



Response of Root-Knot Nematodes and Palmer Amaranth to Tillage and Rye Green Manure

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ABSTRACT

Rye (*Secale cereale* L.) is a frequently used winter cover crop in many agronomic production systems in the United States. Our objective was to determine whether incorporating rye into soil while still green results in greater suppression of root-knot nematodes (*Meloidogyne* spp.) and Palmer amaranth (*Amaranthus palmeri* S. Wats.) compared to conventional cover crop management. Two similar experiments were conducted: one with peanut (*Arachis hypogaea* L.) and the other with cotton (*Gossypium hirsutum* L.). Both experiments were a split-plot design with tillage as the main plot (conventional, green manure, and strip) and cover crop as the subplot. The cover crop treatments were a weedy fallow and the rye cultivars Wrens Abruzzi, Wheeler, Oklon, and Elbon. Wrens Abruzzi produced the greatest amount of biomass, Oklon and Elbon intermediate, and Wheeler the least. Where there was substantial soil disturbance (e.g., conventional tillage and green manure), Palmer amaranth densities were low and not influenced by cover crop. In the strip tillage plots, however, all of the rye cultivars, except Wheeler, reduced establishment of the weed compared to winter fallow. Root galling from nematodes on cotton and peanut was influenced by tillage, but not by rye cover crop. Gall indices on cotton were greater in conventional tillage than in either strip tillage or green manure plots; whereas on peanut, they were greater in the strip tillage than in the conventional tillage or green manure plots. Neither tillage nor cover crop influenced yield except in 2008 in peanut, where yield was lower in strip tillage than in conventional or green manure plots.

WINTER COVER CROPS can reduce soil erosion and loss of nutrients from leaching and runoff, and increase soil organic matter and water infiltration (Reeves, 1994; Teasdale, 1996; Lu et al., 2000; Dabney et al., 2001; Sarrantonio and Galand, 2003). Rye is a frequently used winter cover crop in many agronomic production systems in the eastern and southeastern United States because it establishes reliably, grows rapidly, and produces large amounts of biomass (Reeves, 1994). Rye is typically killed with a nonselective herbicide several weeks before planting the next crop in the spring. In conventional tillage, the residue is chopped with a flail mower and incorporated, whereas in conservation tillage, the rye is either chopped or rolled flat and residue left as a mulch on the soil surface.

Rye may also benefit the succeeding crop by suppressing pests. Suppression of weeds can involve resource competition by the living cover crop, and the residue formed by the killed rye can act as a physical barrier restricting light and seedling emergence (Teasdale and Mohler, 2000; Hoffman and Regnier, 2006). Many cereals, including rye, produce secondary metabolites

called benzoxazinoid hydroxamic acids (syn. benzoxazinones), which are toxic to a broad spectrum of organisms including weeds, insects, and plant pathogens, including nematodes (Yenish et al., 1995; Friebe, 2001; Zasada et al., 2005; Niemeyer, 2009). These compounds are present in the plant as glucosides and are hydrolyzed to the more toxic aglucones following tissue injury (Niemeyer, 2009). The primary benzoxazinoids in rye are DIBOA (2,4-dihydroxy-1,4-benzoxazin-3-one) in aerial tissue and a mixture of BOA (benzoxazolin-2-one), DIBOA, DIMBOA (2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one) and its breakdown product MBOA (6-methoxy-benzoxazolin-2-one) in root tissue (Rice et al., 2005; Copaja et al., 2006); however, only DIBOA was found in the root exudates (Pérez and Ormeno-Nunez, 1991). Several benzoxazinoid compounds in addition to DIBOA have now emerged as possible contributors to the bioactivity from rye, especially when the rye materials decompose in the soil (Fomsgaard et al., 2004; Macías et al., 2005, 2006). Allelopathic suppression of weeds by rye is believed to occur both during the vegetative stage, from benzoxazinoids in the root exudates, and after crop destruction, from leaching of benzoxazinoids in the residue (Pérez and Ormeno-Nunez, 1991; Yenish et al., 1995; Rice et al., 2005).

Palmer amaranth has recently become the most troublesome weed of cotton production in the southern United States due to the development and increase in frequency of plants resistant to glyphosate [N-(phosphonomethyl) glycine] and

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Abbreviations: BOA, benzoxazolin-2-one; DIBOA, 2,4-dihydroxy-1,4-benzoxazin-3-one; DIBOA-glucoside, (2R)-2-β-D-glucopyranosyloxy-4-hydroxy-2H-1,4-benzoxazin-3(4H)-one; DIMBOA, 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one; DIMBOA-glucoside, (2R)-2-β-D-glucopyranosyloxy-4-hydroxy-7-methoxy-(2H)-1,4-benzoxazin-3(4H)-one; HBOA, 2-hydroxy-1,4-benzoxazin-3-one; HBOA-glucoside, (2R)-2-β-D-glucopyranosyloxy-1,4-benzoxazin-3(4H)-one; HMBOA, 2-hydroxy-(2H)-7-methoxy-1,4-benzoxazin-3(4H)-one; J2, second-stage juvenile; MBOA, 6-methoxy-benzoxazolin-2-one.

other commonly used herbicides (Culpepper et al., 2006, 2008; Nichols et al., 2009; Webster 2009). In the absence of glyphosate, control of Palmer amaranth in reduced tillage systems is predicated on the activation of preemergence herbicides by soil moisture. With approximately 50% of the cotton and peanut area in Georgia without supplemental irrigation, many growers are unable to consistently manage Palmer amaranth. Weed control from cover crop residues are one means by which growers could potentially suppress Palmer amaranth emergence and establishment. Previous research has demonstrated that the effectiveness of mulch residues as a component of a weed management system is dictated by the seed size of the weed (Putnam and Defrank, 1983; Burgos and Talbert, 2000; Teasdale and Mohler, 2000). As Palmer amaranth has a relatively small seed (1–1.3 mm) compared with other common weeds in the southern United States, such as sicklepod (*Senna obtusifolia* L.) (4–5 mm), ivyleaf morningglory [*Ipomoea hederacea* (L.) Jacq.] (4–5 mm), and common cocklebur (*Xanthium strumarium* L.) (10–15 mm) (Bryson and DeFelice 2009), rye residues could suppress emergence of this troublesome weed.

The southern root-knot nematode [*Meloidogyne incognita* (Kofoid and White) Chitwood] and the peanut root-knot nematode [*M. arenaria* (Neal) Chitwood] are major pests of cotton and peanut, respectively. Wrens Abruzzi, the predominant rye cultivar planted in the southern United States, is a relatively poor host for these two nematode species (Ibrahim et al., 1993; Timper et al., 2006; Zasada et al., 2007). Several studies have demonstrated that populations of *M. incognita* and *M. arenaria* do not appreciably increase or decrease following a winter cover crop of rye (Johnson and Motsinger, 1990; McSorley, 1994; McSorley and Gallaher, 1994a; Minton and Bondari, 1994; Timper et al., 2006). The lack of detectable population increase is likely due to a combination of low soil temperatures and a low reproductive potential. Additionally, it appears that the traditional method of managing rye (i.e., killing before incorporation or mulching) does not suppress populations of root-knot nematodes compared to winter fallow; however, in a greenhouse study, incorporation of freshly cut rye into soil reduced galling of cotton roots by *M. incognita* (McBride et al., 1999). Greater concentrations of benzoxazinoids may be released by incorporating rye into soil at an earlier stage of growth because the concentration of DIBOA and BOA in aerial tissue declines as rye matures (Rice et al., 2005). Moreover, incorporating organic matter, rather than leaving it on the soil surface, results in more rapid decomposition, which may lead to faster release of benzoxazinoids (Kruidhof et al., 2009).

Our primary objective was to determine whether incorporating rye into soil while still green (i.e., green manuring) results in greater suppression of root-knot nematodes and Palmer amaranth compared to killing rye 2 wk before incorporation or mulching. A secondary objective was to compare different rye cultivars for their effect on population densities of the two pests. The cultivars tested (Elbon, Oklon, Wheeler, and Wrens Abruzzi) contained similar concentrations of total benzoxazinoids when grown under greenhouse conditions, but differed in their host status for root-knot nematodes (Zasada et al., 2007). Reproduction of *M. incognita* was greater on Wheeler than on Wrens Abruzzi and Oklon.

MATERIALS AND METHODS

Experimental Design

Two similar experiments were conducted concurrently, one with cotton and the other with peanut, at the University of Georgia Gibbs Farm in Tifton, GA. The field sites contained a Tifton loamy sand (fine-loamy, kaolinitic, thermic Plinthic Kandudults; 85% sand, 11% silt, 4% clay, <1% organic matter) and were infested with *M. incognita* race 3 and *M. arenaria* race 1 in the cotton and peanut sites, respectively. Cotton and peanut were grown under conventional tillage the previous year in the cotton and peanut sites, respectively. In both experiments, a split-plot design with six replications was used to determine the effect of tillage (main plots) and cover crop (subplots) on densities of *Meloidogyne* spp. and yield of cotton and peanut. In the cotton experiment, the density of artificially-infested Palmer amaranth was also assessed. The three tillage treatments were conventional tillage, green manure, and strip tillage. The five cover crop treatments were a weedy fallow and the following rye cultivars: Elbon, Oklon, Wheeler, and Wrens Abruzzi. The subplots were two rows wide and measured 1.8 by 7.6 m for cotton and 1.8 by 9.1 m for peanut. Both experiments were conducted twice with the harvest of cotton and peanut in 2007 and 2008.

Rye Management and Tillage

Rye was planted in mid-November of 2006 and 2007 with a no-till grain drill at 84 kg ha⁻¹. The drill setting was 8 cm for all of the rye cultivars except Wheeler which was set to 7 cm. In the first week of April when the rye was nearing the end of grain maturation, four plants of each rye cultivar were removed from the plots for analysis of benzoxazinoid content. On 5 Apr. 2007 and 10 Apr. 2008, the rye in the green manure plots was cut to 10 cm with a Carter harvester flail mower. The biomass of the mowed material in each subplot was weighed and a 10% subsample was retained for dry weight determination. The remaining residue was scattered evenly over the plot and incorporated to a depth of 15 to 25 cm with two passes of a rototiller. Glyphosate (0.87 kg a.e. ha⁻¹) was applied on 6 Apr. 2007 and 16 Apr. 2008 to kill weeds and rye in the conventional and strip tillage plots. The rye was mowed before tillage. In early May, the conventional tillage and green manure plots were first disc-harrowed, then for peanut, turned to a depth of 20 to 25 cm with a moldboard plow, and shaped into beds 10 to 15 cm high and for cotton, rip-bedded. Strip-tillage in both experiments consisted of a single subsoil chisel per row with shallow disking (10 cm) and rollers that left a smooth seed-bed 20-cm wide; the remaining space between the rows was undisturbed.

Planting and Harvest of Cotton and Peanut

The cotton cultivar DP 555 BGRR was planted at a rate of 10 seed m⁻¹ on 11 May 2007 and 20 May 2008. Based on soil tests, the cotton was fertilized with 112 kg ha⁻¹ of 0–20–20 (N–P–K) on 9 May 2007 and with 224 kg ha⁻¹ 18–46–0 on 2 May 2008. Additionally, N (101 kg ha⁻¹) was applied on 25 June 2007 and 8 July 2008, and B (2.3 L ha⁻¹) was applied on 20 and 27 June 2007 and 10 and 21 July 2008. Cotton was harvested on 18 Oct. 2007 and 18 Nov. 2008 and seed weight determined for each subplot. Lint yield was estimated as 38% of the seed cotton weight. The peanut cultivar Georgia-02C was planted at a rate of 20 seed m⁻¹ on 15 May 2007 and 22 May 2008. In 2008,

aldicarb (1.7 kg a.i. ha⁻¹) was applied in the planting furrow of all plots to reduce the extremely high populations of *M. arenaria*. Gypsum (560 kg ha⁻¹) was applied on 26 June 2007 and 14 July 2008. The peanuts were dug and inverted based on an optimum maturity index on 27 Sept. 2007 and 30 Sept. 2008. The pods were harvested with a combine when their moisture content was approximately 14%, and then dried to 8% before yield weight was determined. Applications of insecticides and herbicides for both cotton and peanut followed University of Georgia Extension Service recommendations and were the same for all plots (Guillebeau, 2006; Brown et al., 2007). Irrigation was applied as needed through overhead sprinklers.

Nematode, Disease, and Weed Data Collection

Soil samples for nematode counts were collected from the peanut experiment early season (29 May), mid-season (31 July), and before harvest (27 September) in both 2007 and 2008. The samples were collected from the cotton experiment early season (29 May), mid-season (17 or 22 July), late season (7 or 3 September), and near harvest (29 October or 24 November) in 2007 and 2008, respectively. Soil samples consisted of a composite of 8 to 10 cores per plot (2.5-cm diam. and 20-cm deep) collected from the root zone. Nematodes were extracted from 150 cm³ soil by centrifugal flotation (Jenkins, 1964). Root-galling was evaluated on 11 Nov. 2007 and 25 Nov. 2008 for cotton and on the date of inversion for peanut. Ten root systems from each plot were rated for galling based on the percentage of the root system with galls (0–10 scale) where 0 = no galling, 1 = 1 to 10% of the root system galled, 2 = 11 to 20%, etc., with 10 = 91 to 100%. Peanut was assessed for incidence of stem rot (*Sclerotium rolfsii*) and severity of Rhizoctonia limb rot (*Rhizoctonia solani*) immediately after the plants were inverted. Stem rot incidence was based on the number of disease loci per 15.2 m row, where a locus represents one or more plants in 30 cm of row with signs or symptoms of *S. rolfsii*. Rhizoctonia limb rot severity on peanut stems and leaves was visually estimated for the entire plot (0–100%). In the cotton experiment, Palmer amaranth seed were distributed on each plot (40,000 seed spread in an area 6.7 m²) in the early spring (before any tillage treatment). Following cotton planting and emergence, Palmer amaranth densities were quantified using eight 0.25 m² quadrats in each plot.

Plant Chemistry

The aboveground portion of the rye was collected fresh and stored frozen until preparation for extraction by grinding approximately 5 to 10 g of fresh tissue in liquid N using a mortar and pestle. The powder was transferred to a labeled plastic bag and stored frozen for later pressurized solvent extraction with a Dionex ASE 300 model Accelerated Solvent Extractor (ASE). Each extraction cylinder was loaded with two filter membranes, 5 g sand that had been baked at 400°C for 5 h, and 0.5 g of ground plant material. The rest of the cylinder was then filled with sand. The solvent used in the extraction was a MeOH:H₂O:acetic acid mixture (80:19:1). The ASE was set to the following sequence: preheat for 5 min to 80°C, then hold for 5 min, fill with solvent and leave static for 3 min; flush 80% of the cell volume, then purge for 60 s four times at 1500 psi at 80°C (Krogh et al., 2006). The extracts were dried in an evaporator (TurboVap LV Evaporation System) at 40°C and 5 psi for 4 h until the volume was approximately 10 mL. The extracts

were brought to a total volume of 10 mL with methanol (or 50:50 MeOH/H₂O), centrifuged at 3580 rpm for 5 min, and stored at 10°C until analysis by liquid chromatography–mass spectrometry.

The analytical method followed procedures described by Rice et al. (2005). Authentic standards were used to quantify the benzoxazinoids detected in the rye samples. The following compounds were included: BOA, DIBOA, DIBOA–glucoside [(2*R*)-2-β-D-glucopyranosyloxy-4-hydroxy-2*H*-1,4-benzoxazin-3(4*H*)-one], DIMBOA, DIMBOA–glucoside [(2*R*)-2-β-D-glucopyranosyloxy-4-hydroxy-7-methoxy-(2*H*)-1,4-benzoxazin-3(4*H*)-one], HBOA (2-hydroxy-1,4-benzoxazin-3-one; HBOA–glucoside), HBOA–glucoside [(2*R*)-2-β-D-glucopyranosyloxy-1,4-benzoxazin-3-(4*H*)-one], HMBOA (2-hydroxy-(2*H*)-7-methoxy,1,4-benzoxazin-3(4*H*)-one), and MBOA (6-methoxy-benzoxazolin-2-one). For each set of samples, blanks, spikes, and duplicate analyses were included. The average recoveries for the following analytes spiked into actual sample extracts were as follows: BOA–125%; DIBOA–85%; DIBOA–glucoside–100%; HBOA–103%; MBOA–105%. The relative percent differences for duplicate analyses averaged as follows: 14-BOA; 15-DIBOA; 17-DIBOA–glucoside; 40-DIMBOA; 15-HBOA; 14-HBOA–glucoside; and 22-MBOA. Blank values were low for all analytes, except BOA where the average was 60 μg kg⁻¹ dry weight; however, even these were not high enough to affect the total concentration detected in the samples and corrections were not made.

Statistical Analysis

Analysis of variance was used to determine the effect of year, tillage, cover crop, and the interaction of these factors on densities of root-knot nematode juveniles in soil, root-gall indices, disease ratings, crop yield, and chemistry of the rye tissue. Palmer amaranth population densities were square root transformed and the chemistry data were log(*x* + 1) transformed before ANOVA. Fisher's Protected LSD (*P* ≤ 0.05) was used to separate treatment means. Data were combined across years if there was no year × treatment interaction; otherwise, years are presented separately.

RESULTS

Rye Biomass and Plant Chemistry

The rye cultivars differed (*P* < 0.0001) in the amount of aboveground biomass produced from mid-November to early April (Table 1). Wrens Abruzzi produced the greatest amount of biomass, Oklon and Elbon intermediate, and Wheeler the least; this trend was similar among years and experiments. In the peanut experiment, the amount of biomass produced by the rye (averaged across cultivars) was similar in both years; but, in the cotton experiment, more (*P* < 0.0001) biomass was produced in 2007 (1537 kg ha⁻¹) than in 2008 (1051 kg ha⁻¹).

There was no difference in the concentration of benzoxazinoids in the rye between the cotton and peanut experiments, therefore data from the two experiments were combined for analysis (Table 2). There was a difference between years (*P* < 0.01), with higher concentrations of all of benzoxazinoid components (averaged across rye cultivars) in 2007 compared to 2008. In 2007, Wrens Abruzzi always had the lowest concentrations and Wheeler the highest concentrations of benzoxazinoids, regardless of type, and the difference in benzoxazinoid concentrations between these two cultivars was

Table 1. Differences among rye cultivars in the amount of aboveground dry matter and concentration of benzoxazinoids (benz.) before planting cotton and peanut.

Rye cultivar†	Cotton		Peanut	
	Dry matter kg ha ⁻¹	Benz. g ha ⁻¹	Dry matter kg ha ⁻¹	Benz. g ha ⁻¹
<u>2007</u>				
Wrens Abruzzi	2194a‡	58.2	1795a	62.7b
Elbon	1600b	124.4	1581a	220.0ab
Oklon	1640b	132.3	1465ab	214.4ab
Wheeler	714c	65.7	1013b	238.6a
<u>2008</u>				
Wrens Abruzzi	1505a	6.5b	1922a	21.2
Elbon	1096b	11.9b	1362b	13.2
Oklon	1118b	16.8b	1279b	14.7
Wheeler	487c	50.4a	745c	15.3

† Rye was planted mid-November and incorporated as a green manure the first week in April.

‡ Values within a column and year followed by the same letter (or no letters) are not different ($P < 0.05$) according to Fisher's Protected LSD.

significant ($P < 0.001$). Elbon and Oklon were intermediate to Wrens Abruzzi and Wheeler in benzoxazinoid concentrations in 2007. In 2008, Wheeler had higher concentrations of most of the benzoxazinoid components than the other cultivars except for DIBOA- and HBOA-glucose.

Only the aboveground portion of the rye cultivars was chemically characterized and thus, the nonmethoxy benzoxazinoids (DIBOA-glucose, HBOA-glucose, DIBOA, BOA, and HBOA) were the dominant component of the benzoxazinoids in these cultivars. The nonmethoxy benzoxazinoids comprised between 95 and 99% and methoxy benzoxazinoids 1 to 5% of the total benzoxazinoids across cultivars and years. In both 2007 and 2008, DIBOA was the major benzoxazinoid in the rye cultivars comprising 54 to 72% of the total. While there were differences among the cultivars in benzoxazinoid compounds and concentration expressed as milligrams per kilogram, this difference all but disappeared when total benzoxazinoid concentration was calculated as grams per hectare based on dry matter biomass (Table 1). The only exception was in the cotton experiment in 2008, where the rate of total benzoxazinoids applied to soil was significantly higher in Wheeler compared to the other rye cultivars.

Effect of Rye Cover Crop and Tillage on Palmer Amaranth

The effect of rye cover crop on Palmer amaranth emergence was not consistent among tillage treatments (cover crop × tillage interaction, $P = 0.03$). Where there was substantial soil disturbance (e.g., conventional tillage and green manure), Palmer amaranth densities were low and not influenced by cover crop (Table 3). In the strip tillage plots, however, all of the rye cultivars, except Wheeler, reduced establishment of the weed compared to winter fallow. Wheeler had a Palmer amaranth density of 15.9 plants m⁻² in the strip tillage treatments, whereas the other rye cultivars suppressed densities of the weed to a level similar to that of conventional tillage (<5.2 plants m⁻²).

Cotton Experiment

Root galling on cotton caused by *M. incognita* was influenced by tillage ($P = 0.0002$), but not by rye cover crop. Gall indices on cotton were greater in conventional tillage plots than in either strip tillage or green manure plots (Fig. 1), and this trend was consistent across cover crop treatments and years. Densities of *M. incognita* juveniles in the soil showed a similar trend on some sampling occasions. Soil densities of the nematode were greater in conventional and strip tillage plots than in the green manure plots early in the season, and greater in conventional tillage than green manure plots at harvest in 2008 (Table 4). On other sampling occasions, there were no differences among the tillage treatments. Cover crop influenced soil densities of *M. incognita* on only one occasion: late season densities of the nematode were lower in fallow than in most of the rye cultivars except Oklon, which had similar densities to fallow. Cotton yield was lower in 2007 (1186 kg lint ha⁻¹) than in 2008 (1656 kg lint ha⁻¹), but was not influenced by either tillage (Fig. 1) or cover crop.

Peanut Experiment

Root-gall indices on peanut caused by *M. arenaria* were greater ($P < 0.0001$) in 2007 than in 2008 (Fig. 2); averaged across treatments, they were 7.6 and 6.5, respectively. Galling of peanut roots was influenced by tillage ($P < 0.0001$), but not by rye cover crop. Gall indices were greater in the strip tillage plots than in the conventional tillage or green manure plots. Although this trend was consistent between years (i.e., no

Table 2. Concentration of benzoxazinoids in the aboveground rye tissue before incorporation of the cover crop.

Rye cultivar†	DIBOA-glucose	HBOA-glucose	DIBOA	BOA	HBOA	Methoxy‡	Total
<u>2007</u>							
Wrens Abruzzi	1.1	0.5b§	13.0b	4.4b	1.9b	0.6	21.5b
Elbon	1.3	0.8ab	26.7ab	7.0ab	4.0ab	1.1	40.4ab
Oklon	1.2	1.0ab	42.4ab	9.3a	4.6ab	0.6	59.3ab
Wheeler	0.7	1.1a	76.2a	16.1a	10.2a	0.9	105.5a
<u>2008</u>							
Wrens Abruzzi	0.4	0.4	5.4b	1.2b	0.8b	0.4 b	8.6b
Elbon	0.4	0.7	5.4b	2.0b	1.0b	0.5 b	10.0b
Oklon	0.4	0.7	8.1b	3.1b	1.7b	0.5 b	14.3b
Wheeler	0.4	0.4	34.0a	12.9a	8.5a	1.0 a	57.4a

† Rye was planted mid-November and incorporated as a green manure the first week in April.

‡ Methoxy benzoxazinoids are DIMBOA-glucose, DIMBOA, MBOA, and HMBOA.

§ Values within a column and year followed by the same letter (or no letters) are not different ($P < 0.05$) according to Fisher's Protected LSD.

Table 3. Effect of tillage and rye cover crop on the density of Palmer amaranth (*Amaranthus palmeri*) in cotton.

Cover crop/rye cultivar	Conventional tillage	Green manure	Strip tillage
Palmer amaranth plants m ⁻²			
Fallow	3.3c†	2.7c	18.1a
Wrens Abruzzi	3.6c	2.6c	5.2bc
Wheeler	4.1c	3.3c	15.9ab
Elbon	3.4c	4.3c	4.9bc
Oklon	4.1c	6.0bc	4.8c

† Values within the table followed by the same letter are not different ($P < 0.05$) according to Fisher's Protected LSD.

interaction between tillage and year), the data are presented for each year to show the relationship between galling and peanut yield (Fig. 2). Soil densities of *M. arenaria* juveniles tended to be greater in the strip tillage plots than in the other plots, but were only significantly different at mid-season of 2008 (Table 5). Rye cover crop did not influence soil densities of the nematode on any sampling occasion. In 2007, peanut yields were low (1204 kg ha⁻¹) and not influenced by tillage (Fig. 2) or rye cover crop. In 2008, peanut yields were 1.9-fold greater ($P < 0.0001$) than in 2007 and were influenced by tillage, but not by cover crop. Peanut yield in 2008 was lower in strip tillage than in conventional or green manure plots (Fig. 2). Incidence and severity of both stem rot and *Rhizoctonia* limb rot were low and not influenced by any of the treatments. Of the two diseases, stem rot had the highest incidence and was more abundant in 2007 than in 2008, with an average of 4.1 and 2.5% of the row affected by the disease, respectively.

DISCUSSION

The rye cultivars varied in the amount of aboveground biomass produced at our field sites in Tifton, GA. The cultivar Wrens Abruzzi was developed in Georgia and produced the greatest biomass of any of the cultivars. Oklon and Elbon cultivars were developed in Oklahoma and produced intermediate amounts of biomass. The cultivar Wheeler was developed in Michigan and produced the least biomass. In North Carolina, the phenological development of Wheeler was 3 wk behind that of Wrens Abruzzi and 2 to 3 wk behind that of Elbon (Reberg-Horton et al., 2005). As rye matures, there is a decline

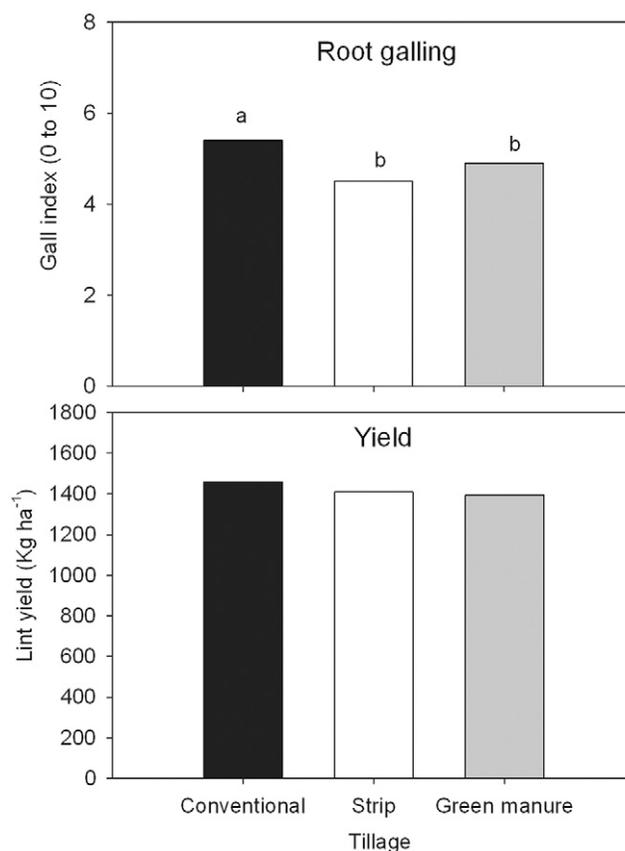


Fig. 1. Root-gall indices on cotton caused by *Meloidogyne incognita* and cotton yield under different tillages. Conventional tillage involved disc harrowing followed by rip and bedding. The green manure treatment received the same tillage as the conventional treatment plus an additional tillage event when the winter rye was rototilled into the soil 4 wk earlier.

in tissue concentrations of benzoxazinoids (Reberg-Horton et al., 2005; Rice et al., 2005). In the North Carolina study, the rate of decline was less in Wheeler than in Wrens Abruzzi, possibly due to the slower development of Wheeler (Reberg-Horton et al., 2005). We also found a greater concentration of benzoxazinoids, including DIBOA, in Wheeler than in Wrens Abruzzi; Oklon and Elbon generally had intermediate concentrations. However, when the rate of benzoxazinoids per hectare

Table 4. Influence of tillage and rye cover crop on population density of southern root-knot nematode (*Meloidogyne incognita*) juveniles in cotton.

Tillage	Early season†	Mid-season	Harvest 2007 2008		
			no./2 150 cm ⁻³		
Conventional	102a ‡	346	1259	728	1225a
Strip	89a	313	1269	757	1040ab
Green manure	50b	268	1064	918	930b
	$P = 0.004$	$P = 0.38$	$P = 0.07$	$P = 0.09$	$P = 0.03$
Cover crop/rye cultivar					
Fallow	89	304	930b	818	
Wheeler	86	292	1237a	1011	
Oklon	84	346	1180ab	918	
Wrens Abruzzi	73	293	1279a	916	
Elbon	72	310	1360a	1000	
	$P = 0.88$	$P = 0.95$	$P = 0.01$		$P = 0.29$

† Unless otherwise indicated, values are the means from 2007 and 2008. There was an interaction between tillage and year ($P = 0.007$) for the harvest sampling time; therefore, data are presented for each year.

‡ Values within a column followed by the same letter (or no letters) are not different ($P < 0.05$) according to Fisher's Protected LSD.

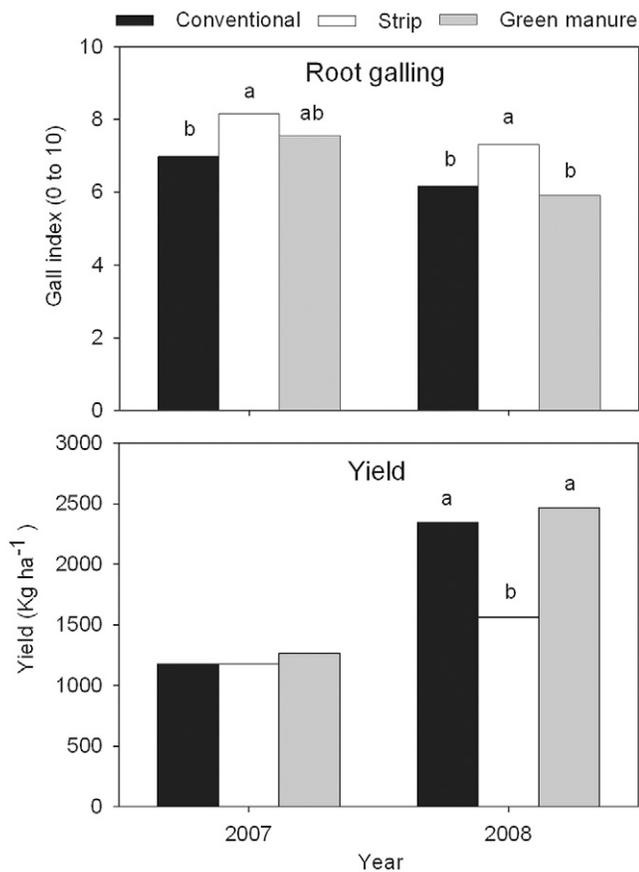


Fig. 2. Root-gall indices on peanut caused by *Meloidogyne arenaria* and peanut yield under different tillages. Conventional tillage involved disc harrowing followed by moldboard plowing and bedding. The green manure treatment received the same tillage as the conventional treatment plus an additional tillage event when the winter rye was rototilled into the soil 4 wk earlier.

was determined (biomass × tissue concentration), there were few consistent differences among the cultivars.

Incorporating rye as a green manure in early April did not enhance suppression of Palmer amaranth compared to conventional tillage or winter fallow. Our results are in agreement

Table 5. Influence of tillage and rye cover crop on population density of peanut root-knot nematode (*Meloidogyne arenaria*) juveniles in peanut.

Tillage	Early season†	Mid-season		Harvest
		2007	2008	
no. J2 150 cm ⁻³				
Conventional	153	104	138b‡	790
Strip	115	138	302a	940
Green manure	121	93	120b	842
	<i>P</i> = 0.15	<i>P</i> = 0.13	<i>P</i> < 0.0001	<i>P</i> = 0.38
Cover crop/rye cultivar				
Fallow	130	137		759
Wheeler	131	131		766
Oklon	139	139		976
Wrens Abruzzi	106	165		841
Elbon	142	174		944
	<i>P</i> = 0.72	<i>P</i> = 0.32		<i>P</i> = 0.41

† Unless otherwise indicated, values are the means from 2007 and 2008. There was an interaction between tillage and year (*P* = 0.0005) for the mid-season sampling time; therefore, data are presented for each year.

‡ Values within a column followed by the same letter (or no letters) are not different (*P* < 0.05) according to Fisher's Protected LSD.

with Kruidhof et al. (2009), who demonstrated that rye was more effective in reducing weed seedling emergence when left on the soil surface as mulch than when incorporated into soil. There are several mechanisms by which cover crops affect weed establishment, including altering light quality, light quantity, temperature, soil moisture content, and nutrient availability (Hoffman and Regnier, 2006). In addition to these factors, the physical barrier created by the rye mulch in the strip tillage plots may have inhibited weed emergence. Wheeler, which produced the smallest quantity of aboveground biomass compared to the other cultivars, did not suppress emergence of Palmer amaranth relative to fallow. The physical effects of the rye residue, however, cannot fully explain the emergence pattern of Palmer amaranth among the rye cultivars. For example, Wrens Abruzzi produced more aboveground biomass than Oklon or Elbon, which, if the mulches only represented a physical barrier, should have led to greater weed suppression. However, these three cultivars had equivalent weed control (Table 3). Though not significant, the total amount of benzoxazinoids (grams per hectare) in the rye biomass was twofold greater for Oklon and Elbon than for Wrens Abruzzi. Previous studies found that weed biomass was reduced 44% by a layer of wood shavings, while a similar amount (by weight) of dried rye residues reduced weed biomass 80%, suggesting an allelopathic component (Putnam and Defrank 1983). Allelopathic residues from rye have been implicated in reducing weed growth (Barnes and Putnam, 1983; Reberg-Horton et al., 2005). Residues from rye shoots (Wheeler) were shown to be more effective in reducing radicle elongation in lettuce (*Lactuca sativa* L.) compared to residues from rye roots (Barnes and Putnam, 1986). Benzoxazinoids reduce root growth by disrupting lipid metabolism and reducing both protein synthesis and transport (Burgos et al., 2004). Burgos et al. (1999) found that aqueous extracts from field-grown rye cultivars Elbon and Bonel had the greatest inhibition of Palmer amaranth root growth. However, there was no correlation between growth inhibition and benzoxazinoid content among the eight cultivars of rye evaluated (Burgos et al., 1999).

In the absence of a cover crop, Palmer amaranth population density was greater in strip tillage than in the green manure and conventional tillage treatments. Palmer amaranth seeds in this study were spread on the soil surface after rye had emerged. In spite of the lack of a naturalized Palmer amaranth soil seedbank, the results of this study were consistent with previous research. Long-term studies with naturalized seedbanks found that weed populations generally declined as soil disturbance increased, especially small-seeded broadleaf species (e.g., *Amaranthus* spp. and *Chenopodium album*) (Cardina et al., 1991; Ramsdale et al., 2006; Sosnoskie et al., 2006). The physical soil disturbance associated with conventional tillage and incorporation of the green manure treatments may have redistributed Palmer amaranth seeds to depths below which these small-seeded weeds could emerge. Keeley et al. (1987) found that Palmer amaranth seedlings emerged more readily from a depth of 2.5 cm or less (36–44% emergence) than from depths of 5.1 cm (7%) or 7.6 cm (2%). Because Palmer amaranth is a very competitive weed in cotton (MacRae et al., 2008), all plots were treated with glyphosate and metolachlor when cotton was at the four-leaf growth stage; this treatment effectively halted

Table 6. Studies evaluating the effect of conventional (C) and minimum (M) tillage on root-knot nematodes (*Meloidogyne* spp.).

Crop	Nematode species	Tillage	Effect of minimum tillage on nematode	Citation
Peanut	<i>M. arenaria</i>	Moldboard (C) Strip† (M)	Galling greater	(Minton et al., 1990)
Peanut	<i>M. arenaria</i>	Moldboard (C) Strip (M)	Galling greater	(Minton et al., 1991)
Soybean	<i>M. incognita</i>	Moldboard (C) Strip (M)	J2 populations lower	(Minton and Parker, 1987)
Soybean	<i>M. incognita</i>	Rototiller (C) No till (M)	J2 populations greater	(McSorley and Gallaher, 1994b)
Soybean	<i>M. incognita</i>	Rototiller (C) No till (M)	J2 populations greater	(Okada and Harada, 2007)
Corn	<i>M. incognita</i>	Disk harrow + Strip (C) Strip (M)	No difference	(Fortnum and Karlen, 1985)
Corn	<i>M. incognita</i>	Rototiller + Strip (C) Strip (M) No till (M)	No difference No difference	(Gallaher et al., 1988)
Corn	<i>M. incognita</i>	Rototiller (C) No till (M)	No difference	(McSorley and Gallaher, 1994a)

† Strip tillage uses a single subsoil chisel in the planting row.

Palmer amaranth emergence in this study, relatively early in the growing season.

Compared to winter fallow, none of the rye cultivars increased or decreased galling of either cotton or peanut roots by *Meloidogyne* spp. in any of the tillage treatments. Soil populations of J2 were also not affected by the rye cover crops except on one sampling occasion in the cotton experiment. In that experiment, *M. incognita* populations late in the season were greater in plots previously planted to Wheeler, Elbon, or Wrens Abruzzi than in fallow plots. Reproduction of the nematode on these rye cultivars is the most likely explanation for the difference between the rye and fallow plots; however, the amount of reproduction was not large enough to increase root galling on cotton. Incorporating the rye into soil as a green manure did not suppress root-knot nematode populations. We had predicted that benzoxazinoids, principally DIBOA, would be released from the incorporated rye tissue at rates toxic to nematodes, but clearly this was not the case. In a recent study, Meyer et al. (2009) showed that the concentration of DIBOA needed to suppress numbers of *M. incognita* eggs on plant roots in soil was two to three times higher than the concentrations previously calculated to kill eggs and J2 based on aqueous bioassays (Zasada et al., 2005). Suppression of egg production by *M. incognita* on plant roots occurred at concentrations well above what could be expected to be released from rye tissue.

Tillage had a consistent effect on root-knot nematodes within each experiment, but the effect of tillage differed between the cotton and peanut experiments. In the peanut experiment, the substantial tillage used in the conventional and the green manure treatments suppressed root galling and soil densities of *M. arenaria* compared to the strip tillage treatment. These results support previous tillage studies involving peanut (Table 6). Tillage may result in greater mortality of root-knot juveniles and eggs due to transfer of these vulnerable stages to the soil surface where they are exposed to desiccation and high temperatures. In support of this mechanism is the observation that fewer J2 of *Meloidogyne* spp. are sometimes found in conventional than in minimal tillage shortly after the tillage event (McSorley and Gallaher, 1994b; Okada and Harada, 2007), although this early-season suppression was

not observed in our study. Tillage also disperses the nematode population and many nematodes may be deposited far from the future root zone.

The response of *M. incognita* to tillage in the cotton experiment is difficult to explain. In that experiment, root galling and soil densities of the nematode were lower in strip tillage than in conventional tillage, the opposite of what we observed in the peanut experiment. To our knowledge, this is the first published report on the response of *M. incognita* in cotton to minimum tillage. However, in another tillage experiment involving cotton, we also found less galling from *M. incognita* in strip than in conventional tillage plots (R.F. Davis, unpublished data, 2007). The primary difference between the cotton and peanut experiment was the host plant for the root-knot nematodes and the type of conventional tillage used, both of which may have played a role in the differential response of the two root-knot species to tillage.

Although no study has examined the interaction between crop species and tillage on nematode populations, several studies with *M. incognita* have shown a tillage effect with soybean [*Glycine max* (L.) Merr.], but not with corn (*Zea mays* L.) (Table 6). Depth and architecture of the root system will influence nematode distribution in the soil. Nematodes deeper in the soil profile may be protected from the disturbance caused by tillage. Moreover, nematode populations concentrated below the planting furrow may show a greater response to strip tillage than populations that are dispersed beyond the furrow.

The type of tillage equipment used may also differentially affect nematode populations. The moldboard plow, used in conventional tillage of peanut, lifts and inverts the soil; whereas, the ripper-bedder, used in conventional tillage of cotton, is similar to a chisel plow which tears and loosens the soil, but no inversion occurs; however, some mixing of soil occurs in the bedding process. Compared to the ripper-bedder, the moldboard plow would cause greater dispersion and exposure of the nematodes to the soil surface. The rototiller, used in both experiments to incorporate the rye green manure, tears and mixes the soil, with some inversion of the soil profile. The only difference in tillage between the conventional and the green manure treatments was the additional

rototilling. Therefore, the lower populations of *M. incognita* in the green manure plots (including the fallow) compared to the conventional plots appear to be due to rototilling. Suppression of *M. incognita* J2 was observed shortly after rototilling indicating that inversion of the soil exposed the nematodes to greater mortality.

It is unclear why root galling from *M. incognita* was lower in strip tillage compared to conventional tillage. If the conventional tillage in cotton was only mildly disruptive to the nematode population, we would expect galling to be similar in conventional and strip tillage. The ability of the J2 to move through soil and infect cotton roots may have resulted in greater galling in the conventional tillage plots. Eo et al. (2007) demonstrated that tillage increased the overall pore volume of soil, which led to greater migration of *M. incognita* in soil that had been subjected to rotary tillage compared to no tillage.

SUMMARY

Substantial soil disturbance as a result of conventional tillage and green manuring decreased Palmer amaranth emergence, but had differential effects on root-knot nematode populations in the cotton and peanut experiments. In the cotton experiment, root galling was greatest in conventional tillage; whereas, in the peanut experiment, galling was greatest in strip tillage. Increased nematode damage in the strip-tilled peanut likely contributed to the lower yield compared to peanut in plots with substantial tillage. Differences in root galling of cotton among the tillage treatments may have been too small to affect yield.

Three of the four rye cultivars (Elbon, Oklon, and Wrens Abruzzi) reduced emergence of Palmer amaranth compared to fallow only under strip tillage. The primary mechanism appeared to be the physical barrier created by the rye mulch. Compared to the other cultivars, Wheeler produced the lowest aboveground biomass, but often had the highest concentration of total benzoxazinoids, including DIBOA, per kilogram of tissue. In cotton in 2008, the total amount of benzoxazinoids (g ha^{-1}) in the rye biomass was greater for Wheeler than for the other cultivars; nevertheless, Wheeler, unlike the other cultivars, did not reduce emergence of Palmer amaranth relative to the fallow. Allelopathy may have contributed to weed suppression in Elbon and Oklon because the biomass of these cultivars was less than that of Wrens Abruzzi, yet these three cultivars provided the same level of Palmer amaranth suppression. None of the rye cultivars suppressed populations of root-knot nematodes in cotton or peanut.

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