Induction of Systemic Acquired Resistance by *Rotylenchulus reniformis* and *Meloidogyne incognita* in Cotton Following Separate and Concomitant Inoculations

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Abstract: Systemic acquired resistance (SAR) can be elicited by virulent and avirulent pathogenic strains and SAR against plant-parasitic nematodes has been documented. Our objective was to determine whether co-infection of cotton by *Meloidogyne incognita* and *Rotylenchulus reniformis* affects the population level of either nematode compared to infection by each species individually. Split-root trials were conducted in which plants were inoculated with i) *R. reniformis* only, ii) *M. incognita* only, iii) both *R. reniformis* and *M. incognita*, or iv) no nematodes. Half of the root system was inoculated with *R. reniformis* or *M. incognita* on day 0 and the other half with *M. incognita* or *R. reniformis* on day 0 or day 14 depending on the experiment. Experiments were conducted on cotton cultivar DP 0935 B2RF (susceptible to both nematodes), LONREN-1 (germplasm line resistant to *R. reniformis*), and M-120 RNR (germplasm line resistant to *M. incognita*), and tests were terminated 8 wk after the last inoculation. Both soil (vermiform) and roots (egg) extracted from each half of the root system to determine the total nematode population levels, and root galling was rated on a 0 to 10 scale. Mixed models analysis and comparison of least squares means indicated no differences in root galling (except on LONREN-1) or population levels when the two nematode species were introduced on the same day. When *M. incognita* was introduced 14 d after *R. reniformis*, reduction in galling (36% on DP 0935 and 33% on LONREN-1) and *M. incognita* population levels (35% on DP 0935 and 45% on LONREN-1) were significant ($P \le 0.05$). When *R. reniformis* was inoculated 14 d after *M. incognita*, reduction in *R. reniformis* population levels (18% on DP 0935 and 26% on M-120) were significant. This study documents for the first time that infection of cotton by a nematode can elicit SAR to another nematode species.

Key words: Cotton, induced resistance, *Meloidogyne incognita,* reniform nematode, root-knot nematode, *Rotylenchulus reniformis*, split-root system, systemic acquired resistance.

Meloidogyne incognita (the southern root-knot nematode) and *Rotylenchulus reniformis* (the reniform nematode) are the two predominant nematodes damaging cotton in the US (Robinson and Cook, 2001). Greenhouse studies have shown that interactions can be antagonistic for either nematode when *M. incognita* and *R. reniformis* are feeding on the same plant. In concomitant inoculations, *M. incognita* inhibited reproduction of *R. reniformis* on black gram (Mishra and Gaur, 1981). *Meloidogyne incognita* also inhibited *R. reniformis* reproduction on soybean (Singh, 1976) and sweet potato (Thomas and Clark, 1981), but *M. incognita* was not affected by *R. reniformis* in either study. In contrast, *R. reniformis* inhibited *M. incognita* on tomato (Kheir and Osman, 1977) and cowpea (Taha and Kassab, 1980). In cotton, both *M. incognita* and *R. reniformis* were capable of reducing the population density of each other when the amount of primary inoculum was higher than that of the other nematode species (Diez et al., 2003).

Interactions between *M. incognita* and *R. reniformis* in cotton fields have not been fully characterized, but it is believed that *R. reniformis* has a competitive advantage over *M. incognita* (Diez et al., 2003; Robinson, 2007). The possibility that induction of systemic resistance might be involved in the interaction between *M. incognita* and *R. reniformis* on cotton has not been studied. The induced plant is resistant to virulent pathogens and other pests as the result of enhanced expression of defense responses resulting from infection or in some cases, as the result of a chemical treatment (Van Loon et al., 1998). Induced resistance is defined as the physiological state of enhanced defense response by the plant which provides both qualitative and quantitative expression of defense mechanisms against subsequent biotic challenges (Van Loon, 1997). At least two forms of induced resistance, systemic acquired resistance (SAR) and induced systemic resistance (ISR) have been described as distinct phenomena based on the type of inducing agents and host signaling pathways that result in resistance expression (Sticher et al., 1997; Van Loon et al., 1998). Both SAR and ISR result in similar phenotypic responses but involve different signaling mechanisms (Pieterse and Van Loon, 2004, Van Loon et al., 2006). Necrotizing pathogenic organisms can trigger SAR and nonpathogenic rhizobacteria can activate ISR (Pieterse and Van Loon, 2007). SAR results in the coordinated expression of pathogenesis-related (PR) genes (Van Loon, 1997; Hammerschmidt, 1999, 2007) that enhance the natural defense systems of plants and provide broad spectrum resistance to a range of pathogens including plant-parasitic nematodes. This process requires prior exposure of plants to a locally infecting pathogen, an avirulent form of a pathogen or some synthetic compounds (Kuc, 1982; Kessmann et al., 1994).

Induced resistance to plant-parasitic nematodes has not been as extensively studied as that to fungi and bacteria, but induced resistance (both ISR and SAR) has been documented for plant-parasitic nematodes in tomato, grape, pine, potato and soybean (Ibrahim and Lewis, 1986; Ogallo and McClure, 1995, 1996; Hasky-Gunther et al., 1998; Kosaka et al., 2001; Siddiqui and Shaukat, 2004; McKenry and Anwar, 2007; Anwar and McKenry,

2008). The goal of this study was to characterize SAR and its effects on nematode reproduction in cotton. We hypothesized that infection of cotton by one nematode species could induce SAR to another nematode species, and that the level of SAR might be affected by constitutive host-plant resistance to one of the nematodes. The specific objectives of this study were (i) to determine whether co-infection of cotton by *M. incognita* and *R. reniformis* affects the population level of either nematode compared to infection by each species individually, and (ii) to determine whether host-plant resistance in cotton to *M. incognita* or *R. reniformis* influences the effect of concomitant infection on nematode population levels.

MATERIALS AND METHODS

Experimental plants and nematode inocula: Cotton plants used in the experiments were Deltapine DP 0935 B2RF, a cotton cultivar susceptible to both *M. incognita* and *R. reniformis*; LONREN-1, a germplasm line that is resistant to *R. reniformis* but susceptible to *M. incognita*; and M-120 RNR, a germplasm line resistant to *M. incognita* but susceptible to *R. reniformis*. Seedlings were grown in a mixture (50:50) of vermiculite and steam-sterilized soil (sand 85%, silt 11%, clay 4%) for 2 to 3 wk in 5-cm-deep, 60-cm^3, biodegradable peat pots (Jiffy-Strips, Seed and Garden LLC, Brighton, MI) with the hole in the bottom of the pot covered by a piece of plastic. For the split-root system, two square plastic pots (10 cm on each side, 950 cm^3) were taped together with a notch the same size and shape as the peat pot cut out of the adjoining sides. A peat pot with a single seedling was placed into the notch, and each pot was filled with 750 cm^3 steam-pasteurized soil. Plants were grown for two to three more weeks to allow roots to grow through the small peat pot into the two adjacent pots thereby creating a split-root system prior to nematode inoculations. Plants were watered as needed up to twice a day. Each plant was supplied with 10 g of slow release granular fertilizer (NPK-14:14:14).

Rotylenchulus reniformis and *M. incognita* were used as the nematode treatments. Both species were obtained from greenhouse cultures maintained on eggplant (*Solanum melongena* var. *esculentum*) cv. Florida Market. Second-stage juveniles of *M. incognita* were obtained using a mist chamber extraction technique (Viglierchio and Schmitt, 1983). Infected roots were gently washed, cut into small pieces, and placed on top of a 10-cm-deep collecting pan covered with an 18-mesh sieve and fine tissue paper. Each pan was kept inside mist chamber for 3-5 d. Mist was sprayed on the roots for 1 min at 5-min intervals. After 72 hr, juveniles were collected using 100-over 400-mesh sieves. Vermiform stages of *R. reniformis* were extracted from soil by using gravity screening and the centrifugal sugar flotation technique (Jenkins, 1964) and collected on a 500-mesh sieve.

Experimental design and inoculation techniques: A series of split-root trials was conducted; each trial included

four treatments and 10 replications in a randomized complete block design. The four treatments were single plants with a split root system inoculated with i) *R. reniformis* to one half only, ii) *M. incognita* to one half only, iii) *R. reniformis* to one half and *M. incognita* to the other half, and iv) a nontreated control. Inoculum density for nematode treatments was 7000 second stage juveniles (J2) of *M. incognita* or 7000 vermiform (mixed life stages) *R. reniformis*. Nematodes were added in three holes (3 cm deep) around the peat pot. On the susceptible DP 0935 and the reniform-resistant LONREN-1, one half of the root system of 6-week-old plants was inoculated with *R. reniformis* (inducer inoculum) and other half was inoculated with *M. incognita* (challenge inoculum) on day 0 or day 14 depending on the experiment. In similar experiments, *M. incognita* was added as the inducer inoculum and *R. reniformis* was added challenge inoculum on susceptible DP 0935 and *M. incognita*-resistant M-120 RNR.

Gall rating and final population assessment: Experiments were terminated 8 wk after inoculation with challenge inoculum, and both soil (vermiform extraction) and roots (egg extraction) from each half of the root system were processed to assess the total nematode population levels. The two halves of the split-root system were cut apart, and soil was carefully removed by hand, then roots were washed lightly to remove the remaining soil, and patted dry with a paper towel. Root-gall rating was assessed on a 0 to 10 scale based on percentage of the root system with galls (0 = no galls, 1=1-10% galls, 2 = 11-20% galls, 3 = 21-30% galls, etc.). The fresh weight was recorded from each half of the root system for root-weight analysis between halves of the root system within a treatment and for total root weight among the treatments. Eggs were extracted from each half of the root system by immersing roots into 20% bleach solution (1.25% NaOCl) and immediately shaking for 4 min on a mechanical shaker (Hussey and Barker, 1973). Vermiform stages were extracted using gravity screening and centrifugal sugar flotation (Jenkins, 1964). Eggs were collected using nested 100-over 500-mesh sieves, and vermiform stages were collected on a 400-mesh sieve. Each experiment with a single cotton genotype was conducted twice as described above.

Data analysis: Data were analyzed using the mixed models (GLIMMIX) procedure of SAS (version 9.2, SAS Institute Inc., Cary, NC). Final populations (eggs + vermiform) were transformed using the function $\log_{10} (X + 1)$ to correct heterogeneity of variances and non-normality prior to analysis. Treatment replications within a trial and repetitions of the trials were considered as random effects. Treatment means were separated by comparison of least squares means ($P \leq 0.05$) using the lines and PDIFF options in SAS.

RESULTS

Effect of R. reniformis on reproduction of M. incognita on susceptible DP 0935: When *R. reniformis* and *M. incognita*

were introduced onto DP 0935 on the same day, root galling was not affected by *R. reniformis*, but the root gall-index was significantly greater on plants inoculated with *M. incognita* alone compared to plants inoculated with *M. incognita* 2 wk after inoculation with *R. reniformis* (Table 1). Populations of *M. incognita* and *R. reniformis* did not differ between plants inoculated with both species and plants inoculated with only one species when both nematode species were added on the same day. However, following inoculation with *R. reniformis* 2 wk earlier, the reproduction of *M. incognita* was reduced by 35% (Table 1).

Effect of M. incognita on reproduction of R. reniformis on susceptible DP 0935: Results showed that following prior inoculations with *M. incognita*, the reproduction of *R. reniformis* was reduced ($P \le 0.0001$). Even though *M. incognita* was introduced 2 wk before *R. reniformis*, the gall index and population levels were also reduced ($P \le 0.0069$) compared to *M. incognita* alone (Table 1).

Effect of host-plant resistance on the reproduction of challenge inoculum: In the reniform-resistant LONREN-1, root galling was reduced regardless of whether *M. incognita* was applied at the same time as *R. reniformis* or 2 wk later (Table 2). There was no significant reduction of *M. incognita* reproduction when the two species were applied at the same time, but the reproduction of *M. incognita* was reduced by 45% when it was applied 2 wk after *R. reniformis* (Table 2). Similarly, in root-knot-resistant M-120 RNR, the reproduction of *R. reniformis* was unchanged when it was added the same day as *M. incognita*, but *R. reniformis* levels were significantly lower ($P = 0.0028$) when

TABLE 2.   Root-gall ratings and final population levels of *Meloidogyne incognita* (*Mi*) and *Rotylenchulus reniformis* (*Rr*) following single and co-inoculations on reniform-resistant cotton LONREN-1[a].

Treatments	Gall index[b]	Final population level[c]	
		Mi	*Rr*
M. incognita and *R. reniformis* inoculated at same day			
Rr + *Mi*	2.9 b[d]	25,721 a	2,010 a
Mi only	3.5 a	29,890 a	0 b
Rr only	0.0 c	0 b	1,658 a
Control	0.0 c	0 b	0 b
M. incognita inoculated 14 days after *R. reniformis*			
Rr + *Mi*	3.30 b	20,843 b	1,000 a
Mi only	4.95 a	37,730 a	0 b
Rr only	0.00 c	0 c	1,154 a
Control	0.00 c	0 c	0 b

[a] LS means of 20 replicates (data were pooled from trials I and II; each trial consisted 10 replicates).
[b] Root-gall index was assessed based on percentage of root system with galls on a 0 to 10 scale.
[c] Final population consisted of total eggs plus vermiform (statistical analysis was performed on $\log_{10}$ (x+1) transformed nematode populations).
[d] Means in each column followed by the same letters are not significantly different according to comparison of least squares means ($P \le 0.05$).

M. incognita was added 2 wk before the challenge inoculation with *R. reniformis* (Table 3).

In each trial, root weight from the two halves of the split-root system within each treatment was compared, and no differences were observed. The total fresh root weight (sum of the two halves) per plant was compared among the four treatments, and no significant differences in root weight were observed among the four treatments (data not shown).

DISCUSSION

In nature, the effects of nematode species interactions are mostly antagonistic among species with

TABLE 1.   Root-gall ratings and final population levels of *Meloidogyne incognita* (*Mi*) and *Rotylenchulus reniformis* (*Rr*) following single and co-inoculations on susceptible cotton DP 0935[a].

Treatments	Gall index[b]	Final population level[c]	
		Mi	*Rr*
M. incognita and *R. reniformis* inoculated at same day			
Rr + *Mi*	4.50 a[d]	44,995 a	29,536 a
Mi only	4.65 a	51,855 a	0 b
Rr only	0.00 b	0 b	31,465 a
Control	0.00 b	0 b	0 b
M. incognita inoculated 14 days after *R. reniformis*			
Rr + *Mi*	3.40 b	28,843 b	23,366 a
Mi only	5.35 a	44,598 a	0 b
Rr only	0.00 c	0 c	32,973 a
Control	0.00 c	0 c	0 b
R. reniformis inoculated 14 days after *M. incognita*			
Rr + *Mi*	3.90 b	61,980 b	53,251 b
Mi only	4.45 a	73,483 a	0 c
Rr only	0.00 c	0 c	64,866 a
Control	0.00 c	0 c	0 c

[a] LS means of 20 replicates (data were pooled from trials I and II; each trial consisted 10 replicates).
[b] Root-gall index was assessed based on percentage of root system with galls on a 0 to 10 scale.
[c] Final population consisted of total eggs plus vermiform (statistical analysis was performed on $\log_{10}$ (x+1) transformed nematode populations).
[d] Means in each column followed by the same letters are not significantly different according to comparison of least squares means ($P \le 0.05$).

TABLE 3.   Root-gall ratings and final population levels of *Meloidogyne incognita* (*Mi*) and *Rotylenchulus reniformis* (*Rr*) following single and co-inoculations on root-knot- resistant cotton M-120 RNR[a].

Treatments	Gall index[b]	Final population level[c]	
		Mi	*Rr*
M. incognita and *R. reniformis* inoculated at same day			
Rr + *Mi*	1.2 a[d]	585 b	48,066 a
Mi only	1.4 a	1,162 a	0 b
Rr only	0.0 b	0 c	48,007 a
Control	0.0 b	0 c	0 b
R. reniformis inoculated 14 days after *M. incognita*			
Rr + *Mi*	1.6 a	2,390 a	34,408 b
Mi only	1.7 a	2,700 a	0 c
Rr only	0.0 b	0 b	46,610 a
Control	0.0 b	0 c	0 c

[a] LS means of 20 replicates (data were pooled from trials I and II; each trial consisted 10 replicates).
[b] Root-gall index was assessed based on percentage of root system with galls on a 0 to 10 scale.
[c] Final population consisted of total eggs plus vermiform (statistical analysis was performed on $\log_{10}$ (x+1) transformed nematode populations).
[d] Means in each column followed by the same letters are not significantly different according to comparison of least squares means ($P \le 0.05$).

similar feeding habits mainly due to the competition for space and food (Eisenback, 1985). The competitive (suppressive) interactions between *R. reniformis* and *M. incognita* have been documented based on population dynamics and attributed to their competition for feeding sites (Thomas and Clark, 1983a, 1983b; Diez et al., 2003). The results from the split-root experiments show that prior infection of susceptible DP 0935 cotton plants with *R. reniformis* significantly suppressed the ability of *M. incognita* to cause galls and reproduce compared to single species inoculations. Because the nematode species were physically separated, this effect could not be due to competition for feeding sites. Our results clearly document a systemic resistance response that we believe to be systemic acquired resistance (SAR). Similarly, when *M. incognita* was added 2 wk before *R. reniformis*, it induced a similar systemic resistance response against *R. reniformis*.

In SAR, active defenses are triggered by a primary infection with certain pathogens or chemical treatments that result in resistance to secondary infections (Wubben et al., 2007). Although the downstream components are similar to induced systemic resistance (ISR) mechanisms, the upstream components differ, mainly involving the salicylic acid (SA) pathway for SAR and the jasmonic acid (JA) or ethylene (Et) pathways for ISR (Pieterse and Van Loon, 2007). Systemic acquired resistance is also involved in the production of pathogenesis-related proteins (Van Loon, 1997). This active resistance mechanism is also characterized by the production of peroxidases, and by the lignin formation and the cell wall modifications (Cohn and Gisi, 1994; Cohen et al., 1999). Systemic acquired resistance induced by virulent or avirulent nematode populations against virulent nematode populations has not been studied as extensively as it has been for bacteria, viruses and fungi (Pieterse and Van Loon, 2007), but similar biochemical pathways are believed to be triggered against plant-parasitic nematodes (Kogan and Paxton, 1983; Zacheo and Bleve-Zacheo, 1995).

Previous reports have documented the ability of nematodes to induce SAR in plants. Centennial soybean, which is normally susceptible to *M. arenaria*, expressed increased resistance to this nematode after prior inoculation with *M. incognita* (Ibrahim and Lewis, 1986). In tomato and pyrethrum, SAR to the root-knot nematode *M. hapla* was observed following prior inoculation with naturally incompatible species of *M. incognita* or *M. javanica* (Ogallo and McClure, 1995). In a split-root assay, SAR against *M. hapla* was obtained on tomato by pre-inoculation with an avirulent strain of *M. incognita* (Ogallo and McClure, 1996). In pine, prior inoculation with an avirulent strain of *Bursaphelenchus xylophilus* induced SAR to a virulent strain of *B. xylophilus* (Kosaka et al., 2001). In split-root experiments, McKenry and Anwar (2007) reported that an avirulent population of *M. incognita* induced SAR to a virulent population of *M. arenaria* in Harmony grape rootstock. In tomato,

challenge inoculations with a virulent population of *M. incognita* to half of the root system 7 d after inoculating the other half with an avirulent population of the same species suppressed reproduction of the virulent population (Anwar and McKenry, 2008). Our study also documents the ability of one nematode species to induce SAR to another species, but ours is the first report of SAR against a nematode in cotton, and it is also the first report of SAR induced by *R. reniformis*.

Little information is available on genotype-specific variation in the level of SAR expression. However, cultivars with constitutive host-plant resistance to the inducer species can exhibit SAR; therefore we also included genotypes with resistance to either *R. reniformis* or *M. incognita*. When *R. reniformis* was added 2 wk before *M. incognita*, reproduction of *M. incognita* was reduced by 45% on the reniform-resistant LONREN-1; and the level of suppression on the susceptible DP 0935 was 35%. Additionally, galling was reduced on LONREN-1 even when *M. incognita* and *R. reniformis* were introduced at the same time, but this was not observed in susceptible DP 0935. Similarly in root-knot-resistant M-120 RNR, *M. incognita* induced SAR to *R. reniformis* and suppressed reproduction by 26%, whereas suppression on DP 0935 was 18%. Although we cannot directly compare the level of SAR between resistant and susceptible genotypes because they were not in the same experiment, there was a trend for a greater level of SAR in resistant genotypes.

We observed SAR in susceptible cotton as well as cotton with resistance to *R. reniformis* or *M. incognita*. Host genotypes have been shown to influence the expression of induced resistance (Walters and Fountaine, 2009). In cucumber, INA (2,6-dichloroisonicotinic acid) induced SAR to the powdery mildew fungus (*Sphaerotheca fuliginea*) and was shown to be cultivar dependent, with the highest levels of SAR expressed in moderately resistant cultivars (Hijwegen and Verhaar, 1994). In soybean, SAR induced by treatment with BTH (benzothiadiazole) or INA reduced the levels of *Sclerotinia sclerotiorum*, and the levels of reduction were greatest in susceptible cultivars (Dann et al., 1998). In contrast, BTH provided control of blue mold (*Peronospora hyocyami* f. sp. *tabacina*) in resistant tobacco plants but not in susceptible tobacco cultivars (Perez et al., 2003). Recently, tomato genotypes treated with BABA (β-aminobutyric acid) expressed significant variability in SAR expression against *Phytophthora infestans*. The level of SAR was not always associated with level of constitutive resistance of the tomato cultivars, but SAR level was influenced notably by pathogen isolates (Sharma et al., 2010). These studies indicate that the level of SAR generally varies among plant genotypes.

In our experiments, the induction of resistance was observed when the inducer inoculum was added 14 d before the challenge inoculum, and that is consistent with previous reports that there is a time delay in the expression of resistance in SAR following infection by

the inducing agent. The delay in induction of systemic resistance is due to the time required for post-infection accumulation of antimicrobial substances. Post-infection accumulation of peroxidase enzymes in tomato plants resistant to *M. incognita* reached maximum levels 10 d after inoculation with an avirulent *M. incognita* population (Zacheo et al., 1983).

It is not known whether other plant-parasitic nematodes, including species that are much less damaging than *M. incognita* and *R. reniformis*, can induce SAR in cotton. It also is not known what level of inducer inoculum is needed to elicit SAR in cotton, if that level varies among nematode species, or how long the induced resistance persists. Further studies will be needed to better understand nematode induced SAR in cotton. But this study documents for the first time that infection of cotton by a nematode can elicit SAR to another nematode species. This post-infection induction of resistance may have a significant direct effect on nematode population dynamics (Ogallo and McClure, 1996) and may help explain results that otherwise might be attributed to nematode competition for feeding sites. Unexpectedly, we found a significant reduction in galling and reproduction of *M. incognita* when it was the inducer inoculum, and that inhibition may contribute to a competitive advantage of *R. reniformis* over *M. incognita*.

Literature Cited

Anwar, S. A., and McKenry, M. V. 2008. Induction of resistance and susceptibility in tomato by two *Meloidogyne incognita* populations. Journal of Nematology 40:276–280.

Cohn, J., and Gisi, U. 1994. Systemic translocation of ^{14}C-DL-3-aminobutyl acid in tomato plants in relation to induced resistance against *Phytophthora infestans*. Physiological and Molecular Plant Pathology 45:441–456.

Cohen, Y., Reuveni, M., and Baider, A. 1999. Local and systemic activity of BABA (DL-3-aminobutyric acid) against *Plasmopara viticola* in grapevines. European Journal of Plant Pathology 195:351–361.

Dann, E., Diers, B., Byrum, J., and Hammerschmidt, R. 1998. Effect of treating soybean with 2,6-dichloroisonicotinic acid (INA) and benzothiadiazole (BTH) on seed yields and the level of disease caused by *Sclerotinia sclerotiorum* in field and glasshouse studies. European Journal of Plant Pathology 104:271–278.

Diez, A., Lawrence, G. W., and Lawrence, K. S. 2003. Competition of *Meloidogyne incognita* and *Rotylenchulus reniformis* on cotton following separate and concomitant inoculations. Journal of Nematology 35:422–429.

Eisenback, J. D. 1985. Interactions among concomitant populations of nematodes. Pp. 193–213 *in* J. N. Sasser, and C. C. Carter, eds. An advance treatise on *Meloidogyne*, vol. 1. North Carolina State University Graphics: Raleigh, NC.

Hammerschmidt, R. 1999. Induced disease resistance: How do induced plants stop pathogens? Physiological and Molecular Plant Pathology 55:77–84.

Hammerschmidt, R. 2007. Introduction: Definition and some history. Pp. 1–8 *in* D. Walters, A. Newton, and G. Lyon, eds. Induced resistance for plant defense: A sustainable approach to crop protection. Oxford, UK: Blackwell Publishing.

Hasky-Gunther, K., Hoffmann-Hergarten, S., and Sikora, R. A. 1998. Resistance against the potato cyst nematode *Globodera pallida* systemically induced by the rhizobacteria *Agrobacterium radiobacter* (G12) and *Bacillus sphaericus* (B43). Fundamental and Applied Nematology 21:511–517.

Hijwegen, T., and Verhaar, M. A. 1994. Effect of cucumber genotype on the induction of resistance to powdery mildew, *Sphaerotheca fuliginea*, by 2,6-dichloroisonicotinic acid. Plant Pathology 44:756–762.

Hussey, R. S., and Barker, K. R. 1973. A comparison of methods of collecting inocula of *Meloidogyne* spp., including a new technique. Plant Disease Reporter 57:1025–128.

Ibrahim, I. K. A., and Lewis, S. A. 1986. Inter-relationships of *Meloidogyne arenaria* and *M. incognita* on tolerant soybean. Journal of Nematology 18:106–111.

Jenkins, W. R. 1964. A rapid centrifugal flotation technique for separating nematodes from soil. Plant Disease Reporter 48:692.

Kessmann, H., Staub, T., Hofmann, C., Maetzke, T., Herzog, J., Ward, E., Uknes, S., and Ryals, J. 1994. Induction of systemic acquired disease resistance in plants by chemicals. Annual Review of Phytopathology 32:439–459.

Kheir, A. M., and Osman, A. A. 1977. Interaction of *Meloidogyne incognita* and *Rotylenchulus reniformis* on tomato. Nematologica Mediterranea 5:113–116.

Kogan, M., and Paxton, J. 1983. Natural inducers of plant resistance to insects. Pp. 153–171 *in* P. A. Hedin, ed. Plant resistance to insects. American Chemical Society Symposium Series, vol. 208. American Chemical Society: Washington, DC.

Kosaka, H., Aikawa, T., Ogura, N., Tabata, K., and Kiyohara, T. 2001. Pine wilt disease caused by the pine wood nematode: The induced resistance of pine trees by the avirulent isolates of nematode. European Journal of Plant Pathology 107:66–675.

Kuc, J. 1982. Induced immunity to plant diseases. Bioscience 32:854–860.

McKenry, M. V., and Anwar, S. A. 2007. Virulence of *Meloidogyne* spp. and induced resistance in grape rootstocks. Journal of Nematology 39:50–54.

Mishra, S. D., and Gaur, H. S. 1981. Effect of individual and concomitant inoculation with *Meloidogyne incognita* and *Rotylenchulus reniformis* on the growth of black gram (*Vigna mungo*). Indian Journal of Nematology 11:25–28.

Ogallo, J. L., and McClure, M. A. 1995. Induced resistance to *Meloidogyne hapla* by other *Meloidogyne* species on tomato and pyrethrum plants. Journal of Nematology 27:441–447.

Ogallo, J. L., and McClure, M. A. 1996. Systemic acquired resistance and susceptibility to root-knot nematodes on tomato. Phytopathology 86:498–501.

Perez, L., Rodriguez, M. E., Rodriguez, F., and Roson, C. 2003. Efficacy of acibenzolar-S-methyl, an inducer of systemic acquired resistance, against tobacco blue mould caused by *Peronospora hyocyami* f. sp. *tabacina*. Crop Protection 22:405–413.

Pieterse, C. M. J., and Van Loon, L. C. 2004. NPR1: The spider in the web of induced resistance signaling pathways. Current Opinion in Plant Biology 7:456–464.

Pieterse, C. M. J., and Van Loon, L. C. 2007. Signaling cascades involved in induced resistance. Pp. 65–88 *in* D. Walters, A. Newton, and G. Lyon, eds. Induced resistance for plant defense: A sustainable approach to crop protection. Oxford, UK: Blackwell Publishing.

Robinson, A. F. 2007. Reniform in US cotton: When, where, why, and some remedies. Annual Review of Phytopathology 45:263–288.

Robinson, A. F., and Cook, C. G. 2001. Root-knot and reniform nematode reproduction on kenaf and sun hemp compared with that on nematode resistant and susceptible cotton. Industrial Crops and Products 13:249–264.

Sharma, K., Butz, A. F., and Finckh, M. R. 2010. Effects of host and pathogen genotypes on inducibility of resistance in tomato (*Solanum lycopersicum*) to *Phytophthora infestans*. Plant Pathology 59:1062–1071.

Siddiqui, I. A., and Shaukat, S. S. 2004. Systemic resistance in tomato induced by biocontrol bacteria against the root-knot nematode,

Meloidogyne javanica is independent of salicylic acid production. Journal of Phytopathology 152:48–54.

Singh, N. D. 1976. Interaction of *Meloidogyne incognita* and *Rotylenchulus reniformis* on soybean. Nematropica 6:76–81.

Sticher, L. B., Mauch-Mani, B., and Metraux, J. P. 1997. Systemic acquired resistance. Annual Review of Phytopathology 35:237–270.

Taha, A. H. Y., and Kassab, A. S. 1980. Interrelations between *Meloidogyne incognita, Rotylenchulus reniformis* and *Rhizobium* sp. on *Vigna sinensis*. Journal of Nematology 12:57–62.

Thomas, R. J., and Clark, C. A. 1981. *Meloidogyne incognita* and *Rotylenchulus reniformis* interaction in a sweet potato field. Phytopathology 71:908 (Abstr.).

Thomas, R. J., and Clark, C. A. 1983a. Effects of concomitant development on reproduction of *Meloidogyne incognita* and *Rotylenchulus reniformis* on sweet potato. Journal of Nematology 15:215–221.

Thomas, R. J., and Clark, C. A. 1983b. Population dynamics of *Meloidogyne incognita* and *Rotylenchulus reniformis* alone and in combination and their effects on sweet potato. Journal of Nematology 15:204–211.

Van Loon, L. C. 1997. Induced resistance in plants and the role of pathogenesis-related proteins. European Journal of Plant Pathology 103:753–765.

Van Loon, L. C., Baker, P. A. H. M., and Pieterse, C. M. J. 1998. Systemic resistance induced by rhizosphere bacteria. Annual Review of Phytopathology 36:453–483.

Van Loon, L. C., Rep, M., and Pieterse, C. M. J. 2006. Significance of inducible defense-related proteins in infected plants. Annual Review of Phytopathology 44:135–162.

Viglierchio, D. R., and Schmitt, R. V. 1983. On the methodology of nematode extraction from field samples: Baermann funnel modifications. Journal of Nematology 15:438–444.

Walters, D. R., and Fountaine, J. M. 2009. Practical application of induced resistance to plant diseases: An appraisal of effectiveness under field conditions. Journal of Agricultural Science 147:1–13.

Wubben, M. J. E., Jin, J., and Baum, T. J. 2007. Cyst nematode parasitism of *Arabidopsis thaliana* is inhibited by salicylic acid (SA) and elicits uncoupled SA-independent pathogenesis-related gene expression in roots. Molecular Plant-Microbe Interactions 21:424–432.

Zacheo, G., Arrigoni-Liso, R., Belve-Zacheo, T., Lamberti, F., and Arrigoni, O. 1983. Mitochondria peroxidase and superoxidase dismutase activities during infection by *Meloidogyne incognita* of susceptible and resistant tomato plants. Nematologia Mediterranea 11:107–114.

Zacheo, G., and Bleve-Zacheo, T. 1995. Plant-nematode interactions: Histological, physiological and biochemical interactions. Pp. 321–353 *in* K. Kohmoto, U. S. Singh, and R. P. Singh, eds. Pathogenesis and host specificity in plant diseases: Histopathological, biochemical, genetic and molecular bases, vol. 3. Oxford, UK: Elsevier Science.