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Response of Resistant and Susceptible Bell Pepper (*Capsicum annuum*) to a Southern California *Meloidogyne incognita* Population from a Commercial Bell Pepper Field

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Abstract: To determine the presence and level of root-knot nematode (*Meloidogyne* spp.) infestation in Southern California bell pepper (*Capsicum annuum*) fields, soil and root samples were collected in April and May 2012 and analyzed for the presence of root-knot nematodes. The earlier samples were virtually free of root-knot nematodes, but the later samples all contained, sometimes very high numbers, of root-knot nematodes. Nematodes were all identified as *M. incognita*. A nematode population from one of these fields was multiplied in a greenhouse and used as inoculum for two repeated pot experiments with three susceptible and two resistant bell pepper varieties. Fruit yields of the resistant peppers were not affected by the nematodes, whereas yields of two of the three susceptible pepper cultivars decreased as a result of nematode inoculation. Nematode-induced root galling and nematode multiplication was low but different between the two resistant cultivars. Root galling and nematode reproduction was much higher on the three susceptible cultivars. One of these susceptible cultivars exhibited tolerance, as yields were not affected by the nematodes, but nematode multiplication was high. It is concluded that *M. incognita* is common in Southern California bell pepper production, and that resistant cultivars may provide a useful tool in a nonchemical management strategy.
Key words: bell pepper, *Capsicum annuum*, *Meloidogyne incognita*, resistance, root-knot nematode.

Bell pepper (*Capsicum annuum*) is an important fruiting vegetable crop in the United States representing a value of $642 million in 2013 (USDA, 2014). With 21,000 acres planted in 2013, California is the number-one producing state in the country (USDA, 2014). In the southern desert valley around Coachella, CA, about 5,000 acres of bell peppers are grown (Anonymous, 2012), usually on raised beds covered with black plastic mulch on sandy soils. Growers in this area often have two pepper crops per year, with a spring planting in February and harvest into June followed by a fall planting in August/September and harvest into December.

Although the southern root-knot nematode (*Meloidogyne incognita*) is an important pest in pepper in most of the production areas (DiVito et al., 1985, 1992; Thies et al., 2008), its distribution and importance in California bell pepper production have not been well established. However, from general observations by growers and from discussions with the California Pepper Commission, it appears that this nematode is not considered an important pest in the growing areas along the coast and the central San Joaquin Valley, but that they can cause serious problems in pepper production under Coachella Valley desert conditions. The relatively warm soil temperatures in combination with the predominant light soil types, sufficient soil moisture, and the almost-continuous cropping of an excellent host crop provides an ideal scenario for root-knot nematodes to increase to damaging population levels. To control nematodes in pepper in the Coachella Valley, soil fumigants are frequently applied before transplanting. For example, 2012 pesticide use data (CDPR, 2014) show that about 196,500 kg (combined 1,3-Dichloropropene and metam-sodium) were used on bell pepper in Riverside County (i.e., Coachella Valley), which represents 62% of California's fumigant use on bell pepper on only 21% of the acreage. Because of the negative impact of fumigants on air quality and human health, soil fumigation in California is subject to ever-stricter regulations with respect to required buffer zones, air quality monitoring, sealing, posting, etc. (CDPR, 2012). Thus, to manage root-knot nematodes in bell pepper in the future, it is necessary that alternative management strategies are tested and developed. One such a strategy would include the use of nematode resistant bell pepper cultivars. An advantage of this strategy is that it requires no or few changes in growing practices, and that it does not have the negative side effects of chemical nematode control. Two open-pollinated bell pepper cultivars: 'Carolina Wonder' and 'Charleston Belle' were released in 1997 by the U.S. Vegetable Laboratory, Charleston, SC (Fery et al., 1998) that are resistant to *M. incognita*. Their resistance is based on the homozygous presence of the *N* gene (Hare, 1957; Fery and Dukes, 1996). Although Thies and Fery (1998) reported that the resistance partially broke down under high (>28°C) soil temperatures, they also found that these cultivars exhibited some level of tolerance even at high soil temperatures, and concluded that the use of resistant cultivars would be a useful component in a strategy to manage *M. incognita*. In Florida field trials on *M. incognita* infested sites, the resistance of these two cultivars did not break even though soil temperatures exceeded 30°C, and they were found to be viable alternatives to the use of soil fumigants (Thies et al., 2008). Despite these promising results, the performance of these resistant cultivars under California Coachella desert growing conditions,

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when exposed to locally occurring nematode populations has not been explored. The purpose of this study was to collect, identify, and multiply a root-knot nematode population from a Coachella Valley bell pepper field, and to evaluate the response of these resistant bell pepper cultivars when inoculated with these root-knot nematodes in greenhouse pot experiments.

Materials and Methods

Field sampling and nematode extraction: To determine the presence of root-knot nematodes in bell pepper in the Coachella Valley, soil and roots of pepper plants were collected on two dates. A limited number of fields were sampled, based on grower reports of a history of suspected nematode damage. Peppers in the sampled fields were planted during the first week of February 2012 (30 January to 3 February). The first sampling (13 samples from eight fields) was on 15 April, 2012 (approximately 77 days after planting), the second sampling (eight samples from three fields) on 31 May, 2012 (approximately 119 days after planting). Plants from each of the sampling areas were dug out with a spade, and the root system with surrounding soil were placed in a plastic bag in a cooler and taken to UC Riverside. There, roots were carefully removed and examined for the presence of root galling. The root systems were weighed, cut into approximately 1-cm long pieces, and a 100-g subsample of the roots were placed in a misting chamber (Niblack and Hussey, 1985) for 5 d to extract nematodes from the roots. Soil from the rhizosphere was thoroughly mixed, and from each sample a 100-g subsample was placed on a modified Baermann funnel for 5 d for nematode extraction (Rodriguez-Kabana and Pope, 1981). Suspensions from the root and soil samples were examined at 40× magnification using a dissecting microscope, and the number of second-stage root-knot nematode juveniles (J2) was counted. If J2 numbers in suspensions were high, two subsamples were taken to each yield between 100 and 200 J2, and water was added to each subsample to a total volume of 5 ml. Nematodes in these subsamples were counted and the average of the two counts was multiplied to derive the total number of J2 in the original suspension. This number is shown in Tables 1 and 4.

Nematode identification: Root-knot nematode females were excised from galled roots of a pepper plant collected on 31 May, 2012 from three different locations, and perineal patterns from 10 females per root system were cut for morphological identification (Riggs, 1990). Patterns were examined under 500× magnification using a Leitz DMR compound light microscope and based on the patterns, nematodes were identified to species level (Eisenback, 1985).

Maintaining and increasing nematode populations for inoculum use: Freshly hatched J2 from pepper roots from one field location (location A, sample 1; see Table 1) were collected after mist chamber extraction and inoculated onto tomato (*Lycopersicum esculentum*) cultivar 'UC82' grown in steam-sterilized sand (93% sand, 4% silt, 3% clay; pH 7.1) in 3.8-liter pots in a greenhouse. Nematodes were further multiplied and maintained by extracting J2 from the tomato roots 8 wk after inoculation, and transferring to new tomato plants. After mist chamber extraction, J2 from roots of these plants were used as inoculum for experiments.

Table 1. Root-knot nematode second-stage juvenile levels in soil and roots of bell peppers collected on 31 May 2012 in the Coachella Valley, CA.

Field code	Sample	J2 per root system[a]	J2 per 100-g soil
A	1	292,000	32,500
	2	92,000	4,500
	3	166,000	16,000
	4	18	4
B	1	56,000	8,500
	2	56,000	1,500
C	1	121,000	5,750
	2	41,500	3,000

[a] J2 per root system calculated as: (J2 extracted from 100-g roots) × (total fresh root weight [g]/100).

Nematode multiplication and effects on susceptible and resistant bell peppers: Susceptible bell pepper cultivars 'Crusader' (Syngenta, Greensboro, NC), 'Baron' (Seminis, Oxnard, CA), and 'Sweet Mini Pepper' (Sunworld, Bakersfield, CA) and the resistant cultivars 'Carolina Wonder' (Reimer Seeds, Saint Leonard, MD) and 'Charleston Belle' (Reimer Seeds, Saint Leonard, MD) were seeded in seedling trays with potting mix (Sunshine Mix 5, Sungro, Vancouver, Canada) in a greenhouse and transplanted 3 wk later to 3.8-liter pots filled with 3-kg steam-sterilized sand. For each pepper cultivar, 20 pots were set up. On the day of transplanting, pots were inoculated with 0, 1,500, 4,500, or 15,000 root-knot nematode J2 that originated from sample A1 (Table 1) and had been multiplied on tomato. There were five replications for each pepper cultivar × inoculum level. The pots were randomized on greenhouse benches, watered with an automated drip system, and fertilized with 10-g slow-release Osmocote fertilizer. Fruits were harvested when mature, and their fresh weight determined. Three months after transplanting, all pepper plants were removed from the pots, root systems examined for galling, and fresh shoot and root weights were determined. Although root galls on peppers are generally not as pronounced as on tomato or cucurbits, galls and egg masses are easily seen with the naked eye. The level of galling and presence of egg masses on the roots was rated on a scale from 0 to 10, corresponding to 0% to 100% of the roots being covered with galls and/or egg masses. J2 were extracted from the root systems in a mist chamber and counted. The entire experiment was conducted twice. Effects of nematode inoculum levels on plant data and root galling, and of the different cultivars on nematode reproduction were analyzed using analysis of variance (ANOVA) procedures, and means were separated using Fisher's protected least significant difference (LSD) test at the 95% confidence level. Before statistical analysis, J2 counts were log10(x+1)-transformed, nontransformed data are shown. SAS statistical software (SAS Institute, Cary, NC) was used for analysis.

Results

Field sampling—Root-knot nematode levels and identification: Soil and root samples were collected on both dates (15 April 2012 and 31 May 2012) from areas within bell pepper fields where plants were stunted, chlorotic, or wilting. At the first sampling date, a total of 12 samples were collected from eight different fields. Only one root-knot nematode J2 was detected in one of the soil samples. No root-knot nematodes were obtained from any of the collected roots or from the soil of the other 11 samples. At the second sampling date, a total of eight soil and root samples were collected from three fields, based on reports of areas in these fields with wilting and yellowing plants. The three fields had been sampled at the earlier sampling date, although the samples collected during the second trip were located in different areas within the field. From all the soil and root samples collected on 31 May 2012, root-knot nematode J2 were obtained. Seven of the eight samples had very high levels of infestations (Table 1). Thirty perineal patterns cut from females obtained from pepper roots from samples A1, B1, and C1 (10 per sample) were examined and all corresponded to the pattern typical for *M. incognita*.

Greenhouse pot trial—Effects on fruit production and plant growth: Averaged over all cultivars and inoculum levels, the average fruit weight per plant was significantly higher in experiment 2 (902.4 g) than in experiment 1 (535.0 g). Averaged over all cultivars, the inoculum level significantly affected fruit weight per plant in the second ($P = 0.03$) but not in the first experiment ($P = 0.35$). Averaged over all inoculum levels, fruit yields were significantly different between the different pepper cultivars in both experiments, with the 'Sweet Mini Peppers' cultivar producing significantly less fruit than the other cultivars (Table 2).

When examining the effects of nematode inoculum levels on fruit yield per plant for the respective cultivars, the results were similar for the two experiments. In both experiments, nematode inoculated resistant 'Carolina Wonder' bell pepper plants appeared to have lower fruit yields than the noninoculated controls, but this effect was not significant. Nematode inoculation appeared to decrease yield in the first experiment but increase yield in the second experiment of the other resistant cultivar 'Charleston Belle', but again differences were not significant. Different nematode inoculum levels also failed to affect the yield of the susceptible 'Crusader' (Table 2). In the susceptible 'Baron', the highest inoculum resulted in a significant loss of 17% and 43% relative to the no-nematode control in the first and second experiment, respectively (Table 2). The susceptible 'Sweet Mini Peppers' was the most sensitive cultivar. In this cultivar the yield was affected by any nematode level in the first experiment, and by the higher two nematode levels in the second experiment. At the two higher inoculum levels, the yields were reduced by approximately 50% compared with the no-nematode control (Table 2).

Effects of the nematode levels on the number of fruits produced per plant were similar to effects on the total weight of the fruits. Significant effects of the inoculum level on the numbers of fruit produced occurred only in the susceptible 'Sweet Mini Peppers' and 'Baron' (data not shown). The nematode inoculum level did not affect the fresh shoot weight of the plants at harvest in any of the five cultivars in either experiment. The highest

Table 2. Effect of second-stage juvenile root-knot nematode (*M. incognita*) inoculum levels on average (n = 5) fruit production (g per plant) of five bell pepper cultivars.

	Pepper cultivar[a]														
Inoculum (J2 per 3.8-liter pot)	CW			CB			CR			SMP			BA		
First experiment															
0	623	(0)[b]	a	871	(0)	a	655	(0)	a	251	(0)	a	585	(0)	b
1,500	530	(-15)	a	643	(-26)	a	868	(33)	a	163	(-35)	b	693	(19)	a
4,500	392	(-37)	a	526	(-40)	a	954	(46)	a	113	(-55)	c	520	(-11)	bc
15,000	502	(-19)	a	798	(-8)	a	534	(-18)	a	146	(-42)	bc	484	(-17)	c
Average[c]	506	b		710	a		735	a		168	c		575	ab	
Second experiment															
0	1,222	(0)	a	1,039	(0)	a	1,035	(0)	a	625	(0)	a	1,063	(0)	a
1,500	996	(-19)	a	1,096	(6)	a	976	(-6)	a	532	(-15)	ab	943	(-11)	a
4,500	855	(-30)	a	1,261	(22)	a	1,032	(0)	a	367	(-41)	b	905	(-15)	a
15,000	932	(-24)	a	1,215	(17)	a	930	(-10)	a	300	(-52)	b	600	(-43)	b
Average[c]	1001	b		1152	a		993	b		447	c		878	b	

[a] Pepper cultivar: CW = Carolina Wonder (R), CB = Charleston Belle (R), CR = Crusader (S), SMP = Sweet Mini Peppers (S), BA = Baron (S).
[b] In parentheses is the percentage yield increase or decrease relative to the no-nematode control. Different letters within the same experiment and column indicate significant differences at the 95% confidence level.
[c] Different letters within this row indicate significant differences at the 95% confidence level.

inoculum level resulted in significantly smaller roots (i.e., less weight) compared with the noninoculated plants of 'Sweet Mini Peppers' in both experiments. In the other cultivars, the nematodes did not result in significant differences in root weight at harvest (data not shown).

Greenhouse pot trial—Effects on root galling and nematode reproduction: In nematode-inoculated plants, and averaged over all cultivars, the inoculum level only affected the level of root galling in the first experiment. In the first experiment the average galling index of 3.8 resulting from an inoculation with 1,500 root-knot nematode J2 was significantly lower than the galling index of 5.4 resulting from the 15,000 J2 inoculum level (Table 3). The severity of root galling was significantly different between the pepper cultivars in both experiments. The resistant 'Carolina Wonder' remained virtually free of root galls. The other resistant cultivar 'Charleston Belle' exhibited a significantly higher level of root galling, although lower than the three susceptible cultivars. Among the three susceptible cultivars, galling on 'Crusader' was significantly less severe than on 'Sweet Mini Peppers' and 'Baron', which had obvious and similarly high levels of root galling (Table 3). Differences in inoculum levels (1,500, 4,500, and 15,000 J2) were not reflected in differences in root galling in any of the cultivars (Table 3).

Final nematode root populations (J2 per root system) were not affected by the inoculum level in the first experiment, but in experiment 2 the highest inoculum level resulted in significantly higher J2 root populations at harvest (Table 4). Final J2 levels differed significantly between cultivars in a similar way in experiments 1 and 2. Lowest nematode levels occurred on the resistant 'Carolina Wonder'. Roots of the other resistant cultivar—'Charleston Belle'—yielded significantly more J2, but fewer than the three susceptible cultivars. At-harvest, J2 levels on roots of the three susceptible cultivars were similarly high and not significantly different (Table 4). Only in one occasion ('Carolina Wonder', experiment 2) did the inoculum level significantly affect the final nematode root population (Table 4).

Table 3. Effect of three second-stage juvenile root-knot nematode (*M. incognita*) inoculum levels on root-galling (scale 0 to 10) of five bell pepper cultivars.

Inoculum (J2 per 3.8-liter pot)	Pepper cultivar[a]					
	CW	CB	CR	SMP	BA	Average
First experiment						
1,500	0.0 a[b]	1.4 a	4.2 a	6.8 a	6.6 a	3.8 b
4,500	0.0 a	2.6 a	6.5 a	7.6 a	7.2 a	4.7 ab
15,000	0.5 a	3.0 a	6.2 a	7.8 a	8.4 a	5.4 a
Average[c]	0.1 d	2.3 c	5.6 b	7.4 a	7.4 a	
Second experiment						
1,500	0.0 a	2.0 a	5.0 a	7.0 a	7.4 a	4.3 a
4,500	0.0 a	1.2 a	5.6 a	6.0 a	7.8 a	4.1 a
15,000	0.0 a	2.4 a	5.6 a	7.6 a	8.4 a	4.8 a
Average[c]	0.0 d	1.9 c	5.4 b	6.9 a	7.9 a	

[a] Pepper cultivar: CW = Carolina Wonder (R), CB = Charleston Belle (R), CR = Crusader (S), SMP = Sweet Mini Peppers (S), BA = Baron (S).
[b] Different letters within the same experiment and within the same column indicate significant differences at the 95% confidence level.
[c] Different letters within this row indicate significant differences at the 95% confidence level.

Discussion

A mid-April 2012 sampling of bell pepper fields in the Coachella Valley of California yielded only one root-knot nematode J2, which would lead us to conclude that these nematodes were largely absent and not likely to cause any significant damage in this crop. However, at a subsequent sampling 46 d later at the end of May 2012, the situation was the reverse as root-knot nematode J2 were found in all of the eight root and soil samples that were collected. Surprisingly, nematode levels both in soil and roots from several samples were very high. Although a direct comparison between the two sampling dates cannot be made as they were not collected from exactly the same locations within the fields, it would suggest that the nematode levels can increase dramatically over a relatively short time span. Ploeg and Maris (1999) showed that *M. incognita* can complete its life cycle in about 20 d at a soil temperature of 30°C. Prot and Van Gundy (1981) reported that at soil temperatures below 18°C *M. incognita* activity is minimal. Average soil temperatures at 15-cm depth in Thermal, in the Coachella Valley, CA, during the period between planting and the first sampling date was 15°C, and between the first and second sampling date was 23°C (http://www.ipm.ucdavis.edu/WEATHER/index.html). However, soil temperatures in the sampled bell pepper fields may have been higher as the peppers were grown on raised beds covered with black plastic tarp. Thus, it is likely that the nematodes were largely inactive before the first sampling date, but completed at least one, and possibly two life cycles between the two sampling dates resulting in the sharp increase in nematode levels. Also, it is possible that plant symptoms resulting from nematode damage (yellowing, stunting) became much more pronounced between the first and the second sampling, which led to a more targeted search for nematode-infested areas within the fields. These results show that root-knot nematodes are present and associated with symptomatic plants in Coachella Valley, CA, pepper fields, clearly demonstrate the erratic nature of root-knot nematode infestation levels in soil and roots, and emphasize the need to collect soil or root samples late in the crop cycle if the goal is to maximize the chance of nematode detection. The fact that the *Meloidogyne* females excised from the pepper roots were identified as *M. incognita* is not surprising as this has been reported as the main *Meloidogyne* species infecting peppers throughout the world (Fery et al., 1998; Thies and Fery, 1998; Ros-Ibanez et al., 2014).

TABLE 4. Effect of three second-stage juvenile root-knot nematode (*M. incognita*) inoculum levels on the average (n = 5) final nematode infestation levels extracted from the roots of five bell pepper cultivars.

Inoculum (J2 per 3.8-liter pot)	CW	CB	CR	SMP	BA	average
	Pepper cultivar[a]					
First experiment						
1,500	150 a[b]	230,500 a	1,700,000 a	4,006,000 a	3,317,000 a	1,850,730 a
4,500	4,650 a	377,000 a	2,950,000 a	4,030,000 a	4,473,000 a	2,342,635 a
15,000	15,000 a	1,874,500 a	2,800,000 a	6,210,000 a	3,877,500 a	3,077,917 a
Average[c]	6,000 c	827,333 b	2,450,000 a	4,748,667 a	3,889,167 a	
Second experiment						
1,500	320 b	296,280 a	1,026,000 a	1,220,000 a	1,130,000 a	734,520 b
4,500	320 ba	264,060 a	1,094,000 a	1,489,400 a	1,096,000 a	788,756 b
15,000	14,400 a	1,022,000 a	1,198,000 a	1,456,000 a	1,712,000 a	1,080,480 a
Average[c]	5,013 c	527,447 b	1,106,000 a	1,388,467 a	1,312,667 a	

[a] Pepper cultivar: CW = Carolina Wonder (R), CB = Charleston Belle (R), CR = Crusader (S), SMP = Sweet Mini Peppers (S), BA = Baron (S).

[b] Different letters within the same experiment and within the same column indicate significant differences at the 95% confidence level. Statistical analysis on log(x+1)-transformed data, nontransformed data shown.

[c] Different letters within this row indicate significant differences at the 95% confidence level. Statistical analysis on log(x+1)-transformed data, nontransformed data shown.

Two repeated greenhouse experiments on the effects *M. incognita* on the growth and fruit production of five bell pepper cultivars gave similar results, although overall fruit production in the second experiment was higher than in the first experiment. This may have been because the second experiment was conducted during the spring and summer with higher light intensity as opposed to the first experiment, which was conducted during the fall and winter. Fruit production of the two resistant pepper cultivars was not different between plants inoculated with *M. incognita* J2 and non-inoculated controls. The same was true for the susceptible cultivar 'Crusader'. Fruit production of the other two susceptible cultivars was severely affected by increasing *M. incognita* inoculum levels. These two cultivars, 'Baron' and 'Sweet Mini Peppers' also had the most severe root galling. Galling on the resistant cultivars was low, but consistently higher on 'Charleston Belle' than on 'Carolina Wonder'. These two cultivars were also included in greenhouse pot trials with *M. incognita* by Thies and Fery (1998) and Kokalis-Burelle et al. (2009), and in field trials by Thies et al. (2008). They also reported low galling indices on roots of these two cultivars, but did not find differences in galling between these two cultivars (Thies and Fery, 1998; Thies et al., 2008; Kokalis-Burelle et al., 2009). The lower galling on roots of the resistant 'Carolina Wonder' was reflected in the nematode reproduction. In both experiments, nematode populations on roots of this cultivar were lower than on the other resistant cultivar 'Charleston Belle' and dramatically lower than on the three susceptible cultivars. This corresponds with findings of Thies et al. (2008) who also reported lower levels of *M. incognita* in roots of 'Carolina Wonder' than in roots of 'Charleston Belle'. *M. incognita* J2 root populations were high and not different between the three susceptible cultivars. Although root galling on the susceptible 'Crusader' was lower compared with the other two susceptible cultivars, and although the nematodes failed to affect fruit production in this cultivar, nematode reproduction on 'Crusader' was not different from the nematode reproduction on the other two susceptible cultivars. Thus, 'Crusader' is more tolerant, but an equally good host for the *M. incognita* population used.

It can be concluded that the two resistant cultivars used in this study could be useful to manage *M. incognita* in Coachella Valley, CA, pepper production, as fruit production did not suffer even under high nematode levels, and as they prevented a high build-up of nematode populations. Evaluation of the usefulness and suitability of these resistant cultivars under local market and environmental conditions remains to be done. Alternatively, resistant cultivars may have a use as a rootstock under susceptible scions in high value production systems (Kokalis-Burelle et al., 2009; Ros-Ibanez et al., 2014).

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