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Effects of Soil Compaction and *Meloidogyne incognita* on Cotton Root Architecture and Plant Growth

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Abstract: The effects of a soil hardpan and *Meloidogyne incognita* on cotton root architecture and plant growth were evaluated in microplots in 2010 and 2011. Soil was infested with *M. incognita* at four different levels with or without a hardpan. The presence of a hardpan resulted in increased plant height, number of main stem nodes, and root fresh weight for cotton seedlings both years. *Meloidogyne incognita* decreased height and number of nodes for seedlings in 2010. Nematode infestation increased seedling root length and enhanced root magnitude, altitude, and exterior path length in 2010. This was also the case for root length and magnitude in 2011 at lower infestation levels suggesting compensatory growth. A hardpan had no consistent effect on these root parameters but increased root volume in both years. A hardpan hastened crop maturity and increased the number of fruiting branches that were produced, while *M. incognita* infection delayed crop development and reduced plant height and number of bolls. Both *M. incognita* infection and a hardpan reduced taproot length and root dry weight below the hardpan in both years. Root topological indices under all the treatments ranged from 1.71 to 1.83 both years indicating that root branching followed a herringbone pattern. The techniques for characterizing root architecture that were used in this study provide a greater understanding of changes that result from disease and soil abiotic parameters affecting root function and crop productivity.

Key words: ecology, host-parasite relationship, root-knot nematode, root topology, soil hardpan.

The southern root-knot nematode, *Meloidogyne incognita* (Kofoid & White) Chitwood, is a detrimental pathogen of cotton (*Gossypium hirsutum* L.) that is distributed throughout the U.S. Cotton Belt (Koenning et al., 2004). Root-knot nematodes cause the greatest crop loss in cotton in sandy soils (Monfort et al., 2007) at temperatures above 25 °C (Thomas and Kirkpatrick, 2001).

Cotton is a taproot crop in which the primary or "tap" root branches giving rise to secondary and tertiary roots (McMichael, 1986). The shape of the root system, the volume of soil explored by the roots, and overall root density is dependent on the development of lateral roots that extend outward from the taproot (McMichael, 1986). The depth of root penetration depends in large part on the taproot. A functional root system is vital for anchorage and nutrient uptake from the soil environment (Lynch, 1995). Impaired root growth and development because of pathogens such as *M. incognita*, or because of physical edaphic factors may limit crop growth and development. A common physical factor that may impact root growth in agricultural fields is compaction (Harveson et al., 2005). Compacted soil has a higher bulk density and resistance to penetration (strength) (Whalley et al., 1995). Root penetration is inhibited by high soil resistance (Taylor and Gardner, 1963; Medvedev, 2009). Compaction restricts root growth of most plants when the soil resistance reaches about 1,500 kPa; at a resistance near 2,500 kPa, vertical root penetration is almost completely inhibited (Coelho et al., 2000). Lowry et al. (1970) reported the distribution of plant roots was partially or fully aggregated to a shallow plowed layer above a compacted soil pan. An inverse linear relationship between soil strength and yield of corn, soybean, and wheat grown in soils with a hardpan has been reported (Busscher et al., 2000).

Meloidogyne incognita distorts cotton root morphology by inducing gall formation resulting in the disruption of the xylem, root epidermis, and cortical tissues (Bird, 1974; Meon et al., 1978; Shepherd and Huck, 1989). Root damage and dysfunction because of alterations in root anatomy may affect host-plant water relations and suppress plant growth and development (Wilcox-Lee and Loria, 1987; Koenning et al., 2004). Reduced leaf stomatal resistance and transpiration (Evans et al., 1975; Kirkpatrick et al., 1995) and water deficit stress symptoms after root-knot nematode infestation have been documented (O'Bannon and Reynolds, 1965). Changes in root system architecture because of this pathogen have been documented in controlled environmental studies (Ma, 2012), but no research has been done to quantify the nature of this reduction in the field. Changes in root architecture, particularly in combination with the effects that may occur with increased soil bulk density as a result of a hardpan could be very important in a loss of crop productivity. The objective of this study was to determine the effect of a hardpan and *M. incognita* on cotton root architecture and plant growth in microplots.

Materials and Methods

Sixty-four concrete microplots (76-cm diam., buried 80-cm deep) located at the Southwest Research and Extension Center, Hope, Arkansas, were used for this study in 2010 and 2011. Prior to planting in 2010, the

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microplots had been used for a soil texture study (Jaraba-Navas et al., 2007). These microplots were left undisturbed after completion of the previous experiment and were compacted because of natural forces (precipitation, hot and cold temperature, and evaporation). Microplots used for the hardpan treatment had soil textures with sand contents ≤ 71%, and soil bulk densities ranged from 1.80 to 2.07 g/cm^3 before the current study was initiated. In preparation for this study, the upper 20 cm of soil was removed and the remaining compacted soil was left in 32 of the microplots to provide a compacted layer or hardpan. A steam-pasteurized (30 min at 70°C), fine loamy sand (87.1% sand, 6.8% silt, 6.1% clay) was then added to the microplots above the compacted zone. The soil in the remaining 32 microplots was removed to a depth of 80 cm and the microplots were refilled with the pasteurized loamy sand to provide a comparison without a hardpan. To ensure that no residual nematodes remained from the previous trial, all the plots were treated with Vapam® HL (sodium methyldithiocarbamate, 42% a.i., Amvac Chemical Corp., Los Angeles, CA) at 35-ml/plot in 3,785-ml water, poured uniformly on the soil surface. Immediately after application, each plot received an additional 8 liters of water to help disperse the fumigant into the soil and to provide a water seal. One week prior to planting, soil samples were taken from all plots and tested for nematodes with a semi-automatic elutriator (Byrd et al., 1976) and sugar flotation (Jenkins, 1964) to ensure the pathogen had been eliminated.

Inoculum of *M. incognita* race 3 was obtained from stock cultures maintained in a greenhouse on tomato (*Lycopersicon esculentum* Mill. cv. 'Rutgers'). In 2010, inoculum was prepared by cutting tomato root systems (60 d old) into segments 1 to 2 cm in length and mixing the root segments thoroughly with the soil in which the plants were grown. All root segments and soil were composited, and subsamples were assayed to quantify the number of nematodes that were present. Nematode egg numbers were determined by collecting all infected root segments from a standard volume of soil and extracting the eggs in 0.05% NaOCl (Hussey and Barker, 1973) for 4 min. Vermiform second-stage juveniles (J2) in the soil were assayed using a semi-automatic elutriator and centrifugal flotation. The soil and *M. incognita*-infected tomato roots were added to specific microplots immediately prior to planting in a sufficient volume to achieve a total density of 4 eggs/cm^3 soil in the upper 15 cm of the microplot. Control plots received root fragments and soil from pots having healthy tomato plants. The soil-root mixture was incorporated thoroughly into each microplot to a depth of 15 cm. Microplots for treatments at higher initial densities (8 or 12 eggs/cm^3 soil) received a second or third inoculation of 4 eggs/cm^3/inoculation at 12 or 24 d later to obtain densities of 8 or 12 eggs/cm^3 soil, respectively. For these inoculations, *M. incognita* eggs extracted with NaOCl and suspended in distilled sterile water were applied into two holes (0.5-cm diam. by 5-cm deep) per microplot.

In 2011, approximately 45 d prior to planting, soils were disinfested in all the microplots by drenching with Vapam® HL and assayed for live nematodes as described previously. The same nematode population was used in 2011, but inoculum consisted exclusively of eggs that were extracted from infected tomato plants. Nematode eggs were applied in three different events starting at planting and then at 12-d intervals to achieve final densities of 4, 8, and 12 eggs/cm^3 soil as described for 2010. Noninfested control plots received sterile water only.

Twenty untreated cotton seeds of the root-knot nematode susceptible cotton cultivar DP 0935 B2RF (Delta and Pine Land Co., Scott, MS) were planted in each plot immediately after infestation. The first *M. incognita* inoculation and planting occurred on 29 April 2010 and 5 May 2011, when the average soil temperature at 15-cm deep was above 16°C for 3 consecutive d. The second and third inoculum applications of *M. incognita* occurred on 11 May and 23 May 2010 and 18 May and 30 May 2011.

The experimental design of this study was completely randomized with eight replications. Treatments included a noninfested control, and *M. incognita* at three different densities (4, 8, and 12 eggs/cm^3 soil) with and without a hardpan.

Model "R" Irrometers (IRROMETER Co., Inc., Riverside, CA) were placed at 10 cm and 20 cm below the soil surface in arbitrarily selected plots to monitor the soil water matric potential in plots with and without a hardpan in both years. In the spring and early summer, 6 mm of water was added to each plot when the matric potential at 10 cm reached -30 J/kg. In midsummer and early fall, 12 mm and 24 mm of water, respectively, were added to each plot when matric potential reached -50 J/kg. Plant watering was stopped on 8 September 2010 and 10 September 2011. Polyethylene rain shields were installed over the microplots in 2010 in an attempt to keep natural rainfall out of the plots. The covers were not used in 2011. Soil temperature was recorded at 20 cm below the soil surface from selected microplots with a Model 450 WatchDog Data Logger (Spectrum Technologies, Inc., Plainfield, IL). Weather data were obtained from the weather station located approximately 100 m from the microplots for both years. In the early season and late season of both years, soil penetration resistance for each plot was measured to a depth of 45 cm with a SC 900 Soil Compaction Meter (Spectrum Technologies, Inc.).

Microplot soil fertility was maintained by applying Jack's Classic Fertilizer, 20-20-20 (J. R. Peters, Inc., Allentown, PA) (2.1% of nitrate nitrogen, 17.9% of urea nitrogen, 20% of P_2O_5, and 20% of K_2O) to each plot periodically throughout the growing season to maintain plant growth. Insect control was accomplished with

esfenvalerate (Asana XL; E.I. du Pont de Nemours and Co., Wilmington, DE) and acephate (Orthene 90S; Valent USA Corp., Walnut Creek, CA) based on scouting according to Arkansas Extension Service recommendations for cotton (Studebaker, 2010). Seedling stand was determined 20 d after planting (DAP), and the plant population was thinned to eight plants per plot. Four seedlings with intact root systems from each plot were excavated 31 and 34 DAP in 2010 and 2011, respectively. Plant height from the cotyledonary node to the tip of the main terminal and the number of main stem nodes were determined for each plant. Leaf and stem tissue above the cotyledonary nodes was dried at 60°C for 48 hr to determine top dry weight.

Excavated root systems were rinsed in running tap water for 20 min, surface-disinfested with 0.5% NaOCl by immersion for 1.5 min, blotted dry and weighed. Each root system was rated for root galling on a scale of 0 to 5, where 0 = no galls, 1 = 1 to 2, 2 = 3 to 10, 3 = 11 to 30, 4 = 31 to 100, and 5 = 101 to 200 galls/root system. Midpoint values, which are the median of the ranges within a category (0 = 0 galls, 1 = 1.5 galls, 2 = 6.5 galls, 3 = 20.5 galls, 4 = 65.5 galls, 5 = 150 galls/root) were used for statistical analysis. Each seedling root was scanned by a high-resolution image scanner (Epson® Expression® 10000XL Scanner, Epson America, Inc., Long Beach, CA). The WinRHIZO image analysis system (Regent Instruments, Inc., Quebec, Canada) was used to analyze each root image to obtain the root morphological data (root surface area, volume, radius, links, tips) and architectural data (altitude, magnitude, and exterior path length) (Fitter, 1986). A link is a segment of root from the root tip to a branch or between branches. Magnitude is a topological parameter that describes the number of exterior links. Altitude is defined as the number of links in the longest path from any exterior link to the base link. Exterior path length (P_e) is the sum of the number of links in all paths. Based on this topological classification system, there are two idealized topological models—herringbone and dichotomous (Fig. 1). With herringbone root systems, branching is confined to the main axis while a dichotomous system has equal branching on all links (Werner and Smart, 1973; Fitter, 1985). The topological index (TI) that describes this branching is determined by the slope of the regression line from double-logarithmic ($\log_e$) plots of the exterior path length against the magnitude (Fitter, 1986; Fitter and Setters, 1988; Larkin et al., 1995, 1996). The values for TI usually range from 1.9 for herringbone models to 1.2 for dichotomous patterns (Werner and Smart, 1973; Fitter, 1986).

Cotton was harvested by hand at maturity. Plant height from the cotyledonary node to the tip of the main terminal for each plant was determined. Plant growth and development were recorded using COTMAP (Bourland and Watson, 1990) to describe the position of the first sympodial branch above the cotyledonary node, total number of sympodial branches, number of sympodial branches with two bolls and total number of bolls per plant. Days to first bloom and number of cracked bolls 114 DAP for each plot was recorded in 2010. At harvest in both 2010 (173 DAP) and 2011 (180 DAP), four mature plants with root systems were excavated carefully from each plot. Excavated roots were washed and nematode galling was rated using the same scale as for the early season galling. A Canon EOS Rebel T2i camera (Canon, USA, Inc., Lake Success, NY) was used to take digital images for each root system and images were analyzed using the WinRHIZO software. Taproot length for each root was measured. Each root was cut at 20 cm below the soil line to evaluate the difference of root biomass above and below hardpan depth and the two portions of roots were dried separately in an oven at 60°C for 5 d and weighed. Soil population densities of nematodes were evaluated at harvest in both years in all plots. Six individual 15-cm-deep soil cores were removed from each plot with a soil sampling tube (2.5-cm diam.) and combined to make a composite sample. A subsample, 100 cm^3 of the composite sample, was processed by sieving and centrifugal flotation (Ayoub, 1980) to extract J2 nematodes.

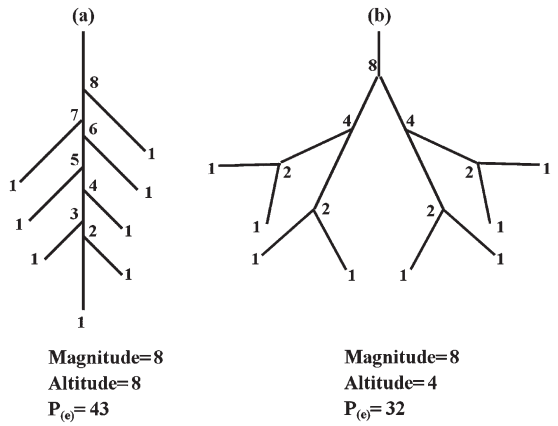

FIG. 1. Characteristics of branching patterns based on the topological classification system of Fitter (1986): a. herringbone; b. dichotomous. Numbers indicate the magnitude of each link. Magnitude is the same as the largest link magnitude. Altitude is the number of links in the longest path from any exterior link to the base link; exterior path length (P_e) is the sum of the number of links in all paths.

Statistical analyses were conducted using the GLM procedure with SAS 9.2 (SAS Institute, Inc., Cary, NC) to evaluate pathogen and hardpan treatment effects on root architecture and plant growth. Treatment means were separated according to Fisher's protected LSD at $P \leq 0.05$.

RESULTS

In the early season of 2010, the mean soil matric potentials 10 cm below soil surface were -0.2 J/kg and -5.0 J/kg for plots with or without a hardpan, respectively. The mean soil matric potentials were -4.5 J/kg and

-9.6 J/kg for plots with or without a hardpan in the early season of 2011. Both 2010 and 2011 (June-October) were below normal for rainfall. Soil temperatures at 20 cm for the first 6 wk (emergence to second true leaf stage) averaged 27.2°C in 2011 and were consistently higher than the 2010 average of 22.6°C. The warm average soil temperature combined with low rainfall during the study in 2011 tended to increase plant growth and nematode activity. Because of environmental differences between 2010 and 2011, data were analyzed by individual years.

There was no soil hardpan by *M. incognita* interaction on cotton seedling growth in either 2010 or 2011, so main effects were examined (Table 1). Seedlings were taller, and the number of stem nodes and root fresh weight were greater in the presence of a hardpan in both 2010 and 2011 (Table 2). *Meloidogyne incognita* suppressed seedling height and number of main stem nodes numerically in both years, but differences were only significant in 2010 (Table 2). Nematodes did not affect root fresh weight in either year (Table 2). The hardpan reduced total root length in 2011, but increased root system volume in both years (Table 3). Nematodes increased total root length, with the greatest density showing the shortest root length (Table 3). Nematodes did not affect root volume in either year (Table 3).

In the early season of 2010, a soil hardpan by *M. incognita* interaction was found for root magnitude, altitude, and exterior path length (Table 1). The presence of *M. incognita* increased root magnitude, altitude, and exterior path length compared with uninfested plots, and consistent increases in these parameters were greater at the levels of 4 or 8 eggs/cm^3 soil than at 12 eggs/cm^3 soil. No consistent differences were found between plants grown with and without a hardpan for lower inoculum levels of *M. incognita* in 2010. *Meloidogyne incognita* effects on root topological parameters were not significant in 2011, with the exception of root magnitude where lower levels (4 and 8 eggs/cm^3) increased root magnitude compared with the uninfested treatment (Table 3).

No hardpan by *M. incognita* interaction was seen for late season cotton plant height and reproductive development in 2010, so main effects were examined (Table 4). The nodal position of the first fruiting (sympodial) branch on the main stem was higher in plots without a hardpan, while the number of cracked bolls (a measure of earliness of crop maturity) was greater in plots with a hardpan (Table 5). Plant height, total number of bolls at harvest, and seed cotton yield were similar in plots with or without a hardpan (Table 5). *Meloidogyne incognita* reduced plant height and the number of cracked bolls, but increased the height of the first fruiting node position, indicating that *M. incognita* infestation delayed development of the crop. Total boll number was reduced by the nematode at 4 eggs/cm^3, but seed cotton yield was not significantly influenced by the presence of the nematode (Table 5).

TABLE 1. Probability values for main and interaction effects of soil hardpan (HP)[a] and *Meloidogyne incognita* (Mi) inoculum densities[b] on cotton seedling characteristics, root morphological parameters and root galling in the early season of 2010 and 2011.

Effect	Plant height[c] (cm)		Number of main stem nodes		Root fresh weight (g)		Total root length (cm)		Root volume (cm^3)		Magnitude[d]		Altitude[e]		Exterior path length[f]		Galling[g]	
	2010	2011	2010	2011	2010	2011	2010	2011	2010	2011	2010	2011	2010	2011	2010	2011	2010	2011
HP	0.0006	<.0001	0.0008	<.0001	0.0060	0.0010	0.1215	0.0084	0.0002	<.0001	0.5740	0.2600	0.8546	0.7976	0.5929	0.1370	0.1792	0.1457
Mi density	0.0028	0.1046	0.0018	0.3790	0.2801	0.4554	0.0026	0.0128	0.2680	0.9970	<.0001	0.0297	<.0001	0.3666	<.0001	0.1079	0.6436	0.1607
HP*Mi density	0.0564	0.2281	0.0879	0.1116	0.2324	0.8727	0.1269	0.1682	0.1251	0.5764	0.0159	0.1970	0.0248	0.6534	0.0088	0.3791	0.5138	0.6299

[a] A soil hardpan was present 20 cm below the soil surface; 0 = no soil hardpan, 1= soil hardpan.
[b] *Meloidogyne incognita* = 0, 4, 8, or 12 eggs/cm^3 soil; Mi = 0 not included in galling analysis because it did not have a variance equal to the other treatments.
[c] Plant height from the cotyledonary node to terminal.
[d] Magnitude is the number of exterior links per root system.
[e] Altitude is the number of links in the longest path from any exterior root link to the base link.
[f] Exterior path length is the sum of links in all paths.
[g] Root galling based on a 0 to 5 scale: 0 = no galls, 1 = 1 to 2, 2 = 3 to 10, 3 = 11 to 30, 4 = 31 to 100, and 5 = 101 to 200 galls/root. Analyses were conducted using midpoint values in which 0 = 0, 1 = 1.5, 2 = 6.5, 3 = 20.5, 4 = 65.5, and 5 = 150 galls/root.
* Interaction between the main effects.

TABLE 2. Effects of a soil hardpan (HP)[a] and *Meloidogyne incognita* (Mi) at various inoculum densities[b] on cotton seedling characteristics in 2010 (31 d after planting) and 2011 (34 d after planting).

	Plant height[c] (cm)		Number of main stem nodes		Root fresh weight (g)	
Treatment	2010	2011	2010	2011	2010	2011
HP						
0	3.65 b[d]	4.65 b	2.95 b	2.66 b	0.27 b	0.56 b
1	4.78 a	8.28 a	3.49 a	4.18 a	0.42 a	0.94 a
Mi density						
0	5.46 a	7.36 a	3.80 a	3.64 a	0.43 a	0.71 a
4	3.88 b	5.77 a	2.84 b	3.23 a	0.34 a	0.68 a
8	3.78 b	6.26 a	3.16 b	3.35 a	0.35 a	0.70 a
12	3.74 b	6.46 a	3.09 b	3.44 a	0.27 a	0.90 a

[a] A soil hardpan was present 20 cm below the soil surface; 0 = no soil hardpan, 1 = soil hardpan.
[b] *Meloidogyne incognita* = 0, 4, 8, or 12 eggs/cm^3 soil.
[c] Plant height from the cotyledonary node to terminal.
[d] Means in a column followed by the same letter are not significantly different according to Fisher's protected least significant difference (LSD) at $P \leq 0.05$.

There was no hardpan by *M. incognita* interaction on root growth late in the season for 2010 or 2011, so main effects were examined (Table 4). Taproot length was suppressed both years by both a hardpan and *M. incognita* for all treatments except the highest inoculum rate in 2010 compared with the uninfested treatment (Table 6). Dry weight of roots that developed above the hardpan was not affected by the hardpan, while root dry weight below the hardpan was reduced by the hardpan in both years (Table 6). Root dry weight in the upper 20 cm (above the hardpan) was reduced at *M. incognita* infestation levels of 4 and 8 eggs/cm^3 in 2010 compared with the uninfested treatment but was not affected by *M. incognita* infestation level in 2011 (Table 6). The lowest density of the nematode (4 eggs/cm^3) suppressed root dry weight below the hardpan consistently in both 2010 and 2011 (Table 6). The presence of a hardpan increased root system magnitude compared with plants grown without a hardpan late in the season in 2010 ($P = 0.0339$) and 2011 ($P = 0.0105$) but did not affect altitude or exterior path length. Root system magnitude in 2010 for treatments having *M. incognita* was increased compared with the uninfested control, ranged 167 to 203 compared with 129, respectively ($P = 0.0092$). A similar trend for magnitude was observed in 2011 for *M. incognita* ($P = 0.0735$) (data not shown). *Meloidogyne incognita* had no effect on root altitude and exterior path length in either year.

Root system topological indices (TI) for all the treatments ranged from 1.71 to 1.83 in both years indicating that the root system conformed to a herringbone root branching pattern. The presence of *M. incognita* tended to lower TI, although effects were variable. In the early season of 2010, root TI was reduced by both 4 and 8 *M. incognita* eggs per cm^3 (1.72 and 1.75, respectively; $P = 0.0137$), comparing with uninfested treatment (1.77), but there was no hardpan effect. In the early season in 2011, root TI were 1.74 and 1.71, for an inoculum density of 4 *M. incognita* eggs/cm^3 with and without a hardpan, respectively, while root TI were 1.78 and 1.79 for the uninfested treatment with and without a hardpan. In the late season of 2010, a hardpan by *M. incognita* interaction was seen ($P = 0.0358$) where a lower TI occurred for all nematode infestation rates with a hardpan compared with plots without a hardpan (data not shown). Over all infestation treatments, the late season TI was reduced from 1.74 to 1.70 in plots having a hardpan ($P = 0.0190$).

Data from noninoculated plots were not included in the analyses for galling and late season J2 because the variance of these plots was not equal to that of the other nematode inoculum levels. There was no soil hardpan by *M. incognita* inoculum density interaction for galling or nematode population density at harvest in 2010 or 2011, so main effects were presented (Tables 1 and 4). Root gall ratings were higher with a hardpan only in the late season of 2011 (Table 7). There were no differences

TABLE 3. Effects of soil hardpan (HP)[a] and *Meloidogyne incognita* (Mi) inoculum densities[b] on cotton seedling root morphological parameters in 2010 (31 d after planting) and 2011 (34 d after planting).

	Total length (cm)		Volume (cm^3)		Magnitude[c]			Altitude[d]			Exterior path length[e]		
Treatment	2010	2011	2010	2011	2010		2011	2010		2011	2010		2011
HP													
0	57.03 a[f]	70.06 a	0.16 b	0.33 b			31.6 a			18.3 a			414.6 a
1	64.81 a	57.66 b	0.22 a	0.63 a			28.7 a			18.0 a			352.5 a
					HP			HP			HP		
Mi density					0	1		0	1		0	1	
0	45.42 c	53.67 b	0.21 a	0.49 a	22.6 e	18.8 e	24.7 b	15.0 d	13.3 d	17.6 a	246.6 f	183.1 f	309.0 a
4	72.37 a	74.95 a	0.20 a	0.48 a	31.7 cd	48.7 a	34.8 a	18.7 c	24.5 a	19.2 a	411.6 de	767.5 a	453.9 a
8	70.95 a	65.52 ab	0.21 a	0.47 a	41.4 b	35.8 c	31.7 a	24.0 ab	22.2 b	18.5 a	662.6 b	528.4 c	404.4 a
12	51.32 b	60.28 b	0.17 a	0.48 a	28.2 d	27.1 d	29.0 ab	20.5 bc	19.0 c	17.1 a	399.3 e	365.1 e	364.4 a

[a] A soil hardpan was present 20 cm below the soil surface; 0 = no soil hardpan, 1 = soil hardpan.
[b] *Meloidogyne incognita* = 0, 4, 8, or 12 eggs/cm^3 soil.
[c] Magnitude is the number of exterior links.
[d] Altitude is the number of links in the longest path from any exterior link to the base link.
[e] Exterior path length is the sum of the number of links in all paths.
[f] Means in a column followed by the same letter are not significantly different according to Fisher's protected least significant difference (LSD) at $P \leq 0.05$.

TABLE 4. Probability values for main and interaction effects of a soil hardpan (HP)[a] and different *Meloidogyne incognita* (Mi) inoculum densities[b] on late season cotton growth and development in 2010 and root growth and disease severity in both 2010 and 2011.

Effect	Plant height[c] (cm)	Cracked bolls[d]	First sympodial node[e]	Total bolls	Yield[f] (g)	Taproot length (cm)		Root dry weight above hardpan (g)		Root dry weight below hardpan (g)		Galling[g]		J2[h]	
						2010	2011	2010	2011	2010	2011	2010	2011	2010	2011
HP	0.0983	< .0001	< .0001	0.6344	0.5913	< .0001	< .0001	0.1950	0.1864	< .0001	< .0001	0.3230	0.0275	< .0001	0.6188
Mi density	0.0051	< .0001	< .0001	0.0434	0.1072	0.0081	0.0155	0.0045	0.2855	0.0026	0.0449	0.3765	0.4597	0.0126	0.9431
HP*Mi density	0.2010	0.6050	0.0506	0.1172	0.5205	0.0996	0.5168	0.3794	0.4976	0.2723	0.3513	0.3765	0.6498	0.4677	0.6175

[a] A soil hardpan was present 20 cm below the soil surface; 0 = no soil hardpan, 1 = soil hardpan.
[b] *Meloidogyne incognita* = 0, 4, 8, or 12 eggs/cm^3 soil; Mi = 0 not included in galling or J2 analyses because it did not have a variance equal to the other treatments.
[c] Plant height from the cotyledonary node to the tip of the main stem terminal.
[d] The total number of cracked bolls at 114 d after planting.
[e] Nodes to the first sympodial branch excluding cotyledonary node.
[f] Seed cotton yield.
[g] Root galling based on a 0 to 5 scale: 0 = no galls, 1 = 1 to 2, 2 = 3 to 10, 3 = 11 to 30, 4 = 31 to 100, and 5 = 101 to 200 galls/root. Analyses were conducted using midpoint values in which 0 = 0, 1 = 1.5, 2 = 6.5, 3 = 20.5, 4 = 65.5, and 5 = 150 galls/root.
[h] Second-stage juveniles (J2) per 100-cm^3 soil were analyzed as $\log_{10}(x+1)$.

TABLE 5. Effect of a soil hardpan (HP)[a] and *Meloidogyne incognita* (Mi) inoculum densities[b] on late season cotton growth and development in 2010 (173 d after planting).

Treatment	Plant height[c] (cm)	Cracked bolls[d]	First sympodial node[e]	Total bolls	Yield[f] (g)
HP					
0	28.60 a[g]	3.5 b	9.3 a	22.1 a	102.79 a
1	30.40 a	7.9 a	7.8 b	23.3 a	109.97 a
Mi density					
0	33.33 a	9.7 a	6.7 c	27.0 a	133.63 a
4	27.92 b	5.0 b	8.5 b	18.4 b	82.83 a
8	27.56 b	4.9 b	9.4 a	20.2 ab	101.98 a
12	29.19 b	3.4 b	9.5 a	25.4 a	107.07 a

[a] A soil hardpan was present 20 cm below the soil surface; 0 = no soil hardpan, 1 = soil hardpan.
[b] *Meloidogyne incognita* = 0, 4, 8, or 12 eggs/cm^3 soil.
[c] Plant height from the cotyledonary node to the tip of the main stem terminal.
[d] The total number of cracked bolls at 114 d after planting.
[e] Nodes to the first sympodial branch excluding cotyledonary node.
[f] Seed cotton yield.
[g] Means in a column followed by the same letter are not significantly different according to Fisher's protected least significant difference (LSD) at $P \leq 0.05$.

in root galling on seedlings or at harvest among *M. incognita* inoculum densities either year. The highest inoculum level, 12 eggs/cm^3, had lower J2 populations late in the season for 2010 than the lowest inoculum level (Table 7). The density of *M. incognita* J2 was lower with a hardpan late in the season of 2010 (Table 7).

DISCUSSION

In the early season for both years, the soil water matric potential at 10 cm below the soil surface (above the hardpan) in hardpan plots tended to be greater than in the plots without a hardpan, indicating that the compaction layer trapped and held water in the upper soil profile to a greater degree than where gravitational water could move vertically in the absence of a hardpan.

TABLE 6. Effects of soil hardpan (HP)[a] and *Meloidogyne incognita* (Mi) inoculum densities[b] rate on late-season cotton root growth in 2010 (173 d after planting) and 2011 (180 d after planting).

Treatment	Taproot length (cm)		Root dry weight above hardpan (g)		Root dry weight below hardpan (g)	
	2010	2011	2010	2011	2010	2011
HP						
0	18.86 a[c]	43.20 a	19.96 a	23.41 a	3.93 a	3.76 a
1	10.68 b	18.50 b	21.75 a	37.79 a	1.78 b	1.39 b
Mi density						
0	18.62 a	40.43 a	24.67 a	25.66 a	4.74 a	3.47 a
4	12.77 b	27.12 b	17.23 c	22.99 a	1.96 b	2.05 b
8	12.44 b	27.79 b	19.67 bc	24.87 a	2.02 b	2.40 ab
12	15.25 a	28.07 b	21.86 ab	48.88 a	2.71 ab	2.34 b

[a] A soil hardpan (HP) was present 20 cm below the soil surface. 0 = no soil hardpan, 1 = soil hardpan.
[b] *Meloidogyne incognita* = 0, 4, 8, or 12 eggs/cm^3 soil.
[c] Means in a column followed by the same letter are not significantly different according to Fisher's protected least significant difference (LSD) at $P \leq 0.05$.

TABLE 7. Effect of soil hardpan (HP)[a] and *Meloidogyne incognita* (Mi) inoculum densities[b] on root galling severity and nematode populations in 2010 and 2011.

	Galling[c]				J2[d]	
	Early season		Late season		Late season	
Treatment	2010	2011	2010	2011	2010	2011
HP						
0	47.8 a[e]	71.3 a	146.5 a	100.0 b	2,089 a	190 a
1	62.4 a	86.3 a	150.1 a	127.9 a	653 b	277 a
Mi density						
4	50.2 a	66.7 a	150.0 a	103.6 a	1,910 a	260 a
8	62.0 a	90.9 a	144.7 a	117.1 a	1,074 ab	242 a
12	53.0 a	78.7 a	150.0 a	121.5 a	776 b	192 a

[a] A soil hardpan (HP) was present 20 cm below the soil surface. 0 = no soil hardpan, 1 = soil hardpan.

[b] *Meloidogyne incognita* = 4, 8, or 12 eggs/cm^3 soil; Mi = 0 not included in analyses because it did not have a variance equal to the other treatments.

[c] Root galling based on a 0 to 5 scale: 0 = no galls, 1 = 1 to 2, 2 = 3 to 10, 3 = 11 to 30, 4 = 31 to 100, and 5 = 101 to 200 galls/root. Analyses were conducted using midpoint values in which 0 = 0, 1 = 1.5, 2 = 6.5, 3 = 20.5, 4 = 65.5, and 5 = 150 galls/root.

[d] Second-stage juveniles (J2) per 100-cm^3 soil were analyzed as $\log_{10}(x + 1)$; back transformed means are presented.

[e] Means in a column followed by the same letter are not significantly different according to Fisher's protected least significant difference (LSD) at $P \leq 0.05$.

Greater soil water availability could explain the increased seedling height, number of nodes, and root fresh weight early in the season of both 2010 and 2011 where a hardpan existed. Ma (2012) found that higher soil bulk density (1.50 g/cm^3) resulted in increased seedling height and greater root surface area, root volume, root magnitude, and exterior path length in comparison with lower soil bulk density (1.25 g/cm^3) in a controlled environment study. The interaction between soil bulk density, water availability, and physical resistance is complex (Taylor and Gardner, 1963; Coelho et al., 2000). Higher soil bulk density and the presence of a hardpan can result in increased plant growth and root development when soil water is sufficient and the physical impedance is relatively low. The average taproot length for the uninfested plots was considerably less than 20 cm early in the season in both 2010 and 2011, indicating that the roots had not reached the hardpan that was 20 cm below the soil surface. Although seedling growth was greater in 2011 than 2010, a significant hardpan effect was still found; the greater seedling growth in 2011was likely because of warmer soil temperatures than 2010. Early in the season of 2011, soil penetration resistance (SPR) was 650 kPa at 10 cm below soil surface, a resistance level that was near the 720 kPa that decreased cotton root growth by 50% (Dexter, 1987). This SPR level above the hardpan likely occurred because of the extremely dry weather during June 2011, and may explain the lower total root length and the numerically smaller root topological parameters for the hardpan treatment early in the season in 2011.

Compacted soil tends to increase soil strength and decrease air permeability and hydraulic conductivity (Allmaras et al., 1988; Whalley et al., 1995). The success of a cotton root in penetrating a compacted soil layer depends on its maximum axial root growth pressure (ranging from 0.6 to 1.6 MPa) (Taylor and Ratliff, 1969). Compacted soil strongly impedes the development of taproots (McKenzie and McBratney, 2001). In their study, roots that encountered a compaction layer were severely tapered and deflected approximately 90° at the top of the compacted layer. These "J" shaped roots were also observed in our study. In the late season of 2011, the SPR at 20 cm deep in the plots without a hardpan was 1,158.0 kPa while the SPR at the beginning of the hardpan layer in the hardpan treatments was 2,075.6 kPa, considerably higher than the 2,000 kPa that has been reported to completely inhibit taproot growth (Taylor et al., 1966). The increased SPR in the late season resulting from the hardpan likely impeded plant taproot penetration. A highly significant linear correlation (r = -0.96) between soil strength and root penetration has been demonstrated (Taylor and Gardner, 1963; Medvedev, 2009).

Increased soil resistance because of soil compaction reduces both the percentage of roots penetrating the soil and the rate of root growth through the soil. Distinct differences in root distribution in heavily compacted versus an uncompacted layer has been shown (Lowry et al., 1970; Horn et al., 1995; Pierret et al., 2007). Similar results were found in this study. In the late season of 2011, although the root biomass above the soil hardpan layer was similar to that in the plots without a hardpan, only 3.5% of the whole root biomass penetrated below the compacted layer in hardpan plots compared with 13.8% of the whole root biomass that was found at the same depth in the plots without hardpan. Given the SPR that existed, it is likely that root penetration in plots with a soil hardpan was the result of a few lateral roots penetrating the soil along the sides of the microplots at the interface between the soil and the concrete wall. Mechanical impedance because of soil compaction, while slowing the rate of root extension, may increase root diameter immediately behind the root tip (Atwell, 1988; Materechera et al., 1991). In this situation, the diameter of individual cortical cells rather than the cell number increases resulting in increased cell volume in impeded roots (Materechera et al., 1991). Soil compaction induced the radial thickening of *Lupinus angustifolius* by 15% (Atwell, 1988). In the late season of 2011, root radius in our study was greater by 18.2% in plots with a hardpan (Ma, 2012). The impedance caused by soil compaction may also alter the pattern of lateral root initiation and sometimes induce the formation of lateral roots (Crossett et al., 1975; Russell, 1977; Goss and Russell, 1980). In our study, proliferation of lateral roots occurred primarily above the soil hardpan in the late season of both years. Because of the increased lateral root formation, the topological parameters, root magnitude, root volume, and root surface area were increased (Ma, 2012).

Off-target drift of 2,4-dichlorophenoxyacetic acid or a similar herbicide from a neighboring farm late in the season of 2011 precluded above-ground cotton development data and yield from being collected. However, based on 2010 data, the soil hardpan appeared to improve rather than delay cotton development, as indicated by the higher number of total cracked bolls at 114 DAP, the lowered first sympodial node position, and numerically increased average seed cotton yield in plots with a hardpan. This may have been an artifact of using microplots for the study. Davidson (1969) suggests that small root systems may still support optimal plant growth when the water and nutrient resources are sufficient. Similarly, Rosolem et al. (1998) found an increased shoot-to-root-dry-weight ratio coupled with increased soil bulk density from 1.13 to 1.82 g/cm^3 indicating that a relatively small root system was able to support the same plant canopy in compacted soils. Iijima et al. (1991) also reported that shoot growth was promoted in "strong soils." In our study, root distribution during the late season of 2010 was mainly above the hardpan, where soil water and nutrients may have been near optimal as a result of water management practices in this study.

Meloidogyne incognita infects the root behind the root cap and at the base of lateral roots or root tips, which causes suppressed root growth. Feeding by the nematode can suppress cotton root growth and shorten root length (Kirkpatrick et al., 1991). In this study, the nematode reduced taproot growth. Detrimental effects on cotton plant growth and root development after nematode infection were also reported by Ma (2012) in a controlled environment in which plant stand, plant height and the root fresh weight, surface area, length, links, magnitude, altitude, and exterior path length were significantly reduced by the nematode. However, in this study, total root length early in the season of both years and root magnitude, altitude, and exterior path length early in 2010 were greater in the presence of *M. incognita* indicating that nematode infection increased these parameters, particularly under lower inoculum densities (4 and 8 eggs/cm^3).

Compensatory root growth in response to invasion by the potato cyst nematode (*Globodera pallida*) has been documented by Smit and Vamerali (1998) using mini-rhizotron root video observation. In their study, compensatory root growth caused by the nematode was restricted to the top 30 cm of soil and nematodes reduced rooting depth. Similarly, De Ruijter and Haverkort (1999) found that nematodes prolonged root formation, and that nematode-infected crops possessed more roots in the top 30 cm of soil than healthy crops. Haase et al. (2007) reported lateral roots of plants infested by a low level of *M. incognita* were elongated, a possible response to wounding and stress on the host plant after nematode invasion. The physiological reaction associated with nematode attack may involve increased production of phytohormones and ethylene in infected root tissue (Glazer et al., 1983; Barker, 1999; Bird and Koltai, 2000). These hormones play a critical role in the formation and elongation of root hairs (Pitts et al., 1998; Ridge and Katsumi, 2002). The mechanism that causes compensatory branching is still unknown. It is not clear why compensatory root growth after nematode infection was observed in the microplot study but not in the previous controlled environment study by Ma (2012). The different soil textures and growth environments may have contributed to these different observations.

Shorter taproot lengths were found for nematode infested soils in both years. Thus it is possible that the taproot length is an important root parameter to ensure sufficient healthy lateral root branching and facilitate the entire root system to absorb enough water and nutrients.

The effects of the nematode on cotton growth in 2010 were similar to reports by Kirkpatrick et al. (1995) and Walker et al. (1998) who also noted a lower number of cracked bolls, total sympodial branches and bolls, and the higher position of the first sympodial branch as well as delayed harvest and reduced yield in nematode-infested plots.

The root TI for this microplot study ranged from 1.71 to 1.83, indicating a herringbone pattern in which branching is primarily on the main root axis (Werner and Smart, 1973; Fitter, 1986). This type of branching pattern is consistent with taproot-producing crops such as cotton (Werner and Smart, 1973). Late in the season, the presence of a hardpan decreased TI. A decrease in root TI in response to nematode infestation was found in the plots with or without hardpan. The lower TI values in the microplot experiment suggest that compensatory branching took place in the microplots in response to *M. incognita* as discussed previously. Changes in the TI in response to other root pathogens have also been reported (Larkin et al., 1995, 1996). Soil infested with *Pythium irregulare* (TI = 1.86) or *P. ultimum* (TI = 1.72) resulted in altered root system architecture in alfalfa compared with the TI of alfalfa roots in uninfested soil (TI = 1.36) (Larkin et al., 1995).

An interaction between a hardpan and root-knot nematode infection was only found for a few root morphological parameters. The season-long effect of a hardpan resulted in most of the root system developing above the hardpan and reduced taproot length. However, the presence of a hardpan in general tended to improve cotton growth and increase seed cotton yields, which was likely because of water and nutrient availability being near optimum in all microplots. This response would not be expected in a field situation because irrigation management would likely not be as intensive. Nematode infection reduced seedling growth and delayed cotton development late in the season. Taproot length was also reduced late in the season. The taproot is crucial for plants with "taproot" systems to penetrate

and explore the soil and maintain functional roots thus supporting plant growth. Root architecture studies allow quantification of root parameters and characterization of root branching structure and may suggest changes in root function across soil environments. Studying root architecture over a range of soil conditions provides a fresh way to investigate soilborne pathogen-host interactions.

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