of all losses attributed to pests and diseases (Whitehead 1998). Root-knot nematodes (RKN) (*Meloidogyne* spp.) are obligate plant endoparasites, found throughout the world, mainly in tropical, subtropical and warm-temperate areas in which several nematode generations can be completed per year. These polyphagous and parthenogenetic nematodes are one of the principal pathogens on many Solanaceous crops throughout the world (Khan and Haider 1991; Sasser 1977). There are four economically important RKN *Meloidogyne* species, *M. incognita* (Kofoid and White) Chitwood, *M. arenaria* (Neal) Chitwood, *M. javanica* (Treub) Chitwood and *M. hapla* Chitwood (Mai 1985; Triantaphyllou 1985), which may be present separately or together. Cultivars resistant to these pests would render soil fumigant and toxic systemic nematicides unnecessary and would be an efficient, durable and nonpolluting method of control. However, resistance genes are rare and limited to a few botanical families. Resistance against RKN usually involves a hypersensitive response. This consists of local root-cell necrosis which prevents the invading juveniles from progressing beyond the infection site (Kaplan and Keen 1980) and inhibits the development of the multinucleate 'giant' cells, essen-

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tial to the development of egg-laying females. As a result, nematode reproduction is almost totally prevented (Whitehead 1998).

Resistance to RKN was first identified 50 years ago in an accession (PI 128657) of *Lycopersicum peruvianum* (L.) Mill., a wild relative of edible tomato (*Lycopersicon esculentum* Mill.) that grows in the western coastal region of south America (Watts 1947). The dominant *Mi* gene of tomato, located on chromosome 6 (Aarts et al. 1991; Erion et al. 1991), confers resistance to *M. incognita*, *M. arenaria* and *M. javanica* (Gilbert and McGuire 1956). Many tomato breeding programs used this resistance source and the *Mi* gene has now been cloned (Milligan et al. 1998). Nevertheless, it has little effect against *M. hapla* (Roberts and Thomason 1989) and some virulent *M. incognita* and *M. arenaria* isolates (Roberts and Thomason 1986; Roberts et al. 1990), and it does not function effectively at temperatures above 28°C (Ammati et al. 1986). A number of RKN resistance genes have since been discovered among diverse members of the Solanaceae, such as tobacco (Powers et al. 1986), tomato (Ammati et al. 1985; Cap et al. 1993; Yaghoobi et al. 1995; Veremis and Roberts 1996), potato (Janssen et al. 1997), eggplant (Boiteux and Charchar 1996) and wild species such as *Solanum sisymbriifolium*, *Solanum wercewiezii* or *Solanum torvum* (Daunay and Dalmasso 1985). Some are used in breeding programmes to develop nematode-resistant cultivars (Fassuliotis 1987).

In pepper (*Capsicum spp.*), the search for resistance to RKN has been on going for some time because parasitism of susceptible plants results in severe yield losses (Lindsey and Clayshutte 1982; Fery and Dukes 1984; Thies et al. 1997). As early as 1956, Hare tested a collection of 162 accessions of pepper for reaction to *M. incognita acrita* Chitwood. Four varieties, all small-fruited hot peppers, were classified as highly resistant and 14 as moderately resistant. A dominant gene for resistance to *M. incognita acrita*, *N*, has been identified in the *C. frutescens* L. 'Santanka XS' line. This gene had variable efficiency limited to certain *Meloidogyne* species when transferred into susceptible cultivars (Hare 1956). More recently, Di Vito and Saccardo (1979) and Di Vito et al. (1992) have discovered high levels of resistance to RKN in some lines of *Capsicum chacoense* Hunz., *Capsicum chinense* Jacq. and *Capsicum frutescens*. Hendy et al. (1983) found that some *C. annuum* L. accessions were resistant to RKN populations. Two new *Capsicum annuum* lines, PM217 and PM687, resistant to a wide variety of RKN populations, were discovered in 1985. At least five main dominant genes are thought to exist, all acting individually in a gene-for-gene interaction.

C. annuum is one of the most cultivated vegetable species after tomato in the United States (Fery and Thies 1997) and in the less-developed countries (FAO 1996). We report here results on three aspects of RKN resistance in *C. annuum*. Resistance of eight lines of *C. annuum* against eight clonal populations of the four main species of *Meloidogyne* was evaluated, and the effect of high temperatures on the resistance of these lines was assessed. Finally, the genetic basis of the resistance of the PM687 line to *M. incognita* was studied at normal and high temperatures.

Materials and methods

Plant material

Eight accessions of *C. annuum* L. from the INRA collection in Montfavet (France) were evaluated. They were from different geographic origins and are all currently used in breeding programmes. Their main characteristics are given in Table 1.

Table 1 List of pepper (C. annuum) accessions characterised for their resistance to RKN

Code	Name of PI	Origin	Characteristics
YW	YoloWonder	Inbred line from Uniersity of California (USA), derived from the accession California Wonder	Parent of several varieties currently cultivated
PM687	PI 322719	Line from local population (India)	Slightly susceptible to *Oidium* and partially resistant to *Xanthomonas vesicatoria* (Doïdoge) Dowson and to *Leveillula taurica* Arnaud (Daubèze, personal communication)
PM217	PI 201234	Line from University of California (USA), originating from Central America, closely related to the wild type	Resistant to *Phytophthora capsici* Leonian (Pochard et al. 1976)
CM334	Criollo de Morelos 334	Line from INIA (Mexico)	Resistant of *P. capsici* (Palloix et al. 1990) and to potyviruses (Dogimont et al. 1996)
YNR	Yolo NR	Line derived from the accesion 45107 Santanka xS(USA)	Line carrying the dominant resistance gene, *N* giving resistance to *M. incognita acrita* (Hare 1956)
H3	H3	Line from local population (Ethiopy), obtained fromcrosses between local and Kenyan populations	Resistant to *L. taurica* (Daubeze et al. 1995)
SC81	SC81	Inbred line from Cuba	Resistant to various pepper viruses (Palloix, personal communication)
DLL	Doux Long des Landes	Line from a french local population (France)	Susceptible to RKN

Tomato plants (*L. esculentum* Mill.) were also studied as a reference for goodness-of-fit to infestation, cv Saint Pierre being susceptible to all RKN, and cv. Piersol (with the *Mi* resistance gene) being resistant to the three main species of *Meloidogyne* (*M. incognita, M. arenaria, M. javanica*).

The genetic basis of resistance to *M. incognita* was studied using 163 plants from the F_2 progeny and 118 androgenetic doubled haploid lines (DH) from the intraspecific F_1 hybrid 'PM687 x YW'. The DH lines were obtained by in vitro culture of F_1 anthers, chromosome doubling by colchicine treatment, self-fertilisation and growth of the DH plants as described by Dumas de Vaulx et al. (1981).

Nematode populations

Eight *Meloidogyne* populations, reared from a single egg mass and maintained on the host tomato *L. esculentum* cv Saint Pierre, were tested. They were taken from the collection of the 'Laboratoire de Nématologie' of the INRA research centre in Antibes. There were two *M. arenaria* (from Marmande, France and Saint Benoit, France), two *M. incognita* (from Calissane, France and Morelos, Mexico), one *M. javanica* (from Avignon, France) and three *M. hapla* (from Canada, England, and La Mole, France) populations. The identity of the populations, at the species level, was checked by determining their isoesterase phenotype before inoculation (Dalmasso and Berge, 1978).

Resistance tests to *Meloidogyne*

Pepper seeds were sown individually in 50-ml polyethylene plastic tubes filled with steam-sterilised sandy soil, irrigated every day. Plants were grown in a growth chamber maintained at 22°C (± 2°C) with a 16-h light cycle. Plants were infested by depositing 24–72-h-old second-stage juveniles of the various *Meloidogyne* isolates into two holes, 2-cm deep, around the plant roots. Juveniles were obtained in a mist chamber, from previously inoculated tomato roots. Seven-week-old seedlings at the five-leaf stage were inoculated with a water suspension of 500 juveniles per seedling. This level of inoculum was based on that used in a previous methodological study of resistance and host lines (Hendy 1984). Ten replicates were produced for each line and each population of nematodes. St. Pierre (susceptible control) and Piersol (with *Mi* gene) tomatoes were included in the tests. Plants were arranged in a completely randomised design. Six weeks after inoculation, which allowed completion of one nematode generation (Tyler 1933), plants were harvested, carefully washed individually with tap-water, then stained for 20 min in a aqueous solution of eosin (0.45%; Fluka Co.), which specifically stains egg masses (EM) red. The roots were then rinsed and examined under a magnifying glass and the number of EM counted for each pepper plant. Lines were considered to be resistant (R) when the mean number of EM was less or equal to 5, and susceptible (S) if there were more than five EM.

The effect of temperature was tested on a range of lines (parental lines, F_1, ten susceptible and ten resistant DH lines). In one experiment, plants were treated at 32°C (± 2°C) for 1 week immediately before infestation (D_{-7} to D_0), 1 week immediately after infestation (D_0 to D_7), 1 week beginning 7 days after infestation (D_7 to D_{14}), or from 1 week before infestation to the end of the cycle (D_{-7} to D_{21}). The plants were held in growth chambers at 22°C for the other period of the 4 weeks which allowed completion of one nematode generation at this temperature. The number of EM were then counted. In another experiment, the plants were treated at 42°C (± 2°C) (for 5–6 h per day then at 32°C) during the same infection phases and for the same time periods of treatment as described for 32°C.

Statistical analysis

Data were analysed using Student's *t* test with a significance level of $P \leq 0.05$ (one-way analysis of variance). Means of EM scores were compared using a Newman-Keuls multiple range test with a significance level of $P \leq 0.05$. The genetic basis of resistance in PM687 was determined by chi-square tests on F_2 and DH progeny data to determine goodness of fit to the hypothetical segregation ratios in resistant and susceptible classes.

Results

Evaluation of the parental lines with the eight *Meloidogyne* populations

The pepper cultivar DLL and the tomato *L. esculentum* cv St. Pierre were susceptible to all *Meloidogyne* populations tested (Table 2). The tomato cv Piersol (carrying the *Mi* gene) was only susceptible to *M. hapla* populations. The other seven pepper lines were highly resistant to *M. arenaria*, *M. javanica* and *M. hapla* from England. Differences were observed in resistance to the other two populations of *M. hapla* (from La Mole and Canada). Only lines PM687, PM217, CM334 and YNR were resistant to *M. incognita.*

Stability of resistance at high temperature

The root systems of the pepper plants tested at 32°C and 42°C were smaller and produced less EM than those kept at 22°C. Nevertheless, the resistance to *M. incognita* of the PM687, PM217, CM334 and YNR cultivars showed that their resistance was stable up to 42°C (Table 2), regardless of the duration of heat treatment (1 week before or throughout the cycle) during nematode infection phases (Table 2, data shown for PM687). In contrast, the resistance of the tomato cv Piersol was lost at 32°C.

Segregation of parents YW, PM687, F_1, F_2 and DH progenies for resistance to *M. incognita*

All plants from the F_1 progenies of the cross 'PM687 x YW' were resistant to *M. incognita* isolates Calissane and Morelos, even at high temperatures (32°C and 42°C) (Table 2). The two *M. incognita* populations tested on 118 DH lines produced the same segregation pattern, 69R/49 S. Nevertheless, *M. incognita* Morelos seemed to be more aggressive in terms of EM production on the roots of susceptible material (Fig 1). In fact, the 69 resistant DH lines had less than 0.1 EM (mean value of ten replications) when infested with *M. incognita* Calissane and up to 5 EM when infested with *M. incognita* Morelos. Moreover, only eight susceptible DH lines had more than 70 EM when infested with *M. incognita* Calissane and 31 susceptible DH lines had more than 70 EM when infested with *M. incognita* Morelos.

The segregation obtained with the DH progeny was unaffected by high temperatures (Table 3). It was not

Table 2 Mean number of egg-masses in inbred pepper accessions, for eight clonal populations of RKN (values for ten replicates)

Pepper-progenitor	Mean egg-masses per root system[1]										
		M. arenaria Marmande Fr.	*M. arenaria* St. Benoit Fr.	*M. javanica* Avignon Fr.	*M. hapla* England	*M. hapla* Canada	*M. hapla* La Mole Fr.	*M. incognita* Morelos	*M. incognita* Calissane Fr.		
		22°C	22°C	22°C	22°C	22°C	22°C	22°C	22°C	32°C[3]	42°C[3]
DLL		66.4 *cde*	87.2 *c*	258.4 *a*	nt[2]	nt[2]	nt[2]	160.5 *b*	111.9 *bc*	159.6 *b*	44.7 *de*
YW		0 *f*	0 *f*	0 *f*	0 *f*	15.7 *ef*	7.2 *f*	80.4 *cd*	76.8 *cd*	51.6 *de*	43.3 *de*
SC81		0 *f*	0 *f*	0 *f*	nt[2]	nt[2]	nt[2]	63.3 *de*	52.9 *de*	50.0 *de*	0 *f*
H3		0 *f*	0 *f*	0 *f*	0 *f*	17.8 *ef*	7.9 *f*	66.0 *de*	49.0 *de*	2.2 *f*	0 *f*
PM687		0 *f*	0 *f*	0 *f*	0 *f*	28.2 *e*	0 *f*	0 *f*	0 *f*	0 *f*	0 *f*
PM217		0 *f*	0 *f*	0 *f*	0 *f*	75.9 *de*	0 *f g*	0.2 *f*	0.1 *f*	0 *f*	0 *f*
CM334		0 *f*	0 *f*	0 *f*	0 *f*	138.2 *b*	98.0 *bc*	0.1 *f*	0 *f*	0 *f*	0 *f*
YNR		0 *f*	0 *f*	0 *f*	nt[2]	nt[2]	nt[2]	0 *f*	0 *f*	0 *f*	0 *f*
Tomato plant(control)	*L. esculentum* cv St. Pierre	35.1 *ef*	142.6 *b*	58.2 *de*	123.2 *b*	130.7 *ab*	57.0 *cde*	68.9 *cde*	189.6 *b*	205.0 *b*	46.7 *de*
	L. esculentum cv Piersol (with *Mi* gene)	0.2 *f*	0 *f*	6.2 *f*	138.8 *bcd*	237.0 *ab*	169.5 *b*	1.2 *f*	0.5 *f*	88.2 *bc*	plants died

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[1] Numbers of egg-masses followed by the same letter are ot statistically different according to the Newman-Keuls multiple range test, with a significance level of P £ 0.05

[2] Not tested

[3] Plants were maintained at 32°C and treated at 42°C only for 5–6 h per a day from 1 week before infestation to the end of the cycle

Table 3 Stability of resistance of *M. incognita* Calissane at high temperatures, for the cultivars YW and PM687 and their F1 and DH progenies (data are based on ten replicates). D_0: day of infestation. R: resistant (EM < 5 EM). S: susceptible (EM > 5 EM)

Treatment	Parental lines			Susceptible DH lines tested					Resistant DH lines tested				
	YW	PM687	F_1	DH128 & DH135	DH146 & DH150	DH152 & DH103	DH106 & DH116	DH129 & DH184	DH107 & DH110	DH118 & DH120	DH133 & DH134	DH160 & DH161	DH169 & DH173
22°C ± 2°C													
D_{-7} to D_{42}	S	R	R	S	S	S	S	S	R	R	R	R	R
32°C ± 2°C													
D_{-7} to D_0	S	R	R	S	–	–	–	–	R	–	–	–	–
D_0 to D_7	S	R	R	–	S	–	–	–	–	R	–	–	–
D_7 to D_{14}	S	R	R	–	–	S	–	–	–	–	R	–	–
D_{14} to D_{21}	S	R	R	–	–	–	S	–	–	–	–	R	–
D_{-7} to D_{21}	S	R	R	–	–	–	–	S	–	–	–	–	R
42°C ± 2°C													
D_{-7} to D_0	S	R	R	S	–	–	–	–	R	–	–	–	–
D_0 to D_7	S	R	R	–	S	–	–	–	–	R	–	–	–
D_7 to D_{14}	S	R	R	–	–	S	–	–	–	–	R	–	–
D_{14} to D_{21}	S	R	R	–	–	–	S	–	–	–	–	R	–
D_{-7} to D_{21}	S	R	R	–	–	–	–	S	–	–	–	–	R

Fig. 1 Distribution of resistant (R) and susceptible (S) DH lines (mean values of ten replicates) infested with two populations of *M. incognita* at 22 °C (data are grouped in classes of x ± 2.5 EM)

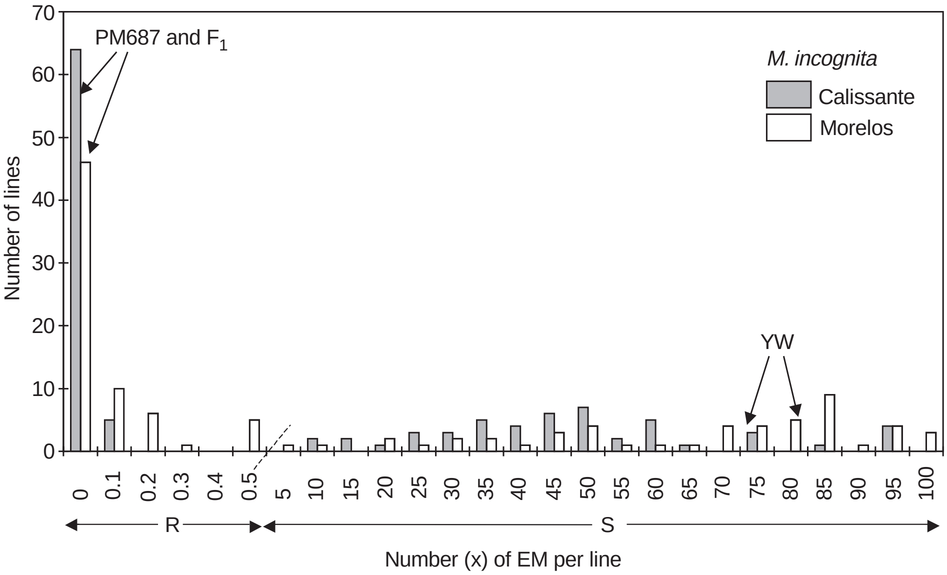

Table 4 Reaction of parents and F1, and segregation of DH and F2 progenies, for resistance to *M. incognita* Calissane at 22°C (same segregation obtained with *M. incognita* Morelos)

Parent or cross	Number of plants			Expected ratio R : S	χ^2	*P* value (%)
	Total	R^a	S^a			
YW	10	0	10			
PM687	10	10	0			
F_1	10	10	0	1 : 0		
DH	118^b	69^b	49^b	1 : 1^c	3.4	6.56
				3 : 1^d	17.2	0.03
				1 : 3^e	70.5	0
F_2	163	118	45	3 : 1^c	0.6	44.20
				15 : 1^d	126.9	0
				9 : 7^e	17.2	0.03

[a] R = resistant, S = S susceptible

[b] Ten replicates for each line

[c,d,e] Expected ratio based respectively on one, two independent, two complementary dominant genes

significantly different from the 1 R:1 S segregation (Table 4) expected for one gene (*P* = 5–10%) but differed significantly from that expected for two independent (3 R:1 S) or complementary (1 R:3 S) genes (*P* <1%). The excess of resistant plants may be due to a distortion in allele frequencies in the DH progeny in favor of PM687 or the presence of two genetically linked resistance genes. In this case, the recombination rate would be 16.9%. We analysed 163 F_2 progenies and found that 72.4% of the plants were resistant. This was consistent with the notion of a single dominant resistance gene, stable at high temperature, with a higher *P* value (*P* = 40–50%) determining resistance against *M. incognita.*

Discussion

The various RKN resistance tests on pepper material demonstrated a diversity in the range and specificity of resistance in *C. annuum* lines. These lines were highly resistant to the three main RKN species (*M. arenaria, M. incognita*, *M. javanica*), but there were differences in resistance to the various populations of *M. hapla*. These results and those of Hare (1956), Di Vito and Saccardo (1979) and Di Vito et al. (1992) suggest that this genus is a useful source of broad-spectrum resistance.

The results obtained for *M. incognita* with the F_1 hybrids between the highly resistant line PM687 and the susceptible host parent YW indicated that resistance to both populations was completely dominant. This is consistent with the results obtained by Hendy (1984) in which the F_1 hybrids ‘PM687 x Yolo Y (other susceptible cultivar)’, ‘PM687 x YW’ and ‘PM687 x DLL’ were all resistant. A single dominant gene *Me3*, conferring resistance to *M. incognita* Calissane, was thought to exist based on an analysis of 56 F_2 progenies of the cross ‘PM687 x Yolo Y’ and 44 DH lines obtained from the F_1 hybrid ‘PM687 x YW’ (Hendy 1984). However, the results of crossing PM687 with the DLL cultivar (165 F_2 analysed) were also consistent with resistance based on two genes. Our results, with segregation ratios for resistance of 1 R : 1 S in the DH lines and 3 R : 1 S in F_2 progenies, clearly support the notion of a single resistance gene.

The mean percentage of resistant DH lines was 58. A result that suggests the resistance gene may increase the chances of survival (possibly due to greater vigor) of seedlings that bear it. The mean percentage of resistant

F_2 clones was 72 (of 163 lines); a result that is not consistent with distortion of segregation in favor of resistant lines. This suggests that in vitro anther culture results in a selection pressure leading to segregation distortion. Allard (1956) previously proposed that DH progenies were less informative than F_2 progenies and Lefebvre et al. (1995) identified several genomic regions in pepper DH lines with aberrant segregation ratios, often favoring the cultivated parent. Nevertheless, analysis of the recombination of parental genes is simplified by the absence of allelic interactions, as all the loci are homozygous (Pochard et al. 1986), and they are useful for mapping projects because self-pollination renders them perennial material, thus facilitating repeat independent tests on every genotype and to map unlimited numbers of markers.

The heat stability of resistance gene expression in the line PM687 was also demonstrated (Tables 2, 3) as for the other pepper lines, but not for the *Mi* gene (cv Piersol). Zacheo et al. (1988) suggested that this decrease in resistance in tomato plants containing the *Mi* gene results from a decrease in superoxide and hydrogen peroxide (linked to lignin synthesis, Bell 1981) due to an increase in superoxide dismutase (SOD) and catalase activities. However, the way in which temperature stress functions in physiological terms is unknown (Ashburner and Bonner 1979; Cooper and Ho 1983). High temperature seems to repress the transcription of the *Mi* gene (Zacheo et al. 1988). The resulting shift in enzymes or substrates leads to changes in resistance to nematodes. This does not seem to occur in resistant pepper lines (Tables 2, 3), or in some tomato cultivars (Roberts and May 1986). Such plants are then able to control RKN populations in soil at temperatures above 30°C, a major advantage in tropical, subtropical and warm-temperate areas where nematodes proliferate.

The resistance in PM687, PM217, CM334 and YNR was highly effective against all RKN species tested (Table 2). Therefore, it would be of interest to investigate whether the same or different genes are involved in resistance to nematodes and whether these genes are allelic with *Mi*. Resistance genes in pepper seem to be different from the *Mi* resistance gene in tomato. Firstly, *Me* and *Mi* genes do not confer an identical resistance spectrum. *Me* genes control all three main species RKN isolates and some *M. hapla* populations. *Mi* is inefficient in the presence of *M. hapla* (Roberts and Thomason 1989), and against virulent isolates of *M. incognita, M. arenaria* (Roberts and Thomason 1986; Roberts et al. 1990) and *M. javanica* (Table 2). Nevertheless, these virulent isolates are controlled by *Me* genes (Hendy et al. 1983, 1985, Table 2). Moreover, the pepper cultivars are resistant to *M. incognita* at high temperature (32–42°C), unlike plants possessing the *Mi* gene. Finally, RKN selected for virulence on *Mi*-resistant tomatoes are not able to reproduce on *Me1*- or *Me3*-resistant peppers, and RKN selected for virulence on *Me3*-resistant peppers are not able to reproduce on *Mi*-resistant tomatoes (Castagnone-Sereno et al. 1996). This evidence points to differences in the resistance mechanisms induced by the *Me* and *Mi* genes. The pepper maps in progress (Lefebvre et al. 1997), and the syntheny observed in the tomato and pepper maps (Lefebvre et al. 1995), should allow a comparison of these *Me* and *Mi* resistance genes to RKN.

The higher susceptibility to *M. incognita* in the cultivar DLL compared to the YW, H3 or SC81 cultivars (Table 2) suggests that some minor genes are also present in these latter pepper lines. A similar quantitative resistance was also noticed in cucurbit cultivars infected with *M. hapla* by Berge et al. (1974) who concluded that the responses may reflect the presence of one or a few partial resistance genes by contrast with the stronger reaction of resistant tomatoes. A molecular approach should provide new insights into the relationships between the diverse RKN resistance genes identified in *C. annuum.*

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