Characterization of Resistance Conferred by the *N* gene to *Meloidogyne arenaria* Races 1 and 2, *M. hapla*, and *M. javanica* in Two Sets of Isogenic Lines of *Capsicum annuum* L.

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ABSTRACT. Two isogenic sets of bell pepper (*Capsicum annuum* L.) lines (differing at the *N* root-knot nematode resistance locus) were characterized for resistance to *Meloidogyne arenaria* (Neal) Chitwood races 1 and 2, *M. hapla* Chitwood, and *M. javanica* (Treub) Chitwood in greenhouse and growth chamber tests. The isogenic sets of *C. annuum* were ‘Charleston Belle’ (NN) and ‘Keystone Resistant Giant’ (nn-recurrent parent), and ‘Carolina Wonder’ (NN) and ‘Yolo Wonder B’ (nn-recurrent parent). *Meloidogyne arenaria* race 1 is pathogenic to *C. annuum*. ‘Charleston Belle’ and ‘Carolina Wonder’ exhibited high resistance to *M. arenaria* race 1. Their respective recurrent backcross parents, ‘Keystone Resistant Giant’ and ‘Yolo Wonder B’, were susceptible to *M. arenaria*. *Meloidogyne arenaria* race 2 and *M. javanica* are not highly pathogenic to pepper. However, ‘Charleston Belle’ and ‘Carolina Wonder’ both exhibited higher ($P \leq 0.05$) resistance to *M. arenaria* race 2 and *M. javanica* than ‘Keystone Resistant Giant’ and ‘Yolo Wonder B’. *Meloidogyne hapla* is pathogenic to pepper. Both ‘Charleston Belle’ and ‘Carolina Wonder’ and their respective recurrent parents, ‘Keystone Resistant Giant’ and ‘Yolo Wonder B’, were susceptible to *M. hapla*. We concluded that the *N* gene confers resistance to *M. arenaria* races 1 and 2, and *M. javanica* in *C. annuum*, but the *N* gene does not condition resistance to *M. hapla*.

The root-knot nematodes *Meloidogyne incognita* (Kofoid & White) Chitwood, *M. arenaria*, *M. javanica*, and *M. hapla* are major pests in bell pepper (*Capsicum annuum*) growing areas of the United States and throughout the world (Di Vito et al., 1985; Lamberti, 1979; Sasser and Freckman, 1987; Thies et al., 1997; Thomas et al., 1995). Preplant soil fumigation with methyl bromide is currently the primary control method for root-knot nematodes in bell pepper, but the proposed cessation of importation and production of this fumigant in the United States has focused significant interest in host resistance.

Information about resistance of *C. annuum* to *Meloidogyne* Goeldi sp. is limited. Martin (1948) observed resistance to root-knot nematodes (unidentified *Meloidogyne* sp.) in a pungent line of *C. annuum* and subsequently released the root-knot nematode resistant cayenne pepper ‘Carolina Hot’ (Martin and Crawford, 1958). Fery et al. (1986) selected ‘Carolina Cayenne’ from a population of ‘Carolina Hot’ that was segregating for many traits including resistance to *M. incognita*. ‘Carolina Cayenne’ is resistant to *M. incognita* races 1, 2, 3, and 4 (Zamora et al., 1994) and *M. arenaria* races 1 and 2 (Noe, 1992). Hare (1956) identified four pepper cultivars with high resistance to the subspecies *M. incognita acrita* Chitwood (no longer recognized as a taxon). Two of these cultivars, ‘Santanka xS’ and ‘405B Mexico’, were also resistant to *M. incognita*, *M. javanica*, and *M. arenaria* (races not specified), but were not resistant to *M. hapla* (Hare, 1956). Hare (1957) demonstrated that resistance to *M. incognita* in

‘Santanka xS’ and ‘405B Mexico’ was conditioned by a single dominant gene which was designated the *N* gene. Hare (1966) backcrossed the *N* gene into pimiento pepper, and subsequently released the *M. incognita*-resistant pimiento pepper cultivar, ‘Mississippi Nemaheart’. Resistance to *M. incognita* in ‘Carolina Cayenne’ is also conferred by the *N* gene and an additional recessive gene (Fery and Dukes, 1996). Recently, ‘Charleston Belle’ and ‘Carolina Wonder’, the first bell pepper cultivars with resistance to *M. incognita*, were developed and released by scientists at the U.S. Vegetable Laboratory, U.S. Department of Agriculture (USDA), Agricultural Research Service (ARS), Charleston, S.C. (Fery et al., 1998). Both of these open-pollinated cultivars are homozygous for the *N* gene. These cultivars provide a feasible alternative to preplant fumigation of soil with methyl bromide for managing the southern root-knot nematode, *M. incognita*, in bell pepper plantings. However, the reaction of these resistant cultivars to the other major species of root-knot nematodes will be important in making cultivar recommendations and in designing cropping systems to manage the four major species of root-knot nematodes. The purpose of these studies was to determine whether the *N* gene confers resistance to *M. arenaria* races 1 and 2, *M. hapla*, and *M. javanica* in two sets of isogenic lines of *C. annuum* that differ in the presence or absence of the *N* gene.

Materials and Methods

NEMATODE INOCULUM. *Meloidogyne arenaria* races 1 and 2 (obtained from S.A. Lewis, Clemson Univ., Clemson, S.C.), and *M. hapla* and *M. javanica* (obtained from K. R. Barker, N.C. State Univ., Raleigh) were maintained in separate cultures on tomato (*Lycopersicon esculentum* Mill. ‘Rutgers’) in the greenhouse. Egg inocula for all tests were collected from tomato roots infected with the appropriate *Meloidogyne* sp. using 0.5% NaOCl (Hussey and Barker, 1973).

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PEPPER CULTIVARS. The pepper cultivars used in all experiments were 'Charleston Belle', 'Carolina Wonder', 'Keystone Resistant Giant', 'Yolo Wonder B', 'Mississippi Nemaheart', 'Carolina Cayenne', and 'California Wonder'. 'Charleston Belle' and 'Carolina Wonder' are *M. incognita*-resistant, open-pollinated bell pepper cultivars that were released by USDA-ARS (Fery et al., 1998). Both of these cultivars are homozygous for the *N* gene that confers resistance to *M. incognita*. 'Keystone Resistant Giant' and 'Yolo Wonder B' are both susceptible to *M. incognita*, and are the respective recurrent parental cultivars used in the backcross breeding procedure (six backcrosses) used to develop 'Charleston Belle' and 'Carolina Wonder' (Fery et al., 1998). 'Mississippi Nemaheart' is resistant to *M. incognita* (Hare, 1966) and is the source of the *N* gene for both 'Charleston Belle' and 'Carolina Wonder' (Fery et al., 1998). 'Carolina Cayenne' is resistant to *M. incognita* (Fery et al., 1986) and its resistance is conferred by the *N* gene and an additional recessive gene (Fery and Dukes, 1996). 'California Wonder' is susceptible to *M. incognita* (Fery and Dukes, 1996).

EXPERIMENTAL DESIGN. The seven pepper cultivars were evaluated in eight separate experiments for reactions to *M. arenaria* races 1 and 2, *M. hapla*, and *M. javanica*. The experimental design for all experiments was a randomized complete block with six replications. There were five plants of each cultivar per replicate.

GREENHOUSE EXPERIMENTS. Five experiments were conducted in the greenhouse: one each for *M. arenaria* race 1, *M. arenaria* race 2, and *M. hapla*, and two for *M. javanica*. Seedlings of each pepper cultivar were germinated and grown in flats containing Metro-Mix 360 (The Scotts Co., Marysville, Ohio) in the greenhouse. Day/night greenhouse temperatures were maintained at 26 ± 3 °C. After 16 to 21 d, 30 seedlings per cultivar were transplanted into a raised $4.0 \times 1.8 \times 0.25$ -m greenhouse bench containing a steam-pasteurized medium of 2 sandy loam soil : 1 fine washed river sand (v/v). At planting, 5 mL tap water containing ≈ 3000 eggs of the appropriate *Meloidogyne* sp./race were pipetted around the base of each plant. The greenhouse environment during the experiments was maintained as described previously for growth of seedlings. Eight to eleven weeks later, the root system of each plant was removed from the growing medium, washed, and rated for severity of root galling and egg mass production using a 1 to 5 scale in which: 1 = 0% to 3% root system galled or covered with egg masses, 2 = 4% to 25%, 3 = 26% to 50%, 4 = 51% to 80%, and 5 = >80% root system galled or covered with egg masses (Thies et al., 1998). Root gall and egg mass indices ≥ 3 were considered susceptible reactions. The fibrous roots were clipped from the tap root, cut into 1- to 2-cm pieces, and root fresh weight recorded. Eggs were extracted from the entire root sample by using 1.0% NaOCl (Hussey and Barker, 1973). Numbers of eggs were counted using a stereomicroscope. Nematode reproduction was assessed by calculating the reproduction factor (R) in which $R = P_f/P_i$, P_i = the initial inoculum level and P_f = the final inoculum level (Sasser et al., 1984).

GROWTH CHAMBER EXPERIMENTS. Three experiments were conducted in growth chambers: one each for *M. arenaria* race 1, *M. arenaria* race 2, and *M. hapla*. Seedlings were grown as described previously in the greenhouse experiments. Twenty-seven days after seeding, single seedlings (30 per cultivar) were transplanted into individual 19×3.8 -cm-diameter polyethylene Cone-tainers (volume = 158 cm^3) (Stueve & Sons, Inc., Corvallis, Ore.) that had been filled with the soil mixture described previously for the greenhouse experiments. About 3,000 eggs of the appropriate *Meloidogyne* sp. were suspended in 3 mL H_2O and

dispensed into the soil surrounding the root system of each plant; then the Cone-tainers were placed in growth chambers programmed to maintain a temperature of 25 °C (*M. hapla* experiment) and 27 °C (*M. arenaria* experiments) with a 16 h photoperiod provided by a combination of fluorescent and incandescent lamps. Visible radiation [measured with a LI-188B spectroradiometer with a LI-1990SB quantum sensor (LI-COR, Lincoln, Neb.)] was $258 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at the plant canopy during the light cycle. About 8 weeks later, each root system was removed from the Cone-tainer, washed, and rated for severity of root galling and for egg mass production using the 1 to 5 scale, and eggs were extracted from the roots and reproduction factor calculated as described above for the greenhouse experiments.

DATA ANALYSIS. Nematode egg and reproductive index data were $\log_{10}(x + 1)$ transformed to normalize the data before analysis (Noe, 1985). Data were analyzed using the GLM procedure of SAS for Windows System Version 6.12 (SAS Inst., Cary, N.C.) and means were separated using Duncan's multiple range test at $P \leq 0.05$.

Results and Discussion

Meloidogyne arenaria race 1 is pathogenic to certain pepper cultivars (Table 1). However, the *N* gene conditions resistance to *M. arenaria* race 1 in the *M. incognita*-resistant cultivars 'Charleston Belle' and 'Carolina Wonder' (Table 1). 'Charleston Belle' and 'Carolina Wonder' exhibited high resistance to *M. arenaria* race 1, while their respective recurrent backcross parents 'Keystone Resistant Giant' and 'Yolo Wonder B' were susceptible. 'Charleston Belle' and 'Carolina Wonder' had no visible root galling (gall index = 1.00 for both cultivars) in contrast to their respective recurrent backcross parents, 'Keystone Resistant Giant' and 'Yolo Wonder B', which exhibited moderate root galling (gall indices = 3.15 and 2.84, respectively, average of two tests). 'Charleston Belle' and 'Carolina Wonder' each had an average of 94% fewer eggs per gram fresh root weight than 'Keystone Resistant Giant' and 'Yolo Wonder B', respectively. The *M. incognita*-resistant controls 'Mississippi Nemaheart' and 'Carolina Cayenne' (both homozygous for the *N* gene) had minimal root galling, but nematode reproduction was equal to 'Keystone Resistant Giant' and 'Yolo Wonder B'. 'California Wonder' was the most susceptible cultivar with a root gall index = 3.36 and 11,494 eggs per g fresh root (average of two tests).

Meloidogyne arenaria race 2 is not highly pathogenic to pepper (Table 2). 'Charleston Belle' and 'Carolina Wonder' and their respective recurrent backcross parents, 'Keystone Resistant Giant' and 'Yolo Wonder B', exhibited little or no root galling in either the greenhouse or growth chamber test. However, in the growth chamber test, the homozygous *N* gene cultivars 'Charleston Belle' and 'Carolina Wonder' had 99% and 95% fewer ($P \leq 0.05$) eggs per gram fresh root weight than their respective recurrent backcross parental cultivars 'Keystone Resistant Giant' and 'Yolo Wonder B', indicating that the *N* gene conditions resistance against *M. arenaria* race 2. 'Charleston Belle' and 'Carolina Wonder' also had lower ($P \leq 0.05$) reproductive indices than their respective recurrent backcross parents, 'Keystone Resistant Giant' and 'Yolo Wonder B' in the growth chamber test. The increased susceptibility of 'Keystone Resistant Giant' and 'Yolo Wonder B' in the growth chamber test was probably due to the constant higher temperature (27 °C) in the growth chamber compared to the fluctuating ambient temperatures in the greenhouse. In growth chamber studies, numbers of *M. incognita*

Table 1. Gall indices, egg mass indices, numbers of eggs per gram fresh root weight, and reproductive index of *Meloidogyne arenaria* race 1 for two isogenic sets of *Capsicum annuum* cultivars (differing for the *N* gene) inoculated with *M. arenaria* race 1.²

Cultivar	Greenhouse test				Growth chamber test			
	Gall index ^y	Egg mass index ^y	No. eggs/g fresh root wt	Reproductive index ^x	Gall index ^y	Egg mass index ^y	No. eggs/g fresh root wt	Reproductive index ^x
Isogenic set I ^w								
Charleston Belle	1.00 a ^v	1.00 a	97 a ^u	0.37 a ^u	1.00 a	1.00 a	404 a ^u	0.06 a ^u
Keystone Resistant Giant	2.62 c	2.19 b	4274 b	2.00 b	3.68 d	3.43 d	4024 b	2.30 b
Isogenic set II ^t								
Carolina Wonder	1.00 a	1.00 a	86 a	0.16 a	1.00 a	1.00 a	182 a	0.03 a
Yolo Wonder B	2.69 c	2.04 b	2373 b	1.38 b	3.00 c	2.72 c	2492 b	0.92 b
Controls								
Mississippi Nemaheart	1.70 b	1.22 a	5210 b	2.84 b	1.72 b	1.51 b	4095 b	1.60 b
Carolina Cayenne	1.12 a	1.15 a	4139 b	3.67 b	1.78 b	1.69 b	4258 b	2.32 b
California Wonder	2.93 c	2.83 c	17036 b	3.93 b	3.80 d	3.25 d	5952 b	6.96 b

²Each plant was inoculated with ≈ 3000 eggs at transplanting. Data are means of six replicates ($n = 30$).

^yRated on a scale of 1 to 5; 1 = 0% to 3% root system galled or covered with egg masses, 2 = 4% to 25%, 3 = 26% to 50%, 4 = 51% to 80%, and 5 = >80% root system galled or covered with egg masses.

^xReproductive index = P_f (final population)/ P_i (initial population).

^w'Charleston Belle' (homozygous for *N* gene); 'Keystone Resistant Giant' (*nn*-recurrent backcross parent).

^vMean separation within columns by Duncan's multiple range test, $P \leq 0.05$.

^uData were $\log_{10}(x + 1)$ transformed before analysis. Untransformed data are shown.

^t'Carolina Wonder' (homozygous for *N* gene); 'Yolo Wonder' (*nn*-recurrent backcross parent).

eggs per gram fresh root were ≈ 4000 , 28,000, and 92,000 in 'Keystone Resistant Giant' grown at 24, 28, and 32 °C, respectively (Thies and Fery, 1998). The controls 'Mississippi Nemaheart' and 'Carolina Cayenne' (both homozygous for the *N* gene) also exhibited high resistance to *M. arenaria* race 2 in both tests. The check cultivar, 'California Wonder', exhibited a low degree of root galling (gall index = 1.87) in response to *M. arenaria* race 2, and numbers of eggs per gram fresh root weight were $38\times$ as great ($P \leq 0.05$) as for the other six cultivars (average of two tests). These results conflict with the differential host range test used for identification of *Meloidogyne* species and races,

which lists 'California Wonder' pepper as a host of *M. arenaria* race 1, but not *M. arenaria* race 2 (Taylor and Sasser, 1978). Differences between our results and those of Taylor and Sasser (1978) may be due to physiological differences in isolates of *M. arenaria* race 2 or to differences in interpretations of resistance. Taylor and Sasser (1978) defined susceptibility as >10 galls and >10 egg masses per root system ≈ 50 d after inoculation with root-knot nematodes. However, Taylor and Sasser (1978) also stated that susceptibility should ultimately be measured by reproduction, not by galling. In the present tests, ratings for severity of root galling (GI = 1.87) and egg mass production (EMI = 2.10) for

Table 2. Gall indices, egg mass indices, numbers of eggs per gram fresh root weight, and reproductive index of *Meloidogyne arenaria* race 2 for two isogenic sets of *Capsicum annuum* cultivars (differing for the *N* gene) inoculated with *M. arenaria* race 2.²

Cultivar	Greenhouse test				Growth chamber test			
	Gall index ^y	Egg mass index ^y	No. eggs/g fresh root wt	Reproductive index ^x	Gall index ^y	Egg mass index ^y	No. eggs/g fresh root wt	Reproductive index ^x
Isogenic set I ^w								
Charleston Belle	1.00 a ^v	1.00 a	319 a ^u	0.11 a ^u	1.00 a	1.00 a	45 ab ^u	0.01 a ^u
Keystone Resistant Giant	1.00 a	1.00 a	362 a	0.09 a	1.06 a	1.09 a	3187 cd	0.74 c
Isogenic set II ^t								
Carolina Wonder	1.00 a	1.00 a	306 a	0.06 a	1.00 a	1.00 a	74 ab	0.03 ab
Yolo Wonder B	1.00 a	1.00 a	267 a	0.06 a	1.02 a	1.04 a	1590 c	0.44 c
Controls								
Mississippi Nemaheart	1.00 a	1.00 a	947 a	0.17 a	1.00 a	1.00 a	34 a	0.00 a
Carolina Cayenne	1.00 a	1.00 a	290 a	0.12 a	1.00 a	1.00 a	624 b	0.12 b
California Wonder	2.15 b	2.27 b	20644 b	6.85 b	1.59 b	1.94 b	30107 d	9.27 c

²Each plant was inoculated with ≈ 3000 eggs at transplanting. Data are means of six replicates ($n = 30$).

^yRated on a scale of 1 to 5; 1 = 0% to 3% root system galled or covered with egg masses, 2 = 4% to 25%, 3 = 26% to 50%, 4 = 51% to 80%, and 5 = >80% root system galled or covered with egg masses.

^xReproductive index = P_f (final population)/ P_i (initial population).

^w'Charleston Belle' (*NN*); 'Keystone Resistant Giant' (*nn*-recurrent backcross parent).

^vMean separation within a column by Duncan's multiple range test, $P \leq 0.05$.

^uData were $\log_{10}(x + 1)$ transformed before analysis. Untransformed data are shown.

^t'Carolina Wonder' (*NN*); 'Yolo Wonder' (*nn*-recurrent backcross parent).

Table 3. Gall indices, egg mass indices, numbers of eggs per gram fresh root weight, and reproductive index of *Meloidogyne javanica* for two isogenic sets of *Capsicum annuum* cultivars (differing for the *N* gene) inoculated with *M. javanica*.^z

Cultivar	Greenhouse test I				Greenhouse test II			
	Gall index ^y	Egg mass index ^y	No. eggs/g fresh root wt	Reproductive index ^x	Gall index ^y	Egg mass index ^y	No. eggs/g fresh root wt	Reproductive index ^x
Isogenic set I ^w								
Charleston Belle	1.01 a ^v	1.01 a	272 a ^u	0.00 a ^u	1.00 a	1.00 a	8 a ^u	0.19 a ^u
Keystone Resistant Giant	1.22 b	1.06 a	493 b	0.03 ab	1.00 a	1.00 a	131 ab	0.33 b
Isogenic set II ^t								
Carolina Wonder	1.00 a	1.00 a	81 a	0.01 ab	1.00 a	1.00 a	65 ab	0.04 a
Yolo Wonder B	1.05 a	1.07 a	506 ab	0.14 b	1.00 a	1.01 a	977 b	0.30 ab
Controls								
Mississippi Nemaheart	1.00 a	1.00 a	249 a	0.00 ab	1.00 a	1.00 a	22 a	0.15 a
Carolina Cayenne	1.07 a	1.08 a	142 a	0.00 a	1.00 a	1.00 a	20 a	0.13 a
California Wonder	1.73 b	1.59 b	3715 b	1.57 c	1.30 b	1.31 b	11432 c	2.16 b

^zEach plant was inoculated with ≈ 3000 eggs at transplanting. Data are means of six replicates ($n = 30$).

^yRated on a scale of 1 to 5; 1 = 0% to 3% root system galled or covered with egg masses, 2 = 4% to 25%, 3 = 26% to 50%, 4 = 51% to 80%, and 5 = >80% root system galled or covered with egg masses.

^xReproductive index = P_f (final population)/ P_i (initial population).

^w'Charleston Belle' (NN); 'Keystone Resistant Giant' (nm-recurrent backcross parent).

^vMean separation within columns followed by Duncan's multiple range test, $P \leq 0.05$.

^uData were $\log_{10}(x + 1)$ transformed before analysis. Untransformed data are shown.

^t'Carolina Wonder' (NN); 'Yolo Wonder' (nm-recurrent backcross parent).

'California Wonder' would be considered in the resistant range; however, the numbers of eggs per gram fresh root (25,375) and the reproductive index (8.06) indicate that 'California Wonder' is susceptible to *M. arenaria* race 2 (average of two tests). Since the numbers of eggs per egg mass may vary greatly among egg masses, we consider numbers of eggs per gram fresh root and the associated reproductive index to be more accurate measures of resistance than counting egg masses or assigning an EMI based on the percentage of the root system covered with egg masses. Therefore, based on nematode reproduction, we consider 'California Wonder' to be susceptible to *M. arenaria* race 2 in our tests.

Meloidogyne javanica is not highly pathogenic to pepper (Table 3). Isolates of *M. javanica* are known to differ in pathogenicity to pepper and only $\approx 10\%$ of *M. javanica* populations parasitize pepper (Sasser and Carter, 1982). 'Charleston Belle' and 'Carolina Wonder' exhibited high resistance to *M. javanica*; e.g., essentially no root galling or nematode reproduction in both tests. However, severity of root galling and numbers of eggs per gram fresh root were greater ($P \leq 0.05$) for 'Keystone Resistant Giant' than for its resistant isogenic line, 'Charleston Belle', in the first greenhouse test with *M. javanica*. Likewise, reproduction of *M. javanica* for 'Keystone Resistant Giant' was greater (P

Table 4. Gall indices, egg mass indices, numbers of eggs per gram fresh root weight, and reproductive index of *Meloidogyne hapla* for two isogenic sets of *Capsicum annuum* cultivars (differing for the *N* gene) inoculated with *M. hapla*.^z

Cultivar	Greenhouse test				Growth chamber test			
	Gall index ^y	Egg mass index ^y	No. eggs/g fresh root wt	Reproductive index ^x	Gall index ^y	Egg mass index ^y	No. eggs/g fresh root wt	Reproductive index ^x
Isogenic set I ^w								
Charleston Belle	2.80 bc ^v	2.78 bc	16338 abc ^u	3.37 b ^u	2.67 b	2.76 bc	10058 a ^u	10.79 a ^u
Keystone Resistant Giant	2.71 abc	2.75 abc	14426 abc	3.37 bc	2.97 c	2.97 c	11071 a	8.72 a
Isogenic set II ^t								
Carolina Wonder	2.48 a	2.50 a	10590 a	1.39 a	2.08 a	2.05 a	5131 a	6.50 a
Yolo Wonder B	2.54 ab	2.60 ab	13146 ab	3.03 b	2.20 a	2.10 a	9678 a	8.60 a
Controls								
Mississippi Nemaheart	2.72 abc	2.65 abc	16224 abc	2.27 b	2.73 bc	2.67 bc	11138 a	7.17 a
Carolina Cayenne	2.83 c	2.88 c	21567 bc	2.83 b	2.58 b	2.60 b	9920 a	10.90 a
California Wonder	2.95 c	2.89 c	22970 c	5.15 c	2.75 bc	2.74 bc	13477 a	10.52 a

^zEach plant was inoculated with ≈ 3000 eggs at transplanting. Data are means of six replicates ($n = 30$).

^yRated on a scale of 1 to 5; 1 = 0% to 3% root system galled or covered with egg masses, 2 = 4% to 25%, 3 = 26% to 50%, 4 = 51% to 80%, and 5 = >80% root system galled or covered with egg masses.

^xReproductive index = P_f (final population)/ P_i (initial population).

^w'Charleston Belle' (NN); 'Keystone Resistant Giant' (nm-recurrent backcross parent).

^vMean separation within columns by Duncan's multiple range test, $P \leq 0.05$.

^uData were $\log_{10}(x + 1)$ transformed before analysis. Untransformed data are shown.

^t'Carolina Wonder' (NN); 'Yolo Wonder' (nm-recurrent backcross parent).

≤ 0.05) than for 'Charleston Belle' in the second greenhouse test. These results suggest that the *N* gene conditions some level of resistance to *M. javanica*. Similar trends of greater reproduction of *M. javanica* were observed for 'Yolo Wonder B' compared to its resistant isogenic line, 'Carolina Wonder'. The check cultivar 'California Wonder' exhibited low levels of root gall (gall index = 1.51) and numbers of eggs per gram fresh root weight were 31× as great ($P \leq 0.05$) as for the other six cultivars (average of two tests). It would be expected that greater differences between the susceptible parents and resistant isolines for root gall severity and nematode reproduction would have been observed if we had used an isolate of *M. javanica* that was more pathogenic to pepper than the one used in our tests.

Meloidogyne hapla is pathogenic to pepper. All seven pepper cultivars tested were susceptible to *M. hapla* in the greenhouse test and the growth chamber test (Table 4). Gall indices ranged from 2.28 to 2.85, and numbers of eggs per gram fresh root ranged from 7860 to 18,225 for 'Carolina Wonder' and 'California Wonder', respectively (average of two tests). Hare (1957) also observed that *C. annuum* cultivars resistant to *M. incognita*, *M. arenaria*, and *M. javanica* were not resistant to *M. hapla*. Our results confirm susceptibility of *C. annuum* to *M. hapla* and demonstrate that the *N* gene does not confer resistance to *M. hapla* in either pair of isogenic pepper lines.

Our results demonstrate that the *N* gene, which confers resistance to *M. incognita* in *C. annuum*, also confers resistance to *M. arenaria* races 1 and 2, and *M. javanica*. Hare (1957) reported that *C. annuum* cultivars resistant to *M. incognita* were also resistant to *M. arenaria* and *M. javanica*, but was unable to conclude that the same gene controlled resistance to all three *Meloidogyne* species. By using two sets of isogenic lines ('Charleston Belle' and 'Keystone Resistant Giant', and 'Carolina Wonder' and 'Yolo Wonder B'), we demonstrated that the *N* gene also conditions resistance to *M. arenaria* races 1 and 2 and *M. javanica*. Knowledge of the specificities of resistance to *Meloidogyne* sp. conditioned by the *N* gene is essential in both the development of root-knot resistant bell pepper cultivars and the development of vegetable cropping systems designed to manage various species of root-knot nematodes. Root-knot resistant pepper cultivars such as 'Charleston Belle' and 'Carolina Wonder' will allow successful production of bell peppers in soils that are heavily infested with *M. incognita*, *M. arenaria* races 1 and 2, and *M. javanica*. However, it will be important to identify alternative sources of resistance to *M. hapla* in *C. annuum*.

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