Applied Soil Ecology 95 (2015) 107–114

Contents lists available at ScienceDirect

Applied Soil Ecology

journal homepage: www.elsevier.com/locate/apsoil

Population dynamics and spatial distribution of Columbia lance nematode in cotton

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ARTICLE INFO

Article history:
Received 24 November 2014
Received in revised form 1 June 2015
Accepted 7 June 2015
Available online 4 July 2015

Keywords:
Lance nematode
Reniform nematode
Spatial distribution
Soil texture
Crop rotation

ABSTRACT

Hoplolaimus columbus, Columbia lance nematode (CLN), can cause severe stunting and considerable yield losses in cotton. A three-year field study was conducted in South Carolina with the purpose of examining the population dynamics and spatial distribution patterns of CLN as influenced by soil texture, the presence of *Rotylenchulus reniformis*, reniform nematode (RN), and a cotton–corn–soybean rotation scheme. Four plots with different soil textures inferred by soil electrical conductivity were sampled at plant and at harvest for each crop. Population densities of CLN were aggregated and the host plant did not affect the pattern of spatial distribution. Columbia lance nematode and RN were found in spatially distinct areas in the field influenced by differences in soil texture. Columbia lance nematode was mainly found in areas with high sand content (above 75%) and RN in areas with 60–65% sand content. Therefore, depending on the sand content, whenever there are concomitant infestations of CLN and RN in a field, only one species is likely to be the key pest. Knowledge of the distribution patterns of CLN is essential for selecting sampling strategies and for site-specific management.

1. Introduction

Hoplolaimus columbus, Columbia lance nematode (CLN), can cause severe stunting and considerable yield losses in cotton (*Gossypium hirsutum*) (Lewis and Fassuliotis, 1982; Noe, 1993; Koenning et al., 2003, 2004). Lance nematodes are migratory endo- and ectoparasites that cause necrotic lesions in cotton roots. The most substantial damage occurs when plants are infected early in the growing season and the tips of tap and secondary roots are damaged (Lewis et al., 1976; Mueller and Sullivan, 1988). Damage thresholds are reported to be approximately 75 CLN per 100 cm^3 of soil, and yield losses normally range from 10% to 25%, but can surpass 50% (Koenning et al., 2004; Mueller et al., 2010).

In South Carolina, CLN, root-knot nematode (RKN) *Meloidogyne incognita*, and reniform nematode (RN) *Rotylenchulus reniformis* are the three main plant-pathogenic nematode species causing yield losses in cotton production (Lewis and Smith, 1976; Lewis and Fassuliotis, 1982; Martin et al., 1994). A survey of cotton-growing counties in the state (Martin et al., 1994) showed that these three species are present in approximately 60% of the cotton acreage in South Carolina and exceed damage thresholds in nearly 50% of that area. Unlike RKN and RN, which are widely distributed across the cotton-growing states in the southeastern United States, CLN has a more limited distribution and is only reported infecting cotton plants in North Carolina, South Carolina, and Georgia (Gazaway, 1994; Koenning et al., 1999).

The relationship between CLN and RKN on cotton has been studied in the field (Bird et al., 1974) and in the greenhouse (Kraus-Schmidt and Lewis, 1981). Populations of RKN can be suppressed in the presence of CLN to the extent that CLN can replace RKN as the predominant plant-pathogenic species (Bird et al., 1974; Kraus-Schmidt and Lewis, 1981). Distribution of these two nematode species in the field is influenced by soil texture. The occurrence of higher population densities of RKN and more severe crop damage in coarser textured soils was documented by Koenning et al. (2004). Reproduction of RKN is greater in soils ranging in sand content from 72% to 91% (Prot and Van Gundy, 1981). Likewise, population densities of CLN are positively correlated to sand content in fields where the sand content ranges from 81% to 90%, and the species is reported to be rare in soils with less than 70% sand (Khalilian et al., 2001).

The relationship between CLN and RN in cotton fields has not been studied, but the two species appear to have different soil texture associations. In a previous field study, Holguin et al. (2015) reported strong correlations between RN densities and percent sand and silt, showing that RN densities peak when sand content is around 60–65% and decline when sand content increases

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http://dx.doi.org/10.1016/j.apsoil.2015.06.004
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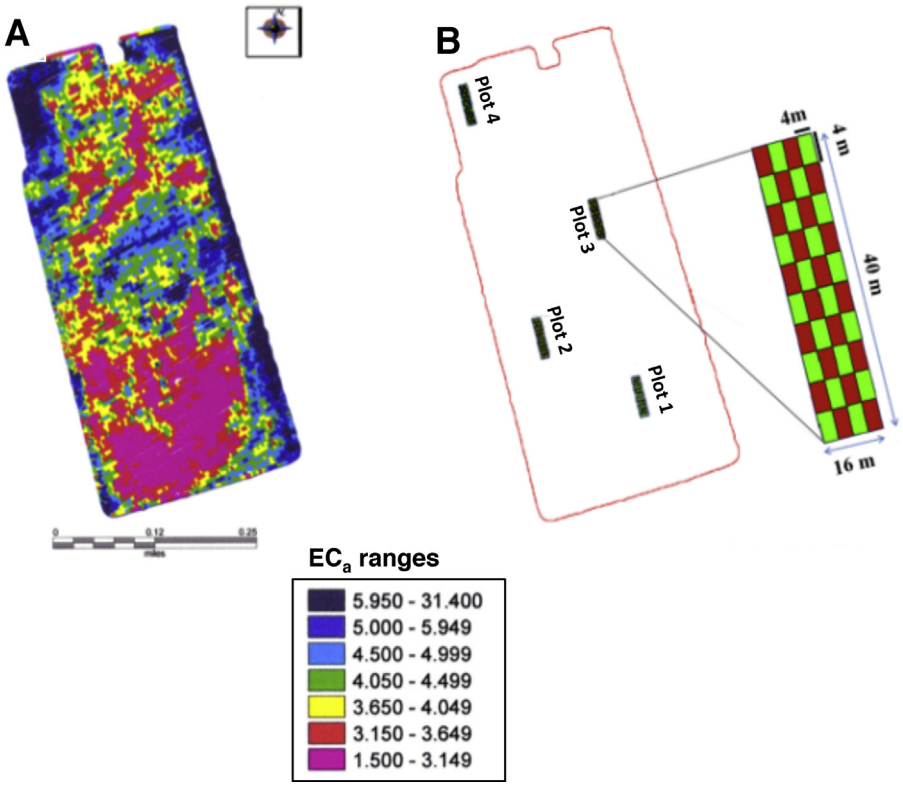

Fig. 1. Sampling design. Electrical conductivity (EC_a) map of readings taken before planting (April 2011). (A) Map showing seven EC_a zones. Each color represents different EC_a ranges. (B) Four plots selected for sampling and each plot divided into 40 (4 m × 4 m) subplots. Eighty total samples taken per date (40/2 * 4 = 80).

above 65%. However, cotton has been shown to be an excellent host for both species (Noe, 1993) and several authors have reported an increase in distribution of these nematodes in cotton-growing regions (Bird et al., 1974; Martin et al., 1994; Koenning et al., 2003). Lewis and Smith (1976) suggest that the high incidence of CLN in South Carolina may be due to continuous cropping with susceptible hosts, such as cotton, corn (*Zea mays*), and soybean (*Glycine max*), and they indicate that continuous cotton may sustain higher densities of CLN than rotations with soybean and corn. The population dynamics and distribution patterns of CLN and RN in cotton fields infested with both species can be especially relevant when considering crop rotation as a management practice (Davis et al., 2000). For example, rotation with corn or RN-resistant soybean, both suitable hosts for CLN, is a commonly prescribed management practice for RN on cotton (Davis et al., 2003; Koenning et al., 2003).

Distribution of CLN within a field is usually in scattered patches determined by soil texture due to the strong positive correlation between CLN population densities and sand content (Khalilian et al., 2001; Koenning et al., 2004). Consequently, the application of nematicides uniformly over the entire field for the control of CLN can be both costly and environmentally questionable (Mueller et al., 2010). Site-specific application of nematicides has been proposed for management of nematodes in cotton fields (Davis et al., 2013; Mueller et al., 2010), so that application of nematicides is restricted to target areas in the field where the nematodes are above threshold (Khalilian et al., 2001; Mueller et al., 2010). By using a soil electrical conductivity meter, the soil texture can be inferred and the distribution of CLN can be predicted (Khalilian et al., 2001; Ortiz et al., 2010; Mueller et al., 2010; Davis et al., 2013). However, soil texture is not the only driver of CLN distribution in the field, and the effective use of site-specific management requires knowledge of the spatial distribution patterns of the nematode species within individual fields (Park et al., 2007; Mueller et al., 2001). The objective of this three-year study was to determine population dynamics and spatial distribution patterns of CLN as influenced by soil texture and the presence of RN, under a cotton–corn–soybean rotation scheme.

2. Materials and methods

Population densities of CLN and RN were monitored over three growing seasons (spring 2011 to winter 2013) in a 36.4 ha irrigated commercial field near Bishopville, South Carolina (80.648° W, 33.736° N). The field was planted with cotton 'Deltapine 1050' in 2011, followed by corn 'Pioneer 1690' in 2012, and soybean 'Asgrow 7231' in 2013.

2.1. Plot selection and sample collection

Prior to this study (April 2011), the soil electrical conductivity (EC_a) was measured in the field with a sensor cart (Veris 3100 from Veris Technologies, Salina, KS, USA) to map the soil EC_a and identify management zones in the field with predictable soil texture similarities (Mueller et al., 2010). Using Global Positioning System (GPS) technology and mapping sensors, each point in the field where the EC_a value was taken was geo-referenced to create a map. The generated map was divided into seven sections according to shallow EC_a (0–30 cm) value ranges (Fig. 1a). For nematode sampling, four zones of the field were selected to represent different EC_a readings and corresponding inferred textures. In each of these four zones, a plot of 40 m × 16 m was divided into 40 subplots of 4 m × 4 m (Fig. 1b). Soil samples were collected from 20 subplots in each plot at planting (May 2011 and August 2013) and after harvest (December 2011 and December 2013). In September 2012, soil samples were collected only after corn harvest. Each soil sample consisted of four subsamples of 200 cc taken from within a one-square-meter area

Table 1
Soil particle size distribution (percentage content of sand, silt, clay) and soil types in the top 15 cm determined by the Bouyoucos method for each plot.

	%			Soil types
	Clay	Silt	Sand	
Plot 1	7.28 ± 0.22 (6.1–8.2)	12.2 ± 0.34 (9.8–16.0)	80.49 ± 0.36 (75.9–81.9)	Loamy sand
Plot 2	14.21 ± 0.51 (10.1–16.4)	21.97 ± 1.37 (11.8–34.1)	63.81 ± 1.50 (51.9–76.0)	Sandy loam, loam
Plot 3	26.21 ± 0.77 (20.1–32.2)	36.89 ± 1.40 (28.0–48.0)	36.95 ± 1.68 (21.9–50.0)	Loam, clay loam, Sandy clay loam
Plot 4	15.38 ± 0.66 (10.1–22.1)	20.46 ± 0.36 (18.1–24.0)	64.16 ± 0.90 (53.9–71.8)	Sandy loam, sandy clay loam

(15 cm deep) and composited into a single sample, for a total of 80 samples per date.

From each sample, nematodes were extracted by sugar centrifugal flotation (Jenkins, 1964) and soil particle distribution (percentage of sand, silt and clay content) was determined using the Bouyoucos method (Bouyoucos, 1962). At the end of the study, after soybean harvest (January 2014), vertical soil cores (1 m deep × 4.3 cm in diameter) were taken in 16 sites in plots 1 and 2 (8 sites per plot) with a hydraulically operated soil sampler (GSTS, Giddings Machine Company, Fort Collins, CO) mounted on a tractor. Each vertical core was divided into four sections: 0–15 cm, 15–30 cm, 30–60 cm, and below 60 cm. From each section of the vertical core, nematodes were extracted and textural analysis performed in the same manner described above.

2.2. Statistical analysis

Descriptive data analysis for nematode density and soil particle size distribution was performed for each plot and for each layer for the vertical sampling. Population densities of CLN and RN were visualized using contour maps for plots where the two nematodes occurred together using JMP v.10 (SAS Institute Inc., Cary, NC). The mean population densities of the two species were compared each year using a two-way analysis of variance (ANOVA) with plots and sampling date as factors using JMP, version 10. Sampling date was included as a repeated measurement statement with a first-order autoregressive covariance structure (ANOVA, PROC MIXED). Densities were $\log_{10}(x+1)$ transformed to normalize the variance prior to ANOVA. Mean densities of the two nematodes collected in the vertical sampling, were also compared using ANOVA with each layer used as factor.

The variance to mean ratio was used as dispersal index (DI) to determine the distribution of CLN densities per plot at each sampling date (Taylor, 1961, 1984). This index takes into account the nematode counts per sample unit and provides an indication of the spatial pattern of the counts. For uniformly distributed counts, variance is around zero and the expected DI is close to 0; for a random distribution, variance and mean are similar therefore DI is approximately 1; and for a clustered distribution, variance is relatively large, thus DI is greater than 1. To assess the significance of the index, the Chi-square test was used at the 0.05 level of significance.

Moran's *I* indices were also calculated to test the spatial autocorrelation between densities of CLN observed within each pair of sampling points and distance classes using the autocorrelation module 3.03 in R version 3.0.2 (Sokal and Oden, 1978; Legendre and Vaudor, 1991). Correlograms were used per plot at each sampling date to show changes in Moran's indices with increasing lag distance and to test for the presence of significant spatial structure (Sokal and Oden, 1978; Legendre and Legendre, 1998). Values of Moran's *I* greater than 1 indicate positive autocorrelation (counts

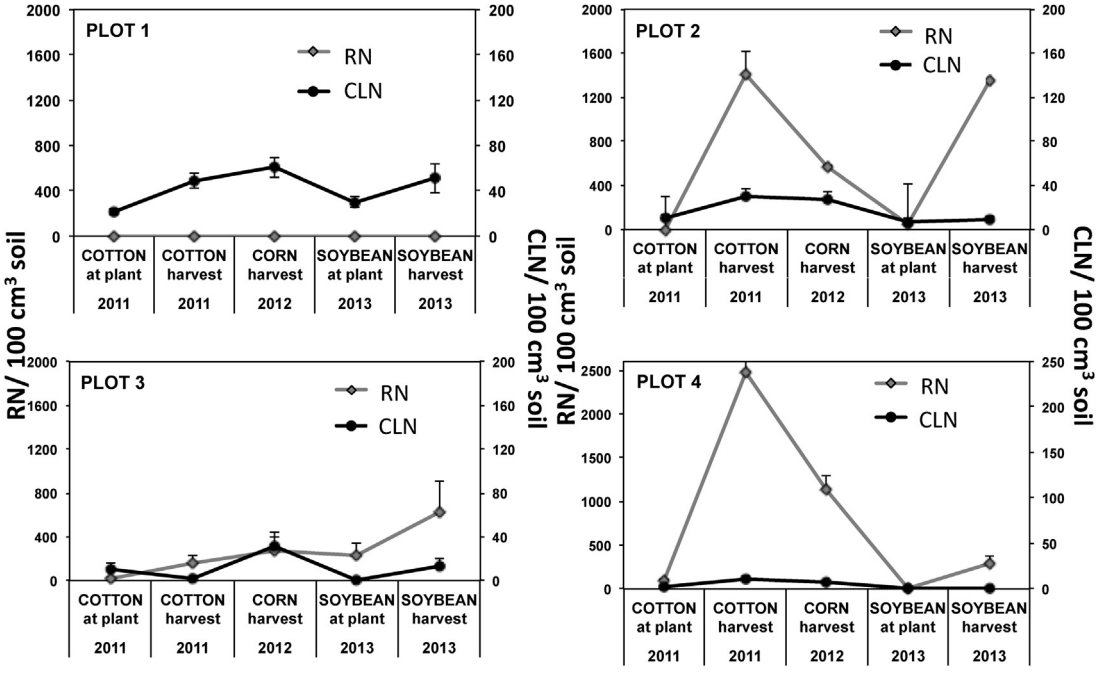

Fig. 2. Population dynamics of Columbia lance nematode (CLN) and reniform nematode (RN) across the three-year study. Densities (±SE) per 100 cm³ soil found in the top 15 cm for all sampling dates in cotton (n = 160) 2011, corn (n = 80) 2012 and soybean (n = 160).

similar in neighbor sites), less than 1 indicate negative autocorrelation (counts dissimilar in neighbor sites) and values close to 1 indicate absence of spatial autocorrelation.

SADIE (Spatial Analysis by Distance Indices) v. 2.0 (Perry, 1998) was used to determine the degree of spatial clustering for CLN counts in each plot for all sampling dates. SADIE characterizes the spatial structure of georeferenced counts and tests for the significance of the spatial pattern by using indices of clustering, with high counts categorized as clusters and low counts as gaps (Perry, 1995). The index of aggregation (I_a) is calculated as: $I_a = D/E_a$, Where D is the minimum distance that densities would need to produce a uniform spatial arrangement, and E_a, the expected distance to regularity (E_a), is the result of randomizing sampling counts among sampling locations. A value of $I_a > 1.0$ indicates an aggregated distribution of counts and $I_a < 1.0$ indicates regular distribution. The significance of I_a was assessed by a randomization method using the default parameters of SADIE v. 2.0. The null hypothesis is rejected at $P_a < 0.025$ (aggregation) and accepted at $P_a > 0.975$ (uniformity) (Perry, 1998).

Additionally, SADIE v. 2.0 was also used to determine the relationship between CLN and RN by calculating the spatial association index for the plots and dates where the two nematodes occurred concomitantly. This analysis compares the cluster indices from two data sets to provide an index that explains the departure from randomness (X). A value of $X > 0$ suggests a positive association between counts, $X < 0$ suggests a negative association, and values near zero indicate that counts are randomly associated to each other. The significance was assessed with a randomization procedure (Perry and Dixon, 2002).

To determine the relationship between CLN and crop as well as the relationship with RN, a non-metrical multidimensional scaling (NMDS) based on Bray–Curtis similarity was computed using the software Primer v.6 (Anderson et al., 2008). To identify which soil factors (% sand, % silt and % clay) explain the pattern detected between CLN and RN (see Section 3), DistLM was used in Primer v.6 to superimpose vector overlays for % sand, % silt and % clay as Pearson correlations and explain the pattern found for the two nematode species.

3. Results

3.1. Soil texture and type for the top layer (0–15 cm)

Plot 1 had the highest sand content (75.9–81.9%) and was the most uniform in soil type with all 20 samples being classified as loamy sand (Table 1). Plot 3 presented the lowest sand content (21.9–50.0%) and was the most variable, containing 12 samples classified as loam, 6 as clay loam, and 2 as sandy clay loam. In plots 2 and 4, the majority of samples were sandy loam, and soil texture for these two plots was similar.

3.2. Population dynamics

Where present, CLN population density ranged from 10 to 240 individuals/100 cm^3 of soil (Fig. 2). Population densities increased moderately from planting to harvest on cotton and soybean, with reproduction factors (Rf = Pf/Pi) ranging from 1.3 to 3.6, except in plot 3 on cotton where populations decreased (Rf = 0.25). Similar CLN densities were detected for the three hosts, with 10–130 individuals/100 cm^3 of soil for cotton, 10–240 individuals/100 cm^3 of soil for corn, and 10–180 individuals/100 cm^3 of soil for soybean. The highest densities were found in plot 1 (80.5% sand content) and the lowest in plot 3 (36.9% sand content). Among plots, densities of CLN were significantly different ($P < 0.0001$ in 2011; $P = 0.0005$ in 2012; and $P < 0.0001$ in 2013) as well as from plant to harvest in 2011 ($P < 0.0001$) and 2013 ($P = 0.0203$) (Fig. 2).

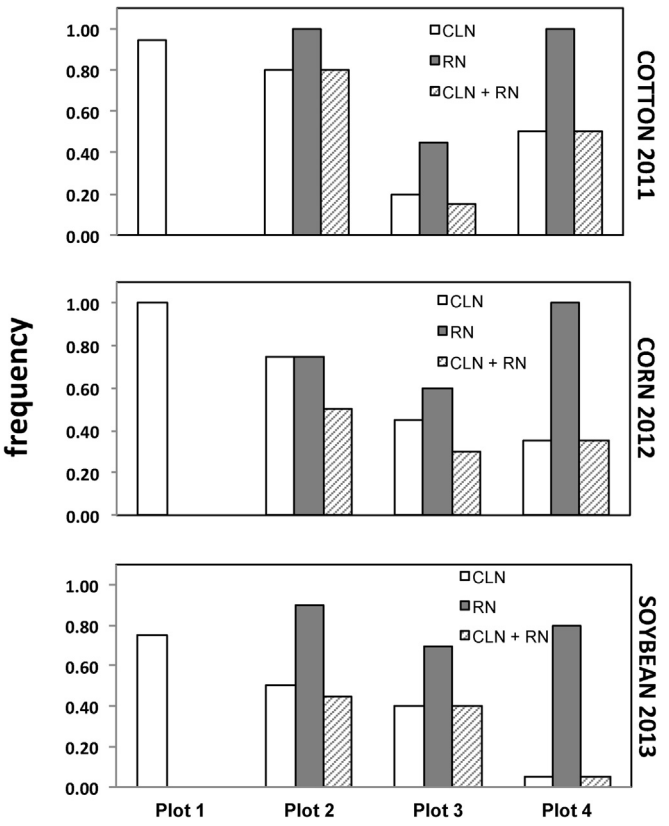

Fig. 3. Frequency of positive samples for Columbia lance nematode (CLN), reniform nematode (RN), and the two species together, for the three hosts (cotton 2011, corn 2012 and soybean 2013) at harvest.

Where present, RN ranged from 10 to 6930 individuals/100 cm^3 of soil. The highest densities and frequencies were found in plots 2 and 4, with relatively low densities in plot 3 and no presence of RN in plot 1. Predictably, the lowest RN densities were found after corn, and populations increased quickly on cotton and soybean. Significant differences were detected among plots across the three years ($P < 0.0001$ in 2011; $P < 0.0001$ in 2012 and $P = 0.0024$ in 2013).

Mixed populations were more frequently found in plots 2 (63.8% sand) and 4 (64.2% sand) with cotton (Fig. 3). The highest frequency of the mixture was in plot 2 with all hosts: 0.80 with cotton, 0.50 with corn, and 0.45 with soybean. However, even in plot 2, it is possible to observe a spatial separation of the species in the field. Fig. 4 illustrates the presence of CLN and RN in plot 2 for the three crops and shows where areas of high density for one species have corresponding low density for the other species.

Table 2
Hoplolaimus columbus, Columbia lance nematode (CLN), dispersal indices (DI)[a] for each of the four plots at each sampling date.

Plot	Cotton 2011		Corn 2012	Soybean 2013	
	At plant	Harvest	Harvest	At plant	Harvest
1	9.93	6.86	23.74	14.38	61.28
2	14.64	18.24	30.96	28.72	24.44
3	60	21.75	108.7	10	89.96
4	9.25	9.47	21.2	–	10

[a] For uniformly distributed counts, variance is around zero and the expected DI is close to 0; for a random distribution, variance and mean are similar therefore DI is approximately 1; and for a clustered distribution, variance is relatively large, thus DI is greater than 1. To assess the significance of the index, the Chi-square test was used at the 0.05 level of significance.

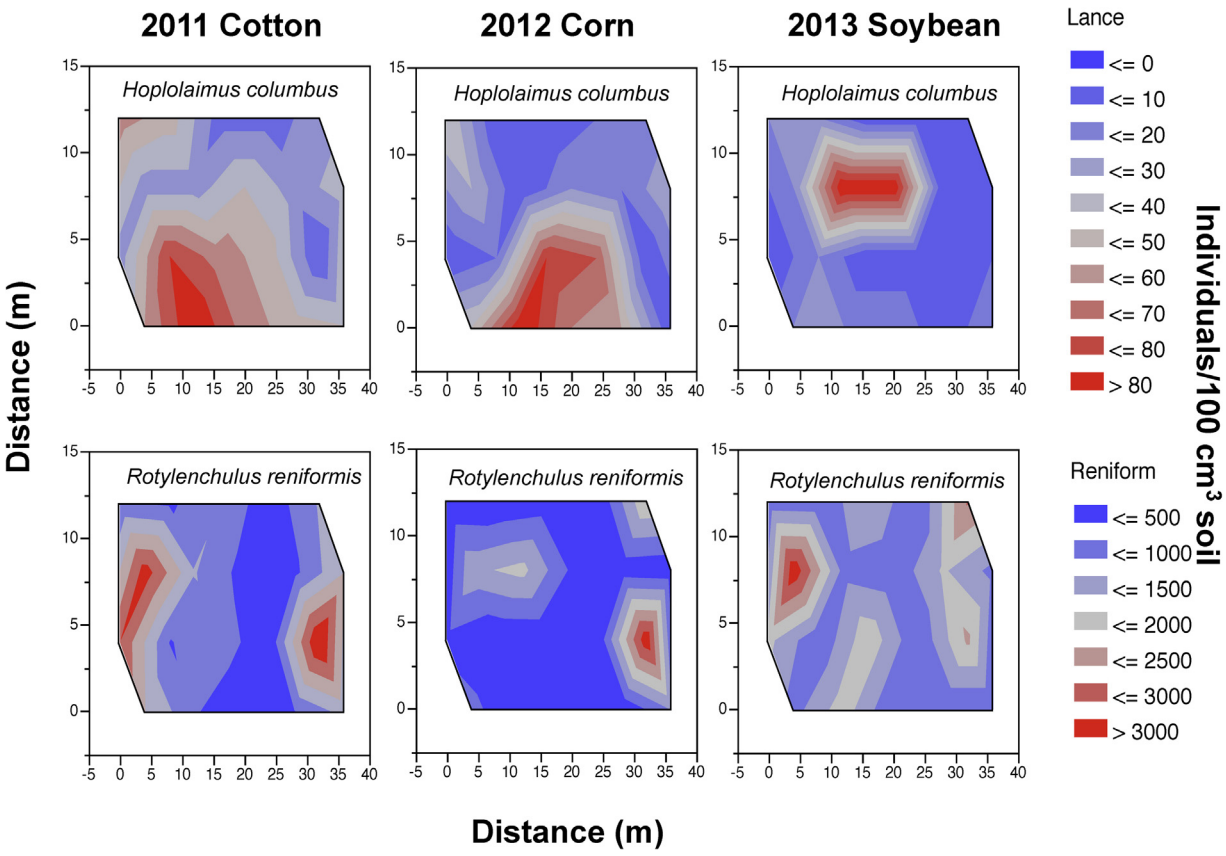

Fig. 4. Contour plots showing densities of Columbia lance nematode (CLN) *Hoplolaimus columbus* and reniform nematode (RN) *Rotylenchulus reniformis* (±SE) per 100 cm^3 soil in plot 2, for the three hosts (cotton 2011, corn 2012 and soybean 2013) at harvest.

3.3. Spatial distribution patterns and associations

An aggregated pattern of CLN densities was observed for all plots at all sampling dates (Table 2), with the lower DI value (6.86, $P < 0.0001$) for cotton at harvest in plot 1 (2011) and the higher value (108.70, $P < 0.0001$) for corn at harvest in plot 3 (2012). However, significant Moran's indices were only detected at harvest and neighborhood structure was not detected at planting for any of the plots during the three years (Fig. 5). Plot 3 was the only one that showed statistically significant Moran's *I* values for the three hosts at harvest at short distance classes (5 m) and at long lag distances (>26 m) when cotton and soybean were the host plants. For the other plots, significant structure was only detected at a single sampling date, in plot 1 at short (5 m) and long distances (26 m) at corn harvest in 2012, for plot 2 at short distance classes (5 m and 8 m) when cotton was the crop in 2011.

However, SADIE indices of aggregation (Table 3), detected densities of CLN significantly aggregated only at harvest. The value for I_a was significant for plot 1 in 2012 with corn ($P = 0.021$) and in 2013 with soybean ($P = 0.012$). In plot 3, significant aggregation was detected in 2011 ($P < 0.001$) with cotton and 2013 ($P = 0.032$) with soybean.

The NMDS results did not indicate differences in the distribution of CLN in relation to crop and date of sampling, suggesting that the crop does not influence the distribution pattern of CLN (Supplementary Fig. 1). However, for the relationship between CLN and RN two distinct clusters were generated, one for each

Table 3
Spatial Analysis by Distance Indices (SADIE)[a] indices of aggregation (I_a) for *Hoplolaimus columbus*, Columbia lance nematode (CLN) in each of the plots and sampling dates where the nematode was detected.

Plot	Cotton 2011				Corn 2012		Soybean 2013			
	Plant		Harvest		Harvest		Plant		Harvest	
	I_a	P_a	I_a	P_a	I_a	P_a	I_a	P_a	I_a	P_a
1	–	–	1.106	0.244	1.636	0.021	0.869	0.652	1.744	0.012
2	–	–	1.239	0.147	0.989	0.397	0.787	0.848	0.928	0.525
3	1.09	0.293	1.956	0.001	1.319	0.103	–	–	1.474	0.0315
4	–	–	–	–	–	–	–	–	–	–

[a] SADIE characterizes the spatial structure of georeferenced counts and tests for the significance of the spatial pattern by using indices of clustering, with high counts categorized as clusters and low counts as gaps (Perry, 1995). The index of aggregation (I_a) is calculated as: $I_a = D/E_a$, where D is the minimum distance that densities would need to produce a uniform spatial arrangement, and E_a, the expected distance to regularity (E_a), is the result of randomizing sampling counts among sampling locations. A value of $I_a > 1.0$ indicates an aggregated distribution of counts and $I_a < 1.0$ indicates regular distribution. The significance of I_a was assessed by a randomization method using the default parameters of SADIE v. 2.0. The null hypothesis is rejected at $P_a < 0.025$ (aggregation) and accepted at $P_a > 0.975$ (uniformity) (Perry, 1998).

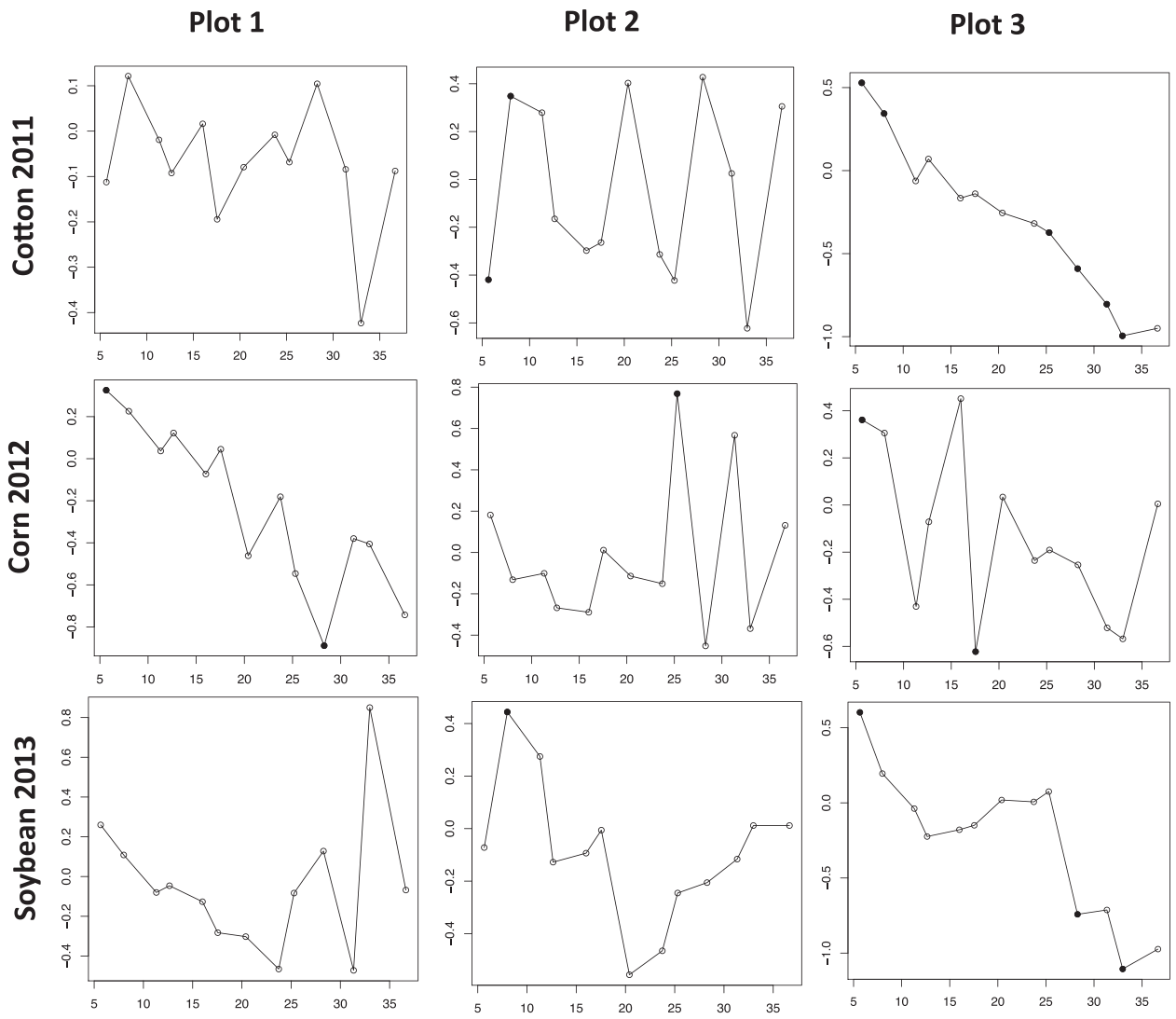

Fig. 5. Moran's *I* correlograms for plots 1, 2 and 3 for the three hosts (cotton 2011, corn 2012 and soybean 2013) at harvest. Solid black circles indicate significant correlation at 0.05 level of significance.

nematode species (Supplementary Fig. 2). Vectors showed that the separation between the two species is caused by soil particle size distribution, indicating that CLN strongly correlates with % sand. The analysis of spatial association between CLN and RN using the SADIE association index (X) for plots and dates where the two nematodes occurred also showed negative associations between the nematodes for all the sampling dates (Table 4).

Table 4
Spatial analysis SADIE spatial association index for Columbia lance and reniform nematodes in each of the plots and sampling dates where the nematodes were detected together. The spatial association statistic (X) indicates association ($X > 0$) or dissociation ($X < 0$).

Plot	Cotton 2011		Corn 2012	Soybean 2013	
	Plant	Harvest	Harvest	Plant	Harvest
1	–	–	–	–	–
2	–	−0.1891	−0.4143	−0.3025	−0.2392
3	−0.1123	−0.0328	−0.2318	–	−0.0013
4	–	–	−0.0724	–	–

3.4. Vertical distribution

For the sections of the vertical cores (Table 5), the highest sand content was found in the 15–30 cm deep layer (86.87% in plot 1 and 87.31% in plot 2), and the lowest sand content was found below 60 cm (78.82% in plot 1 and 64.01% in plot 2). Silt content for both plots was higher below 60 cm (12.22% in plot 1 and 24.78% plot 2) and changed proportionally with soil depth.

In plot 1, CLN individuals were detected in the four layers, but densities were significantly higher ($P = 0.0178$) at 0–15 cm depth and decreased consistently with soil depth (Fig. 6). A mean of 55.71 CLN/100 cm^3 soil, 27.5 CLN/100 cm^3 soil, 20 CLN/100 cm^3 soil and 15 CLN/100 cm^3 soil was recovered at 0–15 cm, 15–30 cm, 30–60 cm and below 60 cm depths, respectively, when only samples containing CLN individuals were considered. In plot 2, densities of CLN were lower than in plot 1 and the nematode was only observed at 0–15 cm and 15–30 cm depths with no significant differences between these two layers ($P = 0.1276$) (Fig. 6). When only samples with CLN were analyzed, the mean for the top layer (0–15 cm) was 20 ± 10 CLN/100 cm^3 soil and for the second layer (15–30 cm) was 16.67 ± 6.67 CLN/100 cm^3.

Table 5
Soil particle size distribution (percentage content of sand, silt, clay) determined by the Bouyoucos method for vertical core samples in plots 1 and 2.

Depth (cm)	% Clay		% Silt		% Sand	
	Plot 1 $X \pm$ SE	Plot 2 $X \pm$ SE	Plot 1 $X \pm$ SE	Plot 2 $X \pm$ SE	Plot 1 $X \pm$ SE	Plot 2 $X \pm$ SE
0–15	7.18 ± 0.4	13.71 ± 0.9	12.65 ± 0.4	20.11 ± 1.7	80.13 ± 0.5	66.17 ± 1.8
	6.2–8.2	10.1–16.3	11.18–14.1	13.8–25.9	77.9–81.9	10.1–16.3
15–30	5.81 ± 1.3	5.01 ± 1.19	7.31 ± 1.6	7.67 ± 1.56	86.87 ± 2.3	87.31 ± 2.3
	2.38–11.54	1.85–12.5	1.67–13.79	2.86–13.79	76.92–95.24	75–93.75
30–60	6.7 ± 1.0	18.93 ± 11.8	10.55 ± 2.8	13.25 ± 2.6	82.75 ± 3.0	67.82 ± 3.9
	3.03–10	3.22–42.3	1.85–23.33	0–20.83	66.67–91.30	0–90.32
>60	8.95 ± 1.3	11.20 ± 2.8	12.22 ± 1.9	24.78 ± 4.1	78.58 ± 1.9	64.01 ± 3.8
	3.57–13.63	2.13–24.32	3.70–23.81	2.78–37.5	69.04–85.71	52.5–82.98

4. Discussion

An aggregated distribution results in high sample variance, so understanding the spatial distribution of plant-parasitic nematodes is essential to accurately measuring population densities (Noe and Campbell, 1985). For CLN, previous studies indicate that densities of this nematode are strongly correlated with sand content (Khalilian et al., 2001) and that the distribution of CLN within a field is typically influenced by sand content (Koenning et al., 2004; Mueller et al., 2010). This study analyzed the distribution pattern of CLN in areas within a field with different levels of sand content and in the presence of RN. Population densities of CLN were aggregated for all plots at all sampling dates, as suggested by the high variance of the counts. The crop did not affect the pattern of CLN spatial distribution, but significant neighborhood structure was only detected at harvest. For nematodes with migratory feeding habits such as CLN, the pattern of distribution is usually less aggregated than for sedentary nematodes because of the movement of the nematodes to find new feeding sites and places to deposit individual eggs (Ferris et al., 1990), which could explain the lack of spatial autocorrelation observed at planting. However, this pattern changed at harvest, likely because the root system was fully grown and concentration of the food source is a determinant factor for the distribution of organisms (Ferris et al., 1990; Belinchón et al., 2011). Thus, for plant-parasitic nematodes, the arrangement and morphology of the host plant root influences the pattern of distribution, causing aggregation (Ferris et al., 1990).

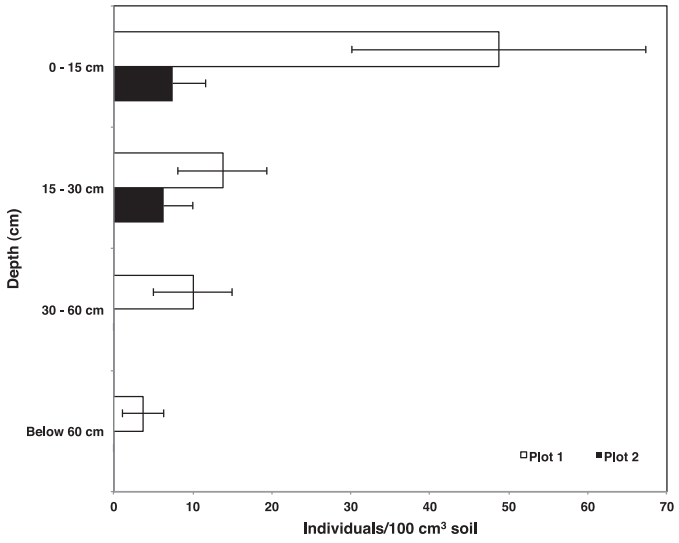

Fig. 6. Columbia lance nematode densities (individuals/100 cm^3 of soil) by depth (±SE) after soybean harvest (2013) in plots 1 and 2. White letters indicate statistical comparisons within plot 2; black letters indicate statistical comparisons within plot 1 (Tukey's means comparison test, $P < 0.001$).

The significant aggregation detected at harvest was not consistent across plots. Additionally, plots 2 and 4 had similar soil texture, but densities of CLN varied between them. These facts suggest that other factors may have influenced the abundance and spatial distribution of CLN. Water content, for instance, has been shown to be an important factor affecting the distribution of nematodes and other soil dwelling fauna (Herring et al., 2010; Davis et al., 2013; Moore and Lawrence, 2013; Petersen et al., 2013). Plot 4 was poorly drained and stayed wet most of the time during growing seasons. Other factors that may affect the distribution of CLN in the field, and that may weigh differently in individual fields, include: initial introduction of nematodes to the field and subsequent dissemination pattern, field crop history, and other edaphic factors such as soil bulk density and soil nutrient status. For example, Lewis and Smith (1976) found that populations of CLN in cotton and soybean samples increased with higher pH and phosphorous and declined as potassium and magnesium increased. During a 4-year study, Khalilian et al. (2002) reported that CLN densities were significantly decreased when organic matter (compost) was added to experimental plots.

In this study, distances between sampling points of (4 m × 4 m) were enough to detect the aggregative pattern of CLN. Future work could consider larger sampling plots to test the pattern of distribution of CLN in field crops. Additionally, more experimental units would allow the implementation of other geostatistical approaches such as semivariograms and kriging interpolations, which require larger sampling size (>30) (Journel and Huijbregts, 1978; Rossi et al., 1992; Webster and Oliver, 2001) and could provide more detailed information to be used in site-specific management.

For vertical cores, densities of CLN were significantly higher in the top layer and decreased consistently with soil depth. Other large plant-parasitic nematodes, such as *Belonolaimus longicaudatus*, have shown higher densities in the top 30 cm layer and migration through the soil profile varies depending on sand content (Brodie, 1976). For this study, it was important to confirm that the highest densities of CLN were found in the layer that is typically sampled for routine nematode assays.

The main driver of dissociation between RN and CLN distribution appears to be soil texture. It was hypothesized that, to a considerable extent, the competition observed by other researchers between RKN and CLN on cotton is probably driven by the fact that both species share the same soil texture associations. An important consideration for ecological studies or when choosing management tactics is the life strategy of the nematode. Our population dynamics data support CLN behaving as a *K* strategist and RN as an *r* strategist. In general terms, *K* species are expected to occur in relatively low and more uniform population densities and *r* species display traits that favor rapid population growth (MacArthur and Wilson, 1967).

5. Conclusion

Based on our results, we predict that any given cotton soil sample is not likely to have both species of nematodes at levels above threshold. Depending on the sand content, whenever there are concomitant infestations of CLN and RN in a field, only one species is likely to be the key pest. Cases in which both species are above threshold will probably only occur in samples with sand content around 60–65%, similar to our plots 2 and 4. Cotton fields with very diverse soil types could have CLN as the key pest in one part of the field and RN in another. Our results contribute to the knowledge of CLN population dynamics, ecological characteristics, and associations with RN in naturally infested fields. This knowledge may improve the effectiveness of management practices in cotton, especially the site-specific application of nematicides and the use of crop rotations.

Acknowledgements

Research was supported by Cotton Incorporated, Project No. 14-506SC and the United States Department of Agriculture USDA-NIFA, Contract Number: 2010–51101-21785.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.apsoil.2015.06.004

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