

Evaluation of 31 Potential Biofumigant Brassicaceous Plants as Hosts for Three *Meloidogyne* Species

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Abstract: Brassicaceous cover crops can be used for biofumigation after soil incorporation of the mowed crop. This strategy can be used to manage root-knot nematodes (*Meloidogyne* spp.), but the fact that many of these crops are host to root-knot nematodes can result in an undesired nematode population increase during the cultivation of the cover crop. To avoid this, cover crop cultivars that are poor or nonhosts should be selected. In this study, the host status of 31 plants in the family Brassicaceae for the three root-knot nematode species *M. incognita*, *M. javanica*, and *M. hapla* were evaluated, and compared with a susceptible tomato host in repeated greenhouse pot trials. The results showed that *M. incognita* and *M. javanica* responded in a similar fashion to the different cover cultivars. Indian mustard (*Brassica juncea*) and turnip (*B. rapa*) were generally good hosts, whereas most oil radish cultivars (*Raphanus sativus* ssp. *oleiferus*) were poor hosts. However, some oil radish cultivars were among the best hosts for *M. hapla*. The arugula (*Eruca sativa*) cultivar Nemat was a poor host for all three nematode species tested. This study provides important information for choosing a cover crop with the purpose of managing root-knot nematodes.

Key words: biofumigation, *Brassica*, host status, *Meloidogyne hapla*, *Meloidogyne incognita*, *Meloidogyne javanica*, root-knot nematode.

Root-knot nematodes (RKN, *Meloidogyne* spp.) are economically the most damaging plant-parasitic nematodes in California vegetable production (Koenning et al., 1999). Nematode control with fumigant pesticides, although still used extensively in some crops, is highly regulated in California because of negative effects on human health and the environment. Fumigants have been identified as contributing to the emission of volatile organic compounds (VOCs), leading to poor air quality in several major crop growing areas of California. Under the 2007 Ozone State Implementation Plan, the California Department of Pesticide Regulation is required to reduce emission of smog forming VOCs from soil fumigants (Wang et al., 2009). Currently, restrictions on fumigant use during the May-October period are in place in five “non-attainment areas” in California. These restrictions may involve covering treated fields with tarpaulin, several postfumigation water treatments, application through drip tubing, reducing rates, increasing injection depths, and requirements for soil compaction (EPA, 2012). These restrictions generally result in higher costs to the grower, and therefore there is a need for economically viable alternatives for soil disinfestation, without the negative side effects. Biofumigation and anaerobic soil disinfestation (ASD) have been proposed as methods that can meet these requirements. With the ASD method, large amounts of fresh organic matter are incorporated in the soil followed by irrigation and sealing with plastic tarp for several weeks. During this period anaerobic conditions and fermentation products with pesticidal activity develop (Lamers et al., 2010). Biofumigation is a similar method and occurs when volatile compounds with pesticidal properties are released into the soil during decomposition of plant material or animal by-products (Halbrendt, 1996; Kirkegaard and Sarwar, 1998; Bello

et al., 2000a, 2000b). Most research on biofumigation, however, has focused on using brassicaceous crops (Kirkegaard and Matthiessen, 2004). Upon tissue disruption, glucosinolate compounds in brassicas produce biocidal isothiocyanates that are released in the soil when the crop is shredded and incorporated (Chew, 1988; Brown et al., 1991). The suppressive effect of brassicaceous biofumigants on soilborne pathogens, weeds, and plant-parasitic nematodes has been demonstrated in numerous laboratory, greenhouse, and field studies (Ploeg and Stapleton, 2001; Ploeg, 2008; Zasada et al., 2010). To qualify as a good cover crop for the management of plant-parasitic nematodes, the crop should be a poor host for the nematodes and lower the population after incorporation of the crop into the soil (Viaene and Abawi, 1998). A complication with growing brassicas or other crops as cover crops for biofumigation or for ASD to control RKN, is that they may multiply the target nematode population (Ploeg, 2008; Zasada et al., 2010). To avoid this, cover crops can be grown when soil temperatures are sufficiently low to prevent nematode activity (Roberts, 1987), or resistant or nonhost cover crop cultivars can be grown (Stirling and Stirling, 2003; Pattison et al., 2006). The objective of this greenhouse study was to compare the host status of a range of brassicaceous crop cultivars for three species of RKN (*M. incognita*, *M. javanica*, *M. hapla*) that are common in California, and identify cultivars that have a low risk of increasing the nematode population when grown as a biofumigant cover crop.

MATERIALS AND METHODS

Nematode origin: Populations of three locally occurring *Meloidogyne* spp. were used in the experiments: *M. incognita* race 3, originally isolated from cotton in the San Joaquin Valley, CA; *M. javanica* from cowpea, Chino, CA; and *M. hapla* from alfalfa in San Bernardino, CA. Species and race identifications were done with isozyme electrophoresis and on differential host tests (Eisenback and Triantaphyllou, 1991). Populations were

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increased and maintained on tomato 'UC82' grown in coarse sand in a greenhouse. To prepare inoculum, *Meloidogyne* eggs were extracted from heavily infested tomato by shaking the roots in a 0.525% NaOCl solution (Radewald et al., 2003). Eggs released from the roots were collected on a 25- μ m pore-size sieve and were counted in two 0.025-ml subsamples. Egg suspensions were then adjusted to contain 20,000 eggs in 5 ml.

Experimental design and treatments: Thirty-one cruciferous cultivars comprising eight species (Table 1) were seeded in 1-gal (3.8-liter) plastic pots filled with steam-sterilized sandy soil (93% sand, 4% silt, 3% clay; pH 7.1). Each pot received 10 seeds, and five pots were seeded for each cultivar. In addition, five pots were planted with one 3-wk-old tomato 'UC82' seedling. Pots were placed in a completely randomized order on a greenhouse bench (17°C to 29°C, natural light), 10-g slow release fertilizer

(Osmocote®) was added to each pot, and pots were watered daily through an automated drip system. Two weeks after emergence, enough seedlings were removed to give three plants per pot. One week later, three 3-cm-deep small holes were made in a triangular pattern over the surface of each pot, 20,000 RKN eggs in 15-ml water were inoculated by adding 5 ml into each hole, and the holes were then covered with soil. Eight weeks after inoculation, three soil cores including root material, were removed from each pot from top to bottom (17 cm) with a 2-cm diam. sampling rod. The soil removed from each pot was thoroughly mixed, and 100g was used for nematode extraction over a 5-d period with a modified Baermann funnel-technique (Rodriguez-Kabana and Pope, 1981). Second-stage *Meloidogyne* juveniles (J2) were counted using a dissecting microscope at 40 \times magnification. Plants were carefully removed from the pots, the root systems were washed free of soil, and were thoroughly examined for the presence of galls. The severity of root-galling was indexed on a scale from 0 (no galls) to 10 (100% of roots galled) (Bridge and Page, 1980). Separate experiments were done with *M. incognita*, *M. javanica*, and *M. hapla* as inoculum, and the entire experiment was repeated once for each of the three *Meloidogyne* spp.

Statistical analysis: Raw nematode data (number of RKN J2 recovered from soil) was log₁₀(X+1)-transformed before analysis. Effects of the plants on RKN J2 levels and root galling were analyzed in an analysis of variance (ANOVA) procedure, and means were compared using Fisher's protected least significant difference (LSD) test ($P \leq 0.05$) using SAS statistical software (SAS Institute, Cary, NC). All data presented are nontransformed means \pm standard errors. Spearman rank correlation coefficients between J2 levels and galling, and between data from the repeated experiments were also calculated using SAS software.

RESULTS

Host status for *M. incognita*: Average J2 counts were significantly different between the two replicated experiments ($P = 0.0001$) and between the 32 plant cultivars tested ($P = 0.0001$). There was no significant interaction between the experiment and cultivar ($P = 0.097$) indicating that the 32 varieties gave similar results in the two experiments. This was confirmed by ranking the cultivars according to J2 levels at harvest and subjecting the ranking to a Spearman rank correlation test. Results show that there was a significant positive correlation of the 32 cultivars in J2 numbers between Experiments 1 and 2 (Spearman rank correlation coefficient 0.73; $P = 0.0001$). In both experiments, *B. rapa* 'Br02206' was as good a host as tomato ($P \leq 0.05$; Table 2). All three *B. juncea* cultivars also were relatively good hosts ranking among the best seven plants in the two experiments. Ratios of J2 populations of brassicaceous plants relative to tomato (P_b/P_t) for

TABLE 1. Thirty-one brassicaceous crop cultivars used in *Meloidogyne* greenhouse pot experiments.

Species	Common name	Cultivar	Source ^a
<i>Brassica carinata</i>	Ethiopian mustard	Bc007	1
<i>Brassica juncea</i>	Indian mustard	ISCI99	2
		Nemfix	3
		Pacific Gold	4
<i>Brassica napus</i>	Oliseed rape	Greenland	1
		Humus	4
		Winfred	1
<i>Brassica oleracea</i>	Broccoli	Liberty	5
<i>Brassica rapa</i>	Turnip	Br02205	1
		Br02206	1
		Rondo	1
		Samson	1
<i>Eruca sativa</i>	Arugula	Nemat	2
<i>Raphanus sativus</i> spp. <i>oleiferus</i>	Oil radish	Adagio	6
		Adios	1
		Boss	6
		Colonel	6
		Comet	6
		Defender	6
		Doublet	1
		Final	1
		Rs05415	1
		TerraNova	1
<i>Sinapis alba</i>	White mustard	Abraham	1
		Absolut	6
		Accent	6
		Achilles	6
		Condor	1
		IdaGold	4
		Maxi	6
		Santa Fe	1

^a Sources of seeds. 1: J. Joordens' Seeds, Kessel, The Netherlands. 2: High Performance Seeds, Inc., Moses Lake, WA. 3: Seed Technology & Marketing Pty Ltd., Adelaide, Australia. 4: University of Idaho, Moscow, ID. 5: Seminis Vegetable Seeds, Oxnard, CA. 6: Petersen Saatzzucht, Lundsgaard, Germany.

TABLE 2. Root galling and *Meloidogyne incognita* second-stage root-knot nematode juvenile numbers 8 wk after inoculating brassicaceous cultivars and tomato with 20,000 eggs (N = 5) per 3.8-liter pot. Ranking from 1 (highest) to 32 (lowest).

Experiment 1 Species	Cultivar	Galling		Ranking	J2/100 g		Ranking
<i>Brassica carinata</i>	Bc007	3.4 (\pm 0.2) ^a	hijk	13	502 (\pm 57) ^a	fghij	18
<i>Brassica juncea</i>	ISCI99	5.0 (\pm 0.3)	de	5	2,422 (\pm 540)	abc	4
	Nemfix	6.2 (\pm 0.4)	bc	3	2,134 (\pm 221)	abcd	5
	Pacific Gold	6.4 (\pm 0.5)	b	2	3,226 (\pm 1,174)	ab	2
<i>Brassica napus</i>	Greenland	3.8 (\pm 0.4)	fghi	10	566 (\pm 149)	fghij	12
	Humus	3.0 (\pm 0.5)	ijkl	14	1,079 (\pm 207)	cdefg	9
	Winfred	2.6 (\pm 0.2)		22	554 (\pm 130)	fghij	15
<i>Brassica oleracea</i>	Liberty	1.0 (\pm 0.0)	op	31	9 (\pm 2)	o	31
<i>Brassica rapa</i>	Br02205	4.6 (\pm 0.2)	def	6	995 (\pm 205)	defg	10
	Br02206	5.4 (\pm 0.2)	cd	4	2,423 (\pm 745)	abcd	3
	Rondo	4.4 (\pm 0.4)	efg	7	1,084 (\pm 210)	cdef	8
	Samson	4.2 (\pm 0.4)	efgh	8	1,369 (\pm 355)	bcde	6
<i>Eruca sativa</i>	Nemat	3.6 (\pm 0.2)	ghij	11	267 (\pm 79)	jklm	25
<i>Raphanus sativus</i>	Adagio	2.6 (\pm 0.2)	klm	23	141 (\pm 18)	lm	29
	Adios	4.2 (\pm 0.4)	efgh	9	277 (\pm 65)	ijkl	24
	Boss	0.4 (\pm 0.2)	p	32	7 (\pm 5)	o	32
	Colonel	3.0 (\pm 0.5)	ijkl	15	201 (\pm 64)	klm	27
	Comet	3.6 (\pm 0.2)	ghij	12	190 (\pm 81)	mn	28
	Defender	2.8 (\pm 0.4)	jkl	17	257 (\pm 70)	jklm	26
	Doublet	2.2 (\pm 0.2)	lmn	28	556 (\pm 107)	efghi	13
	Final	3.0 (\pm 0.3)	ijkl	16	468 (\pm 156)	hijk	21
	Rs05415	2.8 (\pm 0.4)	jkl	18	284 (\pm 70)	ijkl	23
	TerraNova	2.6 (\pm 0.2)	klm	24	63 (\pm 19)	n	30
<i>Sinapis alba</i>	Abraham	1.6 (\pm 0.2)	no	30	351 (\pm 59)	hijkl	22
	Absolut	2.8 (\pm 0.2)	jkl	19	546 (\pm 46)	efghi	16
	Accent	1.8 (\pm 0.2)	mno	29	648 (\pm 105)	efgh	11
	Achilles	2.6 (\pm 0.2)	klm	25	487 (\pm 106)	fghij	19
	Condor	2.8 (\pm 0.4)	jkl	20	1,234 (\pm 163)	bcde	7
	IdaGold	2.8 (\pm 0.2)	jkl	21	480 (\pm 98)	ghij	20
	Maxi	2.4 (\pm 0.2)	lmn	26	554 (\pm 140)	fghij	14
	Santa Fe	2.4 (\pm 0.2)	lmn	27	505 (\pm 180)	hijk	17
<i>Solanum lycopersicum</i>	UC82	7.6 (\pm 0.2)	a	1	4,271 (\pm 1,092)	a	1
Experiment 2							
<i>Brassica carinata</i>	Bc007	3.4 (\pm 0.2)	ghi	12	316 (\pm 76)	defgh	17
<i>Brassica juncea</i>	ISCI99	5.6 (\pm 0.2)	cd	4	662 (\pm 68)	bcde	7
	Nemfix	6.6 (\pm 0.7)	b	2	1,630 (\pm 849)	bc	3
	Pacific Gold	6.4 (\pm 0.5)	bc	3	1,273 (\pm 813)	bcd	4
<i>Brassica napus</i>	Greenland	3.4 (\pm 0.2)	ghi	13	180 (\pm 21)	fghi	22
	Humus	1.8 (\pm 0.4)	ijkl	27	240 (\pm 73)	fghi	21
	Winfred	2.6 (\pm 0.2)	ijkl	20	172 (\pm 41)	fghij	23
<i>Brassica oleracea</i>	Liberty	0.6 (\pm 0.2)	op	32	0 (\pm 0)	k	32
<i>Brassica rapa</i>	Br02205	5.0 (\pm 0.3)	de	6	360 (\pm 115)	defgh	14
	Br02206	5.4 (\pm 0.4)	d	5	2,624 (\pm 1,448)	ab	2
	Rondo	4.4 (\pm 0.2)	ef	7	458 (\pm 298)	defgh	9
	Samson	4.4 (\pm 0.2)	ef	8	1,088 (\pm 483)	bcde	5
<i>Eruca sativa</i>	Nemat	3.4 (\pm 0.2)	ghi	14	164 (\pm 59)	hij	25
<i>Raphanus sativus</i>	Adagio	3.4 (\pm 0.2)	ghi	15	116 (\pm 29)	hij	27
	Adios	4.2 (\pm 0.2)	efg	9	308 (\pm 78)	defgh	18

(Continued)

TABLE 2. Continued.

Experiment 1 Species	Cultivar	Galling		Ranking	J2/100 g		Ranking
	Boss	0.8 (± 0.4)	p	31	6 (± 4)	k	31
	Colonel	3.0 (± 0.0)	hij	17	164 (± 50)	fghij	24
	Comet	4.2 (± 0.4)	efg	10	142 (± 36)	ghij	26
	Defender	2.6 (± 0.2)	ijkl	21	74 (± 42)	j	30
	Doublet	2.6 (± 0.2)	ijkl	22	408 (± 128)	cdefgh	11
	Final	3.8 (± 0.4)	fgh	11	422 (± 111)	cdefg	10
	Rs05415	3.2 (± 0.4)	hij	16	390 (± 152)	efgh	12
	TerraNova	2.8 (± 0.2)	ijk	18	80 (± 46)	j	29
<i>Sinapis alba</i>	Abraham	1.4 (± 0.2)	no	30	88 (± 34)	ij	28
	Absolut	2.8 (± 0.4)	ijk	19	332 (± 230)	fghi	15
	Accent	2.0 (± 0.5)	mno	25	324 (± 63)	defgh	16
	Achilles	1.8 (± 0.2)	klm	28	912 (± 495)	cdef	6
	Condor	2.0 (± 0.3)	jkl	26	304 (± 64)	defgh	19
	IdaGold	2.6 (± 0.2)	ijkl	23	518 (± 353)	fghi	8
	Maxi	1.8 (± 0.4)	lmn	29	286 (± 95)	defgh	20
	Santa Fe	2.4 (± 0.2)	jkl	24	372 (± 190)	defgh	13
<i>Solanum lycopersicum</i>	UC82	7.8 (± 0.2)	a	1	5,460 ($\pm 1,816$)	a	1

^a Values shown are the mean of five replicates ($n = 5$) \pm SE. Root galling index on a scale from 0 to 10 with 0 = no galls, 10 = 100% of roots galled. Values in a column followed by different letters are significantly different ($P \leq 0.05$) according to Fisher's LSD-test within one experiment. Raw nematode data (egg counts) were $\log_{10}(x+1)$ -transformed before analysis; nontransformed data are presented.

B. juncea ranged from 0.75 ('Pacific Gold', Experiment 1) to 0.12 ('ISCI99', Experiment 2). The poorest hosts for *M. incognita* were broccoli (*B. oleracea*) 'Liberty' and *R. sativus* 'Boss', both reducing J2 numbers compared with tomato on average by more than 99%, and resulting in significantly lower J2 levels than any of the other cultivars. Other cultivars that were among the 10 poorest hosts in both experiments included the five *R. sativus* cultivars 'Adagio', 'Colonel', 'Comet', 'Defender', and 'TerraNova', *E. sativa* 'Nemat', and *S. alba* 'Abraham'.

Average galling was not significantly different between the two experiments ($P = 0.81$), nor was the interaction between "experiment" and "cultivar" ($P = 0.37$). Gallings on *R. sativus* 'Boss' was very minor in both experiments, but none of the cultivars remained free of root-galling. Cultivars of *B. juncea* and *B. rapa* all showed very obvious root-galling. The severity of gallings was positively correlated with the J2 levels in both experiments (Spearman rank correlation coefficient 0.59, $P = 0.0003$; and 0.59, $P = 0.0004$ for Experiments 1 and 2, respectively) (Table 2).

Host status for M. javanica: There was a significant effect of the "experiment" ($P = 0.0001$), of the "cultivar" ($P = 0.0001$), and of the interaction between "experiment" and "cultivar" ($P = 0.0001$) on average J2 counts. Still, the ranking of the cultivars according to J2 numbers was very similar between the two experiments (Spearman rank correlation coefficient 0.73; $P = 0.0001$). Good hosts for *M. javanica* in both experiments included *B. juncea* 'ISCI99' and 'Nemfix' and *B. rapa* 'Rondo'. These cultivars resulted in J2 numbers that were not significantly lower than after tomato. In the first experiment, *R. sativus* 'Boss', 'TerraNova', and 'Defender', and *E. sativa*

'Nemat' yielded significantly fewer J2 than the other cultivars. These four cultivars were also among the five poorest hosts in Experiment 2. Broccoli 'Liberty' was a very poor host in Experiment 2 (ranking 30 of 32; $P_b/P_t = 0.003$), but a moderately good host in Experiment 1 (ranking 18 of 32; $P_b/P_t = 0.26$).

"Experiment," "cultivar," and "experiment \times cultivar" effects on gallings were also significant ($P = 0.0001$). Like with *M. incognita*, cultivars of *B. juncea* and *B. rapa* generally showed obvious root gallings, where as gallings on *R. sativus* 'Boss' was very minor. None of the cultivars remained free of gallings, and there was a significant positive correlation between root-galling and J2 levels (Spearman rank correlation coefficient 0.67, $P = 0.0001$; and 0.68, $P = 0.0001$ for Experiments 1 and 2, respectively) (Table 3).

Host status for M. hapla: J2 levels were quite different between the two replicated experiments ($P = 0.0001$). For example, in the first experiment on average only 804 J2/100 g soil were obtained after 8 wk under tomato, whereas in the second experiment 27,272 J2/100 g soil were found. Effects of "cultivar" and "experiment \times cultivar" were also highly significant ($P = 0.0001$). In the first experiment, J2 numbers after *B. rapa* 'Br02005' and 'Br02006', and *R. sativus* 'Colonel', 'Doublet', 'Final', and 'TerraNova' were not significantly different from those after tomato. In the second experiment, none of the brassicaceous cultivars were as good a host as tomato. The two *B. rapa* cultivars 'Rondo' and 'Samson', and the two *R. sativus* cultivars 'Colonel' and 'TerraNova' were among the 10 best brassicaceous hosts for *M. hapla* in both experiments. Conversely, 'Adagio', 'Condor', and 'Nemat' were among the five poorest hosts in both experiments. Reductions in J2 numbers by the latter

TABLE 3. Root galling and *Meloidogyne javanica* second-stage root-knot nematode juvenile numbers 8 wk after inoculating brassicaceous cultivars and tomato with 20,000 eggs (N = 5) per 3.8-liter pot. Ranking from 1 (highest) to 32 (lowest).

Experiment 1 Species	Cultivar	Galling		Ranking	J ₂ /100 g		Ranking
<i>Brassica carinata</i>	Bc007	4.0 (±0.3) ^a	gh	11	552 (±95) ^a	jk	25
<i>Brassica juncea</i>	ISCI99	6.0 (±0.3)	cde	5	3,816 (±1,070)	abcde	6
	Nemfix	7.0 (±0.3)	b	2	3,980 (±966)	abcd	4
	Pacific Gold	6.0 (±0.5)	cde	6	2,812 (±806)	bcdefg	11
<i>Brassica napus</i>	Greenland	4.8 (±0.4)	fg	9	1,972 (±445)	defgh	13
	Humus	3.4 (±0.2)	hij	14	1,620 (±303)	efgh	17
	Winfred	5.8 (±0.2)	de	7	3,096 (±809)	abcdef	10
<i>Brassica oleracea</i>	Liberty	1.6 (±0.2)	no	30	1,584 (±413)	fghi	18
<i>Brassica rapa</i>	Br02205	6.8 (±0.4)	bc	3	3,868 (±819)	abcd	5
	Br02206	6.6 (±0.2)	bcd	4	4,684 (±874)	abc	3
	Rondo	4.8 (±0.4)	fg	10	6,524 (±1,723)	a	1
	Samson	5.2 (±0.4)	ef	8	3,584 (±1,082)	abcdef	8
<i>Eruca sativa</i>	Nemat	3.0 (±0.3)	ijkl	18	144 (±76)	l	29
<i>Raphanus sativus</i>	Adagio	3.2 (±0.4)	hijk	17	450 (±106)	k	28
	Adios	3.6 (±0.4)	hi	12	1,280 (±302)	ghi	19
	Boss	0.4 (±0.2)	p	32	92 (±48)	l	32
	Colonel	2.6 (±0.4)	jklm	20	646 (±73)	ijk	24
	Comet	3.4 (±0.2)	hij	13	1,816 (±384)	defgh	15
	Defender	2.6 (±0.2)	jklm	21	122 (±52)	l	30
	Doublet	1.6 (±0.2)	no	29	508 (±166)	k	27
	Final	2.2 (±0.4)	lmno	24	1,008 (±248)	ijk	21
	Rs05415	2.2 (±0.2)	jkl	25	552 (±121)	jk	26
	TerraNova	3.0 (±0.3)	lmno	19	96 (±26)	l	31
	<i>Sinapis alba</i>	Abraham	2.2 (±0.4)	lmno	23	3,544 (±575)	abcde
Absolut		3.2 (±0.6)	hijk	15	1,620 (±323)	efgh	16
Accent		1.8 (±0.2)	mno	27	732 (±193)	ijk	23
Achilles		3.2 (±0.4)	hijk	16	3,708 (±1,423)	abcdef	7
Condor		2.4 (±0.2)	klmn	22	2,526 (±556)	cdefg	12
IdaGold		2.0 (±0.5)	mno	26	1,896 (±477)	defgh	14
Maxi		1.4 (±0.2)	o	31	1,256 (±329)	ghij	20
Santa Fe		1.8 (±0.2)	mno	28	908 (±84)	hij	22
<i>Solanum lycopersicum</i>		UC82	8.0 (±0.3)	a	1	6,120 (±1,405)	ab
Experiment 2							
<i>Brassica carinata</i>	Bc007	2.8 (±0.2)	de	7	74 (±24)	mn	26
<i>Brassica juncea</i>	ISCI99	2.4 (±0.2)	efg	11	1,364 (±449)	abc	3
	Nemfix	4.4 (±0.3)	b	2	1,628 (±575)	ab	2
	Pacific Gold	3.4 (±0.8)	cd	5	670 (±291)	bcdefg	11
<i>Brassica napus</i>	Greenland	2.0 (±0.0)	efghi	17	602 (±104)	bcdefg	13
	Humus	2.2 (±0.5)	efgh	14	848 (±119)	abcde	7
	Winfred	2.8 (±0.4)	de	9	728 (±126)	bcdef	9
<i>Brassica oleracea</i>	Liberty	1.0 (±0.3)	jkl	29	8 (±6)	pq	30
<i>Brassica rapa</i>	Br02205	3.4 (±0.4)	cd	4	74 (±12)	klm	27
	Br02206	2.8 (±0.5)	de	8	954 (±444)	bcdefg	5
	Rondo	3.4 (±0.2)	cd	6	972 (±153)	abcd	4
	Samson	3.8 (±0.2)	bc	3	754 (±79)	bcdef	8
<i>Eruca sativa</i>	Nemat	1.0 (±0.5)	jkl	30	44 (±30)	op	28
<i>Raphanus sativus</i>	Adagio	1.2 (±0.4)	ijk	25	222 (±95)	ijkl	20
	Adios	2.2 (±0.2)	efgh	13	858 (±106)	abcde	6

(Continued)

TABLE 3. Continued.

Experiment 1 Species	Cultivar	Galling	Ranking	J2/100 g	Ranking		
	Boss	0.2 (± 0.2)	l	32	6 (± 3)	pq	31
	Colonel	1.8 (± 0.6)	fghij	19	150 (± 104)	lmn	23
	Comet	1.4 (± 0.2)	hij	24	722 (± 153)	bcdefg	10
	Defender	0.4 (± 0.2)	kl	31	4 (± 2)	q	32
	Doublet	5.6 (± 0.2)	bcd	20	486 (± 184)	cdefgh	14
	Final	1.2 (± 0.2)	ijk	26	330 (± 97)	defghi	17
	Rs05415	1.2 (± 0.4)	ijk	27	86 (± 15)	jklm	25
	TerraNova	1.2 (± 0.4)	ijk	28	40 (± 15)	no	29
	<i>Sinapis alba</i>	Abraham	1.8 (± 0.4)	fghij	18	400 (± 149)	defghi
Absolut		2.6 (± 0.4)	def	10	254 (± 69)	fghijk	19
Accent		1.6 (± 0.2)	ghij	22	108 (± 27)	ijklm	24
Achilles		1.4 (± 0.2)	hij	23	274 (± 24)	efghij	18
Condor		2.0 (± 0.3)	efghi	16	220 (± 64)	ghijk	21
IdaGold		1.8 (± 0.4)	fghij	21	640 (± 153)	bcdefgh	12
Maxi		2.2 (± 0.4)	efgh	15	208 (± 110)	hijkl	22
Santa Fe		2.4 (± 0.5)	efg	12	384 (± 96)	cdefgh	16
<i>Solanum lycopersicum</i>	UC82	7.2 (± 0.2)	a	1	2,840 (± 443)	a	1

^a Values shown are the mean of five replicates ($n = 5$) \pm SE. Root galling index on a scale from 0 to 10 with 0 = no galls, 10 = 100% of roots galled. Values in a column followed by different letters are significantly different ($P \leq 0.05$) according to Fisher's LSD-test within one experiment. Raw nematode data (egg counts) were $\log_{10}(x+1)$ -transformed before analysis; nontransformed data are presented.

three cultivars relative to tomato ranged from 90% ($P_b/P_t = 0.10$) to 99% ($P_b/P_t = 0.01$) for 'Condor' in Experiments 1 and 2, respectively. Despite the variability in J2 numbers between the two experiments, the ranking of the cultivars regarding J2 numbers was significantly positively correlated (Spearman rank correlation coefficient 0.52, $P = 0.002$).

The overall average galling was similar between the two experiments ("experiment"; $P = 0.416$), although there was some variability in galling on the individual cultivars between the two experiments ("experiment \times cultivar": $P = 0.015$). Galling occurred on all brassicaceous cultivars, ranging from a galling index of 1.8 on *B. napus* 'Winfred' and *B. oleracea* 'Liberty' in Experiment 1, to 6.6 on *R. sativus* 'TerraNova' in Experiment 2. In both experiments, cultivars that ranked high in galling generally also ranked high in J2 numbers and vice versa (Spearman rank correlation coefficient 0.51, $P = 0.0028$; and 0.74, $P = 0.0001$ for Experiments 1 and 2, respectively) (Table 4).

DISCUSSION

Our results show that there are significant differences within and between brassicaceous species with regard to host status for RKNs, and furthermore that the host suitability of a particular brassicaceous cultivar for RKNs can differ depending on the nematode species. Therefore, identification of the target RKN to species level is important to optimize this management strategy. Results for *M. incognita* and *M. javanica* were similar, with *B. juncea* and *B. rapa* cultivars generally being good hosts, and *E. sativa* Nemat and the *R. sativus* cultivars Boss and TerraNova consistently ranking

among the poorest hosts. Whether inoculated with *M. incognita* or *M. javanica*, reproduction on the latter two cultivars was reduced by at least 98% compared with reproduction on tomato. These results are in agreement with findings by Curto et al. (2005) who also reported that *B. juncea* cultivars were among the better hosts for *M. incognita*, and that *R. sativus* Boss and *E. sativa* Nemat were poor or nonhost. Broccoli, in our study a poor host for *M. incognita* and to a lesser degree for *M. javanica*, was also identified by McSorley and Frederick (1995) as a crop that showed potential to reduce *Meloidogyne* populations, although they used a different cultivar. *Brassica juncea* Nemfix, in our study among the best hosts for *M. incognita* and *M. javanica*, was also found a good host for *M. javanica* by Stirling and Stirling (2003), which led them to conclude that "it is imperative that in warm climates only poor hosts are grown" and that "a screening program could identify such material." Monfort et al. (2007) included *B. juncea* Pacific Gold in a cover crop field study on a *M. incognita*-infested site and showed that the nematodes reproduced on the cover crop. They also concluded that information on the level of susceptibility of *Brassica* species to RKN is needed for biofumigation to become a successful nematode management strategy. Johnson et al. (1992) and McLeod et al. (2002) reported that *M. javanica* and/or *M. incognita* caused galls on *B. napus* Humus and that populations were maintained on this cultivar. In our study, both these *Meloidogyne* species also caused galls on Humus roots, and the cultivar was not a particularly good or bad host, despite containing high levels of glucosinolates (Johnson et al., 1992). The *R. sativus* cultivar Adagio, in our study a poor host for both *M. incognita* and *M. javanica*, was also a poor host for

TABLE 4. Root galling and *Meloidogyne hapla* second-stage root-knot nematode juvenile numbers eight weeks after inoculating brassicaceous cultivars and tomato with 20,000 eggs (N = 5) per 3.8-liter pot. Ranking from 1 (highest) to 32 (lowest).

Experiment 1 Species	Cultivar	Galling		Ranking	J ₂ /100 g		Ranking
<i>Brassica carinata</i>	Bc007	3.0 (±0.3) ^a	hijkl	20	96 (±40) ^a	klmn	26
<i>Brassica juncea</i>	ISCI99	3.0 (±0.3)	hijkl	21	196 (±58)	efghijk	18
	Nemfix	3.6 (±0.2)	fghijk	16	148 (±48)	ghijkl	21
	Pacific Gold	5.2 (±0.2)	bcde	7	212 (±94)	ghijkl	17
<i>Brassica napus</i>	Greenland	2.8 (±0.4)	ijkl	24	252 (±58)	bcdefghi	13
	Humus	2.6 (±0.2)	jkl	27	128 (±19)	ghijkl	22
	Winfred	2.2 (±0.8)	kl	31	42 (±20)	n	32
<i>Brassica oleracea</i>	Liberty	2.0 (±0.3)	l	32	290 (±95)	bcdefghi	10
<i>Brassica rapa</i>	Br02205	3.8 (±0.9)	efghij	13	520 (±115)	abc	3
	Br02206	4.2 (±0.4)	defghi	12	408 (±138)	abcdef	7
	Rondo	4.4 (±0.2)	defgh	11	350 (±96)	bcdefg	8
	Samson	4.8 (±0.6)	cdefg	10	324 (±88)	bcdefg	9
<i>Eruca sativa</i>	Nemat	2.4 (±0.6)	jkl	29	44 (±12)	mn	31
<i>Raphanus sativus</i>	Adagio	5.6 (±0.8)	bcd	4	68 (±21)	lmn	30
	Adios	3.4 (±0.8)	ghijkl	17	272 (±50)	bcdefgh	11
	Boss	5.2 (±0.4)	bcde	6	228 (±62)	cdefghi	16
	Colonel	3.8 (±0.5)	efghij	14	476 (±129)	abcd	4
	Comet	3.8 (±0.8)	efghij	15	112 (±26)	hijkl	23
	Defender	3.2 (±0.7)	ijkl	19	92 (±30)	jklmn	28
	Doublet	5.6 (±0.6)	bcd	5	460 (±105)	abcde	6
	Final	6.0 (±0.3)	abc	3	472 (±112)	abcde	5
	Rs05415	5.0 (±0.6)	cdef	9	96 (±15)	ijklm	27
	TerraNova	6.6 (±0.5)	ab	2	632 (±116)	ab	2
	<i>Sinapis alba</i>	Abraham	3.2 (±0.5)	hijkl	18	148 (±48)	ghijkl
Absolut		2.8 (±0.4)	ijkl	22	100 (±50)	jklmn	25
Accent		2.2 (±0.2)	kl	30	104 (±48)	lmn	24
Achilles		2.8 (±0.2)	ijkl	23	168 (±59)	fghijkl	19
Condor		2.6 (±0.4)	jkl	26	80 (±18)	jklmn	29
IdaGold		5.0 (±0.6)	cdef	8	260 (±96)	defghijk	12
Maxi		2.8 (±0.5)	ijkl	25	240 (±80)	cdefghij	15
Santa Fe		2.6 (±0.5)	jkl	28	248 (±102)	cdefghi	14
<i>Solanum lycopersicum</i>		UC82	7.4 (±0.2)	a	1	804 (±94)	a
Experiment 2							
<i>Brassica carinata</i>	Bc007	2.4 (±0.4)	mno	25	228 (±90)	n	32
<i>Brassica juncea</i>	ISCI99	4.2 (±0.2)	efghi	15	5,952 (±857)	b	2
	Nemfix	4.4 (±0.2)	efghi	13	5,090 (±1,360)	bcd	3
	Pacific Gold	5.2 (±0.4)	bcde	5	4,032 (±1,332)	bcde	6
<i>Brassica napus</i>	Greenland	3.6 (±0.2)	hijkl	18	2,432 (±434)	cdefg	12
	Humus	2.4 (±0.4)	mno	27	1,440 (±365)	fghi	19
	Winfred	1.8 (±0.2)	o	31	744 (±174)	ijkl	24
<i>Brassica oleracea</i>	Liberty	1.8 (±0.2)	o	32	1,384 (±261)	fghi	20
<i>Brassica rapa</i>	Br02205	5.2 (±0.4)	bcde	6	2,296 (±515)	cdefgh	13
	Br02206	4.4 (±0.8)	efghi	14	1,976 (±233)	cdefgh	17
	Rondo	4.0 (±0.5)	fghij	16	2,472 (±685)	cdefg	11
	Samson	5.0 (±0.6)	bcdef	8	3,316 (±602)	bcde	9
<i>Eruca sativa</i>	Nemat	2.4 (±0.2)	mno	28	520 (±157)	klm	27
<i>Raphanus sativus</i>	Adagio	3.6 (±0.4)	hijkl	19	488 (±170)	lmn	29
	Adios	4.6 (±0.5)	defgh	10	1,044 (±330)	hijk	23

(Continued)

TABLE 4. Continued.

Experiment 1 Species	Cultivar	Galling	Ranking	J2/100 g	Ranking		
	Boss	5.2 (± 0.5)	hijkl	6	304 (± 95)	mn	31
	Colonel	4.6 (± 0.2)	defgh	11	3,520 (± 728)	bcde	7
	Comet	4.8 (± 0.2)	cdefg	9	4,292 ($\pm 1,140$)	bcde	5
	Defender	2.8 (± 0.4)	klmno	24	536 (± 107)	jklm	26
	Doublet	4.6 (± 0.4)	defgh	12	2,272 (± 625)	defgh	14
	Final	5.6 (± 0.5)	bcd	4	1,952 (± 485)	efgh	18
	Rs05415	5.8 (± 0.4)	bc	3	3,464 ($\pm 1,071$)	bcdef	8
	TerraNova	5.2 (± 0.5)	bcde	7	2,840 ($\pm 1,196$)	cdefgh	10
<i>Sinapis alba</i>	Abraham	3.8 (± 0.4)	ghijk	17	2,064 (± 752)	efgh	16
	Absolut	3.0 (± 0.5)	jklmn	23	700 (± 98)	ijkl	25
	Accent	2.4 (± 0.4)	mno	29	520 (± 168)	klm	28
	Achilles	2.8 (± 0.2)	hijkl	23	1,176 (± 222)	ghij	22
	Condor	2.2 (± 0.2)	no	30	404 (± 153)	mn	30
	IdaGold	6.0 (± 0.3)	b	2	4,684 (± 826)	bc	4
	Maxi	2.8 (± 0.2)	ijklm	25	2,090 (± 306)	cdefgh	15
	Santa Fe	2.6 (± 0.4)	lmno	25	1,330 (± 235)	fghi	21
<i>Solanum lycopersicum</i>	UC82	7.6 (± 0.2)	a	1	27,272 ($\pm 4,625$)	a	1

^a Values shown are the mean of five replicates ($n = 5$) \pm SE. Root galling index on a scale from 0 to 10 with 0 = no galls, 10 = 100% of roots galled. Values in a column followed by different letters are significantly different ($P \leq 0.05$) according to Fisher's LSD-test within one experiment. Raw nematode data (egg counts) were $\log_{10}(x+1)$ -transformed before analysis; nontransformed data are presented.

M. javanica in a study by McLeod et al. (2001). Gardner and Caswell-Chen (1994), however, reported that both *M. incognita* and *M. javanica* produced numerous females in the roots of this cultivar, and recommended that it should not be grown on *M. incognita*- or *M. javanica*-infested sites for risk of nematode population increase. The response of *M. hapla* to the different brassica cultivars was sometimes very different from results with *M. incognita* or *M. javanica*. For example, *R. sativus* Colonel and TerraNova were among the best hosts for *M. hapla*, but poor hosts for *M. incognita* and *M. javanica*. Also, the variability in host status for *M. hapla* within the same brassica species was greater. For example, within *R. sativus* there were good hosts (Colonel, TerraNova) as well as poor hosts (Adagio, Condor). The fact that plants resistant to *M. incognita* and *M. javanica* are often susceptible to *M. hapla* (Roberts, 1992) is thought to be the result of basic differences in the inheritance of resistance (Bünthe et al., 1997). Within *R. sativus* lines, it is also thought that differences in response to *M. incognita* or *M. javanica*, and *M. hapla* may be because of a single gene resistance mechanism for the former two species, and a polygenic resistance mechanism for *M. hapla* (Bünthe et al., 1997). Ongoing breeding efforts may lead to more cultivars with resistance to the range of economically important *Meloidogyne* species. In our study, poor hosts for all three *Meloidogyne* species include *R. sativus* Adagio and *E. sativa* Nemat. The latter cultivar was also reported a poor host for *M. hapla* by Melakeberhan et al. (2006, 2010). Others (Curto et al., 2005; Melakerberhan et al., 2006) studied the mechanism responsible for the differences in host status of brassica crops, and found that in poor or nonhosts, the nematodes do

invade the root systems but fail to develop into females and/or develop very slowly, rendering the crops a trap crop.

Although this study did not include the biofumigant effect that occurs during cover crop decomposition after soil incorporation of the crop, it would be unproductive to grow a host crop as a biofumigant. This was also concluded by Monfort et al. (2007) who observed a large net reduction in *M. incognita* population levels from brassica cover crop incorporation to planting of the next vegetable crop, but also noted that the increase in nematode levels during cover crop growth was a major obstacle. This study clearly demonstrates that large differences occur between different brassica cultivars with respect to their host status for three *Meloidogyne* species. Based on this study, the *R. sativus* cultivars Boss, Terranova, or *E. sativa* Nemat would be good choices for cover crops on *M. incognita*- or *M. javanica*-infested sites. Conversely, *B. rapa* or *B. juncea* cover crops would carry a risk of substantial nematode multiplication. On *M. hapla*-infested sites, *E. sativa* Nemat would carry little risk of nematode multiplication, whereas *B. juncea* cultivars should be avoided. Evaluation of the validity of these recommendations under field conditions is an important next step.

LITERATURE CITED

- Bello, A., López-Pérez, J. A., and Díaz-Veruliche, L. 2000a. Biofumigación y solarización como alternativas al bromuro metilo. Pp. 25–50 in J. Z. Castellanos and F. Guerra O'Hart, eds. Memorias del Simposium Internacional de la Fresa. Zamora, Mexico.
- Bello, A., López-Pérez, J. A., Sanz, R., Escuer, M., and Herrero, J. 2000b. Biofumigation and organic amendments. Pp. 113–141 in Regional workshop on methyl bromide alternatives for North Africa and

- Southern European countries. Paris, France: United Nations Environment Program (UNEP).
- Bridge, J., and Page, S. L. J. 1980. Estimation of root-knot nematode infestation levels on roots using a rating chart. *Tropical Pest Management* 26:296–298.
- Brown, P. D., Morra, M. J., McCaffrey, J. P., Auld, D. L., and Williams, L., III, 1991. Allelochemicals produced during glucosinolate degradation in soil. *Journal of Chemical Ecology* 17:2021–2034.
- Büntel, R., Müller, J., and Friedt, W. 1997. Genetic variation and response to selection for resistance to root-knot nematodes in oil radish (*Raphanus sativus* ssp. *oleiferus*). *Plant Breeding* 116:263–266.
- Chew, F. S. 1988. Biological effects of glucosinolates. Pp. 155–181 in H. G. Cutler, ed. *Biologically active natural products: potential use in agriculture*. Washington, DC: American Chemical Society.
- Curto, G., Dallavalle, E., and Lazzeri, L. 2005. Life cycle duration of *Meloidogyne incognita* and host status of Brassicaceae and Capparaceae selected for glucosinolate content. *Nematology* 7:203–212.
- Eisenback, J. D., and Triantaphyllou, H. H. 1991. Root-knot nematodes: *Meloidogyne* species and races. Pp. 191–274 in W. R. Nickle, ed. *Manual of agricultural nematology*. New York: Marcel Dekker.
- EPA. 2012. Soil fumigant mitigation factsheet. Washington, DC: U.S. Environmental Protection Agency.
- Gardner, J., and Caswell-Chen, E. P. 1994. *Raphanus sativus*, *Sinapis alba*, and *Fagopyrum esculentum* as hosts to *Meloidogyne incognita*, *Meloidogyne javanica*, and *Plasmodiophora brassicae*. *Journal of Nematology* 26(Suppl.):756–760.
- Halbrendt, J. M. 1996. Allelopathy in the management of plant-parasitic nematodes. *Journal of Nematology* 28:8–14.
- Johnson, A. W., Golden, A. M., Auld, D. L., and Summer, D. R. 1992. Effects of rapeseed and vetch as green manure crops and fallow on nematodes and soilborne pathogens. *Journal of Nematology* 24:117–127.
- Kirkegaard, J., and Matthiessen, J. 2004. Developing and refining the biofumigation concept. *Agroindustria* 3:233–239.
- Kirkegaard, J. A., and Sarwar, M. 1998. Biofumigation potential of brassicas. I. Variation in glucosinolate profiles of diverse field-grown brassicas. *Plant and Soil* 201:71–89.
- Koenning, S. R., Overstreet, C., Noling, J. W., Donald, P. A., Becker, J. O., and Fortnum, B. A. 1999. Survey of crop losses in response to phytoparasitic nematodes in the United States for 1994. *Journal of Nematology* 31(Suppl.):587–618.
- Lamers, J. G., Runia, W. T., Molendijk, L. P. G., and Bleeker, P. O. 2010. Perspectives of anaerobic soil disinfestation. *Acta Horticulturae* 883:277–283.
- McLeod, R. W., Kirkegaard, J. A., and Steel, C. C. 2001. Invasion, development, growth and egg-laying by *Meloidogyne javanica* in Brassicaceae crops. *Nematology* 3:463–472.
- McLeod, R. W., Steel, C., and Kirkegaard, J. A. 2002. Effects of some crop management practices on reproduction of *Meloidogyne javanica* on *Brassica napus*. *Nematology* 4:381–386.
- McSorley, R., and Frederick, J. J. 1995. Responses of some common Cruciferae to root-knot nematodes. *Journal of Nematology* 27(Suppl.):550–554.
- Melakeberhan, H., Xu, A., Kravchenko, A., Mennan, S., and Riga, E. 2006. Potential use of arugula (*Eruca sativa*) as a trap crop for *Meloidogyne hapla*. *Nematology* 2006:793–799.
- Melakeberhan, H., Kravchenko, A., Dahl, J., and Warncke, D. 2010. Effects of soil types and *Meloidogyne hapla* on the multi-purpose uses of arugula (*Eruca sativa*). *Nematology* 12:115–120.
- Monfort, W. S., Csinos, A. S., Desaegeer, J., Seebold, K., Webster, T. M., and Diaz-Perez, J. C. 2007. Evaluating *Brassica* species as an alternative control measure for root-knot nematode (*M. incognita*) in Georgia vegetable plasticulture. *Crop Protection* 26:1359–1368.
- Pattison, A. B., Versteeg, C., Akiew, S., and Kirkegaard, J. 2006. Resistance of Brassicaceae plants to root-knot nematode (*Meloidogyne* spp.) in northern Australia. *International Journal of Pest Management* 52:53–62.
- Ploeg, A. T. 2008. Biofumigation to manage plant-parasitic nematodes. Pp. 239–248 in A. Ciancio and K. G. Mukerji, eds. *Integrated management of plant pests and diseases, vol. 2, Integrated management and biocontrol of vegetable and grain crops nematodes*. Dordrecht, The Netherlands: Springer.
- Ploeg, A. T., and Stapleton, J. J. 2001. Glasshouse studies on the effects of time, temperature and amendment of soil with broccoli plant residues on the infestation of melon plants by *Meloidogyne incognita* and *M. javanica*. *Nematology* 3:855–861.
- Radewald, K. C., Darsow, J., Stangelini, M. E., and Becker, J. O. 2003. Quantitative comparison of methods for recovery of root-knot nematode eggs from plant roots. *Phytopathology* 93:S129.
- Roberts, P. A. 1987. The influence of planting date of carrot on *Meloidogyne incognita* reproduction and injury to roots. *Nematologica* 33:335–342.
- Roberts, P. A. 1992. Current status of the availability, development and use of host plant resistance to nematodes. *Journal of Nematology* 24:213–227.
- Rodriguez-Kabana, R., and Pope, M. H. 1981. A simple incubation method for the extraction of nematodes from soil. *Nematropica* 11:175–186.
- Stirling, G. R., and Stirling, A. M. 2003. The potential of *Brassica* green manure crops for controlling root-knot nematode (*Meloidogyne javanica*) on horticultural crops in a subtropical environment. *Australian Journal of Experimental Agriculture* 43:623–630.
- Viaene, N. M., and Abawi, G. S. 1998. Management of *Meloidogyne hapla* on lettuce in organic soil. *Plant Disease* 82:945–952.
- Wang, D., Browne, G., Gao, S., Hanson, B., Gerik, J., Qin, R., and Tharayil, N. 2009. Spot fumigation: Fumigant gas dispersion and emission characteristics. *Environmental Science and Technology* 43:5783–5789.
- Zasada, I. A., Halbrendt, J. M., Kokalis-Burelle, N., LaMondia, J., McKenry, M. V., and Noling, J. W. 2010. Managing nematodes without methyl bromide. *Annual Review of Phytopathology* 48:311–328.