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Diversity and Occurrence of Plant-parasitic Nematodes Associated with Golf Course Turfgrasses in North and South Carolina, USA

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Abstract: One hundred and eleven golf courses from 39 counties in the Carolinas were surveyed for plant-parasitic nematodes. Species diversity within habitats was analyzed with five diversity indices including Diversity index (*H'*), Evenness (*J'*), Richness (*SR*), Dominance (λ) and Diversity (H_2). The results revealed a remarkably high diversity of 24 nematode species belonging to 19 genera and 11 families. Of those, 23 species were found in SC, 19 species in NC, and 18 species were detected in both states. *Helicotylenchus dihystera, Mesocriconema xenoplax, Hoplolaimus galeatus, Tylenchorhynchus claytoni, Belonolaimus longicaudatus, Meloidogyne graminis* and *Paratrichodorus minor* were the most prevalent and abundant species in golf course turfgrasses in both states. Twelve species were new records of plant parasitic nematodes in turfgrasses in both NC and SC. The results also revealed effects of different habitats on diversity of nematode species in turfgrass ecosystem. *H'* and *SR* values were higher in SC than in NC. *H', J'* and H_2 values were significantly higher in sandy than in clay soil in NC, but no significant differences between sand and clay soil were detected in SC or in pooled data from both states. There were no significant differences for all indices among the management zones (putting green, fairway and tee) in NC. However, in SC and pooled data, *H', SR* and H_2 were significantly higher in putting greens than in fairways and tees. Significant differences from different grass species (bermudagrass, creeping bentgrass and zoysiagrass) were detected only in *H'*, which was significantly higher in zoysiagrass than in bentgrass or bermudagrass in NC. In pooled data, *H'* was significantly higher in zoysiagrass samples than in creeping bentgrass samples but was not significantly different from bermudagrass samples.

Key words: North Carolina, South Carolina, detection, distribution, diversity, ecology, golf course, identification, plant-parasitic nematode, turfgrass.

Turfgrasses are among the most widely planted ornamental plants in the world, serving important functions in soil stabilization and providing safe surfaces for recreational activities. In the United States, there are currently over 19,000 golf courses (http://www.thegolfcourses.net), including 451 in South Carolina (SC) (http://www.mapsofworld.com/usa/states/south-carolina/south-carolina-golf-courses.html) and 644 in North Carolina (NC) (http://www.mapsofworld.com/usa/states/north-carolina/north-carolina-golfcourses.html). However, maintenance of golf courses is becoming more challenging due to economic pressures and changes in the availability of pesticides. Of all turfgrass pests, nematodes are probably the least understood and most often overlooked. Due to lack of understanding of the nematodes associated with turfgrasses and their impact on turfgrass health, it is very difficult to accurately diagnose nematode problems. More research is needed in this area so that nematode problems can be effectively diagnosed and managed in turfgrass systems.

Over the past 40 years, numerous research papers have been published on plant-parasitic nematodes associated with turfgrass worldwide, including the US (Sikora et al., 2001; Lucas et al., 1974; Crow and Walker, 2003; Hixson et al., 2004; Karssen et al., 2004; Crow, 2005; Mitkowski, 2007), Canada (Yu et al., 1998; Mitkowski and Jackson, 2003; Bélair et al., 2006; Simard et al., 2008, 2009), Argentina (Echeverría and Chaves, 1998), Germany, Sweden and Norway (Magnusson and Hammeraas, 1997; Knuth, 1998), Belgium (Viaene et al., 2007; Vandenbossche et al., 2011), and Israel (Oka et al. 2004).

In the United States, 38 species in 23 genera of plant-parasitic nematodes associated with turfgrasses have been recorded so far. Despite the importance of turfgrasses and the prevalence of nematode problems in NC and SC turfgrasses, little research has been carried out on the nematodes in this region. In SC, species from genera of *Mesocriconema, Helicotylenchus, Trichodorus, Meloidogyne, Hoplolaimus* and *Belonolaimus* are known to be problematic in warm and cool season turfgrasses (http://www.clemson.edu/extension/horticulture/turf/pest_guidelines/2011_pest_guidelines/nematodes_2011.pdf). Lucas et al. (1974) showed that *Mesocriconema ornata, Helicotylenchus dihystera, Trichodorus christiei, Meloidogyne* sp., *Tylenchorhynchus claytoni, Hoplolaimus galeatus* and *B. longicaudatus* were the common plant-parasitic nematodes; and *Pratylenchus zeae, Xiphinema americanum* and *Paratylenchus* sp. were occasionally found in soil samples from golf greens in NC. Little detailed, systematic and updated information about the species, occurrence, population levels and distribution of turf nematodes in NC and SC has been presented since this initial work in 1974.

In recent years, diversity indices have become common tools for describing the diversity and distribution of plant-parasitic nematodes. Useful indices include Shannon diversity index (*H'*), Evenness (*J'*), Richness (*SR*), Dominance (λ) and Diversity (H_2). In conjunction with proper sampling strategies, these indices can be used to make inferences on the influence of soil type, host species composition, or other factors on

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nematode populations. A study on diversity and distribution of nematode communities in grassland from Romania, and a survey of plant-parasitic nematodes in natural and semi-natural mountain grassland in southern Spain were undertaken (Popvici and Ciobanu, 2000; Talavera and Navas, 2002). The related results revealed that index *H'* did not differ significantly between the different types of grasslands (Popvici and Ciobanu, 2000), and there were no significant differences between mountainous areas (Talavera and Navas, 2002). However, our knowledge of the diversity of nematodes associated with golf grasses is very scarce compared with agricultural crops.

The purpose of this study was to determine species diversity, incidence and distribution of plant-parasitic nematodes associated with golf course turfgrasses in NC and SC to determine how grass species, soil type, and management zone influence the distribution of plant-parasitic nematodes.

Material and Methods

Soil sampling: A total of 282 soil samples were collected from 111 golf courses in 39 counties of NC and SC during the summer of 2011 (Fig. 1). Sampling locations were selected to represent the different grass species [hybrid bermudagrass (*Cynodon dactylon* × *C. transvaalensis*), creeping bentgrass (*Agrostis stolonifera*) and zoysiagrass (*Zoysia matrella* and *Zoysia japonica*)], soil textures (sandy and clay which did not include sandy clay and clay loam, etc.) and management zones (putting greens, fairways, and tees). Preference was given to locations that had previously experienced or reported problems with plant-parasitic nematodes, but some exploratory sampling was also done in areas where no nematode problems had been previously reported. Each sample consisted of 12 soil cores (1.5 cm diam. × 20 cm deep) sampled at roughly equal intervals in a zig-zag pattern across an area of 1000 m^2 or less. Soil samples were placed in sealed plastic bags, which were then placed in sample boxes and stored at 4°C before analysis to minimize changes in nematode populations.

Nematode extraction: Nematodes were extracted from soil samples by a combination of elutriation (Byrd et al., 1976) and centrifugation (Jenkins, 1964) methods. A 500-cm^3 subsample was taken from each composite and assayed for enumeration and identification of plant-parasitic nematodes. These tests were carried out by the Nematode Assay Section of the NCDA&CS Agronomic Division.

Nematode identification and counting: Nematodes were identified and counted under the inverted microscope. For further species identification, nematodes were picked, killed by heating (70°C), then fixed in FG solution (1 ml glycerol, 10ml formalin, and 80ml distilled water). Specimens were dehydrated slowly into 100% glycerol and mounted on slides (Southey, 1970). Measurements were performed with the aid of a drawing tube using a LEICA DM 2500 microscope and a stage micrometer. Morphometric data were collected and analyzed using Excel software as described by Ye (1996). In addition to morphological identification, most of the species were characterized by sequencing of the near full-length small subunit (SSU) and internal transcribed spacer region subunit 1 (ITS1) of the rDNA locus in a separate study.

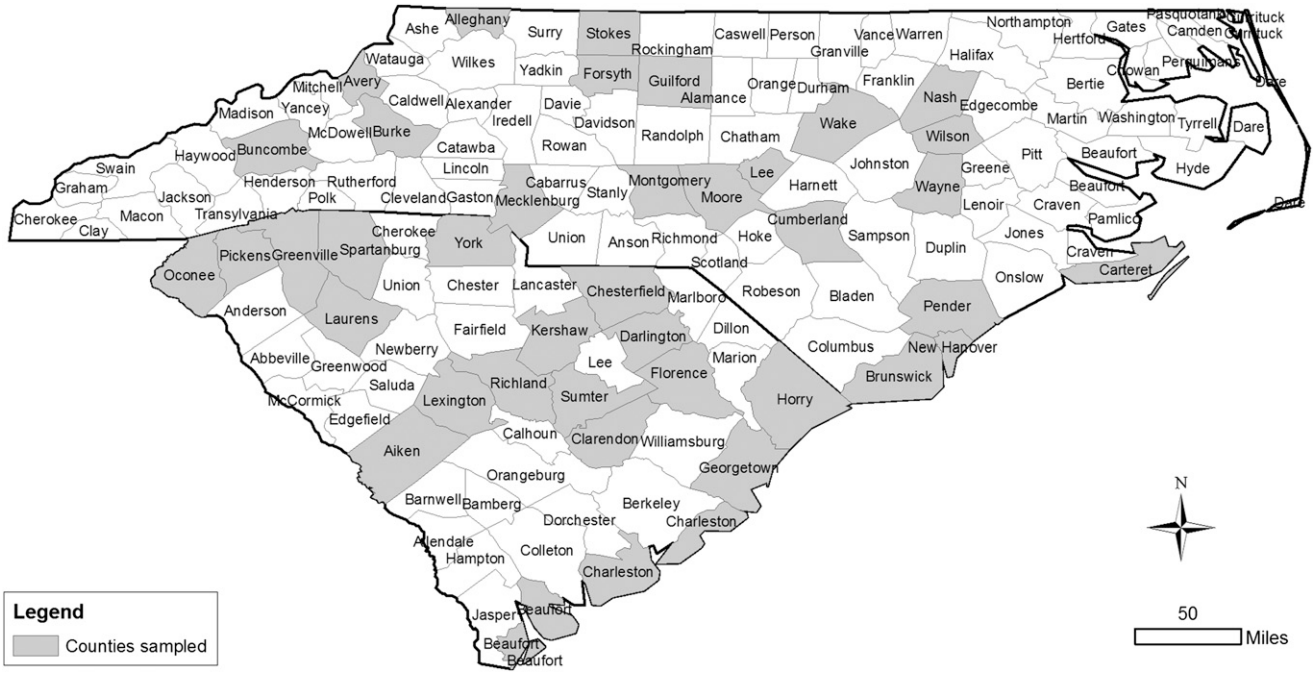

Fig. 1. Map of North Carolina and South Carolina showing 39 sampled counties (shaded).

Data analysis: Nematode diversity and incidence were assessed by calculating prevalence, mean intensity, and maximum density (Boag, 1993). *Prevalence* was defined as the number of samples having a particular nematode species divided by the number of samples examined, expressed as a percentage. *Relative abundance* was calculated as the total number of individuals of a particular nematode species per 500 cm^3 soil in all the samples divided by the number of samples including those with zero counts for that species. *Mean intensity* was defined as the number of individuals of a particular nematode species per 500 cm^3 soil in the positive samples divided by the number of positive samples, and *maximum density* was determined as the maximum number of individuals of a particular nematode species per 500 cm^3 soil recovered from a sample. Several diversity indices were also calculated according to Yeates and Bird (1994):

$$\text{Shannon-Weaver diversity } H' = -\sum_{i=1}^{s} p_i \ln p_i$$

Richness $SR = (s\text{-}1)\ ln\ N$
Evenness $J' = H'/H'max$
Simpson's dominance $\lambda = \Sigma\ p_i^2$

$$\text{Diversity } H_2 = -\ln \lambda$$

Where s = number of taxa (species) in the sample; N = total number of nematodes identified in the sample; p_i = proportion of individuals of taxa i in the total population; $H'max = ln\ s$.

Differences in the diversity indices among various factors (grass species, management zone, and soil type) were analyzed by Duncan's multiple range test ($p < 0.05$) in SAS 9.2 (SAS Institute, Cary, NC, USA).

Results

Survey: Twenty-four species of plant-parasitic nematodes in 19 genera of 11 families were identified from the 282 soil samples collected from 111 golf courses in 39 counties in NC and SC. Detailed nematode morphological identification and a new species description were published in earlier papers (Zeng et al., 2012a, b). Among those nematodes, 23 species were found in SC, 19 in NC, and 18 species in both states (Tables 1-2). The following species are new records of plant-parasitic nematodes associated with turfgrasses: 12 species (*Cactodera* sp., *Dolichodorus heterocephalus, Hemicaloosia graminis, Hemicriconemoides wessoni, Hemicycliophora conida, Heterodera* sp., *Longidorus paralongicaudatus, Loofia thienemanni, Ogma floridense, Paratrichodorus allius, Pratylenchus penetrans, Xiphinema bakeri*) in both NC and SC; 12 species (*Cactodera* sp., *Dolichodorus heterocephalus, Hemicaloosia graminis, Heterodera* sp., *Hemicycliophora conida, Longidorus paralongicaudatus, Loofia thienemanni, Ogma floridense, Paratrichodorus allius, Pratylenchus penetrans, Scutellonema brachyurum and Tylenchorhynchus claytoni*) in SC; and 10 species (*Hemicaloosia graminis, Hemicriconemoides wessoni, Hemicycliophora conida, Mesocriconema xenoplax, M. curvatum, M. sphaerocephala, Ogma floridense, Paratrichodorus allius, Pratylenchus penetrans* and *Xiphinema bakeri*) in NC.

Data concerning prevalence, relative abundance, mean intensity, and maximum density of nematodes are presented in Table 1. The most prevalent nematodes on golf courses in both states were *Mesocriconema xenoplax* (69.9%), *Helicotylenchus dihystera* (60.3%), *Belonolaimus longicaudatus* (46.5%), *Paratrichodorus minor* (42.9%), *Meloidogyne graminis* (36.9%), *Hoplolaimus galeatus* (35.1%), and *Tylenchorhynchus claytoni* (25.2%). These seven species were also most prevalent on golf course putting greens, but in a different order of occurrance: *Mesocriconema xenoplax* (70.8%), *Helicotylenchus dihystera* (43.8%), *B. longicaudatus* (40.6%), *Hoplolaimus galeatus* (33.3%), *P. minor* (33.3%), *T. claytoni* (28.1%), and *Meloidogyne graminis* (27.1%) (Table 1).

The most abundant species were *Helicotylenchus dihystera* (196 per 500 cm^3 of soil), *Mesocriconema xenoplax* (168), *B. longicaudatus* (85), *Hoplolaimus galeatus* (59), *T. claytoni* (56), *Meloidogyne graminis* (40), *M. naasi* (24), and *P. minor* (22) (Table1).

Other species found occasionally at high densities were *Mesocriconema curvatum* (maximum density 1235 in NC), *Hemicycliophora conida* (1200 in SC; 510 in NC), *Xiphinema americanum* (673 in SC), *Pratylenchus penetrans* (420 in SC), *Hemicriconemoides wessoni* (350 in SC), *Mesocriconema sphaerocephala* (340 in SC), and *Paratrichodorus allius* (328 in SC; 500 in NC) (Table 1).

The species with the highest mean intensities and maximum densities were *B. longicaudatus* (173 and 1200 in SC respectively; 211 and 1040 in NC), *Helicotylenchus dihystera* (173 and 1200 in SC; 211 and 1040 in NC), *Hoplolaimus galeatus* (137 and 850 in SC; 230 and 1472 in NC), *Mesocriconema xenoplax* (225 and 8200 in SC; 274 and 2720 in NC), *T. claytoni* (149 and 840 in SC; 318 and 3112 in NC), *Meloidogyne naasi* (283 and 1160 in SC), and *Hemicycliophora conida* (252 and 1200 in SC; 127 and 510 in NC) (Table 1).

The total numbers of nematode species recovered were greater in SC (23 species) than in NC (19). In addition, the numbers of species exceeding 10% prevalence (11 in SC *vs* 9 in NC), relative abundance exceeding 30 nematodes per 500 cm^3 of soil (7 *vs* 5), mean densities exceeding 100 individuals (15 *vs* 9) and maximum densities exceeding 500 individuals (11 *vs* 9) were all greater in SC than in NC (Table 1).

Occurrence, frequency and total numbers of plant-parasitic nematodes among different grass species, management zones, and soil types are presented in Table 2. The numbers of species recovered in bermudagrass were greater than in creeping bentgrass and zoysiagrass in both states. In bermudagrass, a greater number of species occurred in SC than in NC (21 species and 15, respectively); and *B. longicaudatus, P. minor, Meloidogyne graminis,*

TABLE 1. Frequency of occurrence and population density of plant-parasitic nematodes from golf courses in North and South Carolina.

	Prevalence (%)			Abundance (numbers per 500 cm^3soil)			Nematodes (numbers per 500 cm^3soil)				Golf courses with nematodes (%)		Total golf courses with nematodes (%)	Greens with nematodes (%)		Total greens with nematodes (%)
							SC		NC							
Nematode species	SC	NC	SC+NC	SC	NC	SC+NC	Mean	Max	Mean	Max.	SC	NC	NC+SC	SC	NC	NC+SC
Belonolaimus longicaudatus	49.7	41.0	46.5	85.5	82.7	84.5	172.9	1200	210.5	1040	39.1	20.9	60	50.00	36.36	40.63
Hoplolaimus galeatus	37.9	30.5	35.1	51.7	69.9	58.5	136.5	850	229.3	1472	34.5	20.0	54.5	33.33	33.33	33.33
Helicotylenchus dihystera	55.9	67.6	60.3	102.5	352.6	195.7	183.3	1720	551.3	8313	52.7	40.0	92.7	60.00	36.36	43.75
Scutellonema brachyurum	0.6		0.4	3.3		2.1	78.2	100			0.9		0.9		1.52	1.04
Meloidogyne graminis	43.5	25.7	36.9	47.9	25.7	39.6	112.2	570	95.2	360	38.2	17.3	55.5	6.67	36.36	27.08
Meloidogyne naasi	12.4	5.7	9.9	35.1	4.8	23.8	283.0	1160	83.8	250	9.1	3.6	12.7	3.33	16.67	12.50
Heterodera sp.	1.9		0.7	1.5		1.0	135	180			0.9		0.9			
Cactodera sp.	1.1	1.0	1.1	2.2	0.2	1.5	195	270	20	20	2.7	0.9	3.6			
Tylenchorhynchus claytoni	22.6	29.5	25.2	33.6	93.8	56.0	148.7	840	317.6	3112	26.4	21.8	48.2	50.00	18.18	28.13
Pratylenchus penetrans	14.1	10.5	12.8	7.9	3.9	6.4	56.0	420	37.0	140	17.3	10.0	27.3	6.67	4.55	5.21
Hemicycliophora conida	2.8	7.6	4.6	7.1	9.6	8.1	252.4	1200	126.6	510	3.6	7.3	10.9		3.03	2.08
Loofia thienemanni	1.7		1.1	3.3		2.1	172.5	220			1.8		1.8			
Hemicaloosia graminis	1.1	1.0	1.1	1.6	0.8	1.3	145.0	240	80	80	1.8	0.9	2.7			
Hemicriconemoides wessoni	19.8	14.3	17.7	12.2	7.5	10.5	61.8	350	55.4	230	21.8	11.8	33.6		10.61	7.29
Mesocriconema xenoplax	75.7	60.0	69.9	171.1	161.8	167.6	225.2	8200	274.0	2720	52.7	31.8	84.5	53.33	78.79	70.83
Mesocriconema curvatum	0.6	7.6	3.2	1.8	14.2	6.4	310	310	212.6	1235	0.9	3.6	4.5	6.67	1.52	3.13
Mesocriconema sphaerocephala	1.7	1.9	1.8	2.8	0.7	2.0	166.7	340	35	60	0.9	0.9	1.8		1.52	1.04
Ogma floridense	1.0	1.0	0.7	0.3	0.3	0.3	60	60	30	30	0.9	0.9	1.8			
Paratrichodorus allius	7.9	1.9	5.7	7.1	5.7	6.6	96.2	328	300	500	7.3	1.8	9.1	6.67	3.03	4.17
Paratrichodorus minor	49.7	31.4	42.9	26.1	14.5	21.8	52.0	520	46.1	305	42.7	21.8	64.5	40.00	30.30	33.33
Xiphinema americanum	13.0	6.7	10.6	7.2	1.6	5.2	54.4	673	24.6	62	15.5	5.4	20.9		1.52	1.04
Xiphinema bakeri		1.0	0.4		0.1	0.04			12	12		0.9	0.9			
Longidorus paralongicaudatus	0.6		0.4	0.1		0.07	20	20			0.9		0.9			
Dolichodorus heterocephalus	0.6		0.4	0.06		0.04	10	10			0.9		0.9			

TABLE 2. Prevalence of plant-parasitic nematodes in different habitats of golf courses in North and South Carolina.

	Prevalence (%)															
	SC								NC							
Nematode species	Bermudagrass	Bentgrass	Zoysiagrass	Green	Fairway	Tee	Sand	Clay	Bermudagrass	Bentgrass	Zoysiagrass	Green	Fairway	Tee	Sand	Clay
Belonolaimus longicaudatus	56.4	10.5	50.0	50.00	49.0	52.6	56.4		50.0	40.0	100.0	36.36	45.0	50.0	51.3	
Hoplolaimus galeatus	42.0	20.8		33.33	37.3	43.9	44.8		16.7	33.3	50.0	33.33	10.0	25.0	32.3	
Helicotylenchus dihystera	58.1	67.6		60.00	82.4	61.4	58.8	100.0	54.2	70.0	75.0	36.36	50.0	62.5	64.6	50.0
Scutellonema brachyurum	4.2											1.52			1.9	
Meloidogyne graminis	50.4		100.0	6.67	54.9	45.6	47.6	80.0	58.3	13.3	50.0	36.36	55.0	62.5	34.2	50.0
Meloidogyne naasi	11.9	15.6		3.33	17.6	12.3	9.8	20.0	8.3	10.0	25.0	16.67	15.0	12.5	7.6	50.0
Heterodera sp.	1.4					1.8	1.4									
Cactodera sp.	1.4				3.9		1.4	20.0			25.0			12.5	1.9	
Tylenchorhynchus claytoni	18.2	62.4	25.0	50.00	35.3	15.8	21.7	80.0	12.5	53.3		18.18	15.0		32.3	25.0
Pratylenchus penetrans	14.0	10.5		6.67	21.6	17.5	13.3	60.0	25.0	6.7		4.55	25.0	12.5	9.5	50.0
Hemicycliophora conida	3.5				2.0	1.8	2.1			3.3		3.03		12.5	1.9	
Loofia thienemanni	1.4		25.0		2.0	1.8	2.1									
Hemicaloosia graminis	0.7		25.0			1.8	1.4									
Hemicriconemoides wessoni	21.7				21.6	26.3	20.9		8.3			10.61	5.0	12.5	3.8	
Mesocriconema xenoplax	78.6	73.6	100.0	53.33	74.5	77.2	80.5	80.0	45.8	70.0	50.0	78.79	45.0	50.0	57.0	25.0
Mesocriconema curvatum		5.2		6.67			0.7		20.8	3.3	25.0	1.52	20.0	12.5	9.5	25.0
Mesocriconema sphaerocephala	2.1				2.0	1.8	2.1		4.2		25.0	1.52	5.0	12.5	3.8	
Ogma floridense	0.7				2.0		0.7		4.2					12.5	1.9	
Paratrichodorus allius	8.4	5.2		6.67	9.8	12.3	4.2	20.0		3.3		3.03			1.9	
Paratrichodorus minor	49.0	62.4	100.0	40.00	52.9	66.7	56.0	40.0	29.2	40.0	75.0	30.30	30.0	37.5	43.7	
Xiphinema americanum	15.4				29.4	12.3	14.0		4.2			1.52	10.0		1.9	25.0
Xiphinema bakeri									4.2				5.0		1.9	
Longidorus paralongicaudatus		5.2				1.8										
Dolichodorus heterocephalus	0.7					1.8	0.7									
Total number of species	21	10	7	11	16	19	21	9	15	12	10	16	14	14	19	8

Mesocriconema xenoplax, *Helicotylenchus dihystera,* and *Hoplolaimus galeatus* were most prevalent species in SC. A similar species profile was observed in bermudagrass in NC, except that prevalence of *H. galeatus* was relatively low. In zoysiagrass, the number of nematode species identified was greater in NC (10 species) than in SC (7 species). *B. longicaudatus*, *P. minor*, *Meloidogyne graminis* and *Mesocriconema xenoplax* were the most prevalent species in SC; these species plus *Helicotylenchus dihystera* and *Hoplolaimus galeatus* were most prevalent in NC. In creeping bentgrass, in addition to *B. longicaudatus, H. dihystera, M. xenoplax* and *P. minor, T. claytoni* was most prevalent in NC. A similar profile was observed, except that *B. longicaudatus* was less prevalent in SC (Table 2).

In putting greens, the number of nematode species identified were greater in NC (16 species) than in SC (11), lower in golf course tees in NC (14) than in SC (19), but similar in fairways across both states (16 in SC, 14 in NC).*B. longicaudatus*, *P. minor*, *Mesocriconema xenoplax*, *Helicotylenchus dihystera* were prevalent species in all management zones in NC and SC. *H. galeatus* was prevalent in all management zones in SC but only in putting greens in NC. *Meloidogyne graminis* was dominant in all management zones in NC but only in fairways and tees in SC. *T. claytoni* was prevalent only in SC putting greens and fairways (Table 2).

The total number of nematode species identified in sandy soil was greater than in clay soil in both states. However, there was no clear difference between NC and SC in the number of species identified in different soil types. In sandy soils, *B. longicaudatus*, *P. minor*, *Mesocriconema xenoplax*, *H. dihystera, H. galeatus*, *Meloidogyne graminis* and *T. claytoni* were prevalent in both states. In clay soils, *H. dihystera, M. graminis* and *P. penetrans* were prevalent species in both states, but *T. claytoni, M. xenoplax* and *P. minor* were prevalent only in SC, and *M. nassi* was only in NC (Table 2).

Distribution: The distribution of nematodes on golf courses in NC and SC is shown in Table 3. The most widespread species over the two states were *P. minor* (19 counties in SC; 16 in NC), *Meloidogyne graminis* (18 in SC; 12 in NC), *Mesocriconema xenoplax* (19 in SC; 13 in NC), *H. dihystera* (18 in SC; 18 in NC), *T. claytoni* (14 in SC; 12 in NC), *B. longicaudatus* (11 in SC; 10 in NC), *H. galeatus* (13 in SC; 11 in NC) and *P. penetrans* (15 in SC; 9 in NC) (Table 3).

Some species were not evenly distributed among the two states. For example, *Hemicriconemoides wessoni* was documented in 10 counties in SC but only 5 counties in NC, and *X. americanum* in 9 counties in SC but only 4 counties in NC. Other species were found only in one state. For instance, *Scutellonema brachyurum, Heterodera* sp., *Loofia thienemanni, Longidorus paralongicaudatus* and *Dolichodorus heterocephalus* were only found in SC, whereas *X. bakeri* was only found in NC (Table 3).

Nematode diversity: The effects of different habitats on nematode biodiversity are presented in Tables 4–7. Of the five indices reflecting biodiversity, Diversity (*H'*), Richness (*SR*) and Dominance (λ) values were significantly different between NC and SC (Table 4). *H'* and *SR* were higher in SC than in NC, while λ was higher in NC (Table 4).

Nematode biodiversity as influenced by soil type presented in Tables 5 shows that the indices *H'*, λ, *J'* and H_2 were significantly different between sandy and clay soil in NC. *H'*, *J'* and H_2 are significantly higher in sandy samples than in clay ones, but λ was significantly higher in clay samples, indicating dominance by a smaller number of species. However, no significant differences between sandy and clay soil were detected in SC or in pooled data from both states (Table 5).

The effects of management zone on nematode diversity indices are shown in Tables 6. There were no significant differences among the management zones in NC. However, in SC, *H'*, *SR* and H_2 were significantly higher in putting greens than in fairways and tees. Pooled data from NC and SC showed similar differences for *H'*, λ, *SR* and H_2 (Table 6).

Comparing samples from different grass species (Tables 7), significant differences were detected only in Diversity (*H'*), which was significantly higher in zoysiagrass than in bentgrass or bermudagrass in NC. In pooled data from NC and SC, *H'* was significantly higher in zoysiagrass samples than in creeping bentgrass samples but was not significantly different from bermudagrass samples.

Discussion

Twenty-four species of plant-parasitic nematodes were identified among 282 soil samples collected from 111 golf courses in NC and SC. Of those nematodes, 23 and 19 species were detected in SC and NC, respectively. Eighteen species were documented in both states (Tables 1–2). Of the 38 nematode species previously reported from turfgrasses in the USA, 65.8% of them were documented in the current study. These results revealed a great diversity of nematode species associated with golf course turfgrasses in NC and SC.

The overall nematode populations in NC and SC were very similar; 75% of species were present in both adjacent states. However, some differences between the two states were observed. For example, *Heterodera* sp., *Loofia thienemanni*, *Longidorus paralongicaudatus* and *D. heterocephalus* were found only in SC, but *Xiphinema bakeri* only in NC. In addition, the numbers of species that exceeded 10% prevalence (11 in SC *vs* 9 in NC), relative abundance exceeding 30 nematodes per 500 cm^3 of soil (7 *vs* 5), mean densities exceeding 100 nematodes (15 *vs* 9) and maximum densities exceeding 500 nematodes (11 *vs* 9) were all greater in SC than in NC.

The results in this survey indicated that *Helicotylenchus dihystera, Mesocriconema xenoplax, Hoplolaimus galeatus, T. claytoni, B. longicaudatus, Meloidogyne graminis* and

TABLE 3. Distribution of plant-parasitic nematodes in North and South Carolina.

Nematode species	States	Counties	Number of counties
Belonolaimus longicaudatus	NC	Brunswick, Cumberland, Lee, Montgomery, Moore, Nash, New Hanover, Wake, Wayne, Wilson	10
	SC	Aiken, Beaufort, Charleston, Chesterfield, Clarendon, Darlington, Florence, Georgetown, Greenville, Horry, Kershaw, Lexington, Richland, Sumter	14
Hoplolaimus galeatus	NC	Brunswick, Buncombe, Carteret, Cumberland, Lee, Mecklenburg, Moore, New Hanover, Pender, Stokes, Wake	11
	SC	Beaufort, Charleston, Chesterfield, Clarendon, Florence, Georgetown, Horry, Kershaw, Lexington, Pickens, Richland, Sumter, York	13
Helicotylenchus dihystera	NC	Alleghany, Avery, Brunswick, Buncombe, Burke, Carteret, Cumberland, Guilford, Mecklenburg, Montgomery, Moore, Nash, New Hanover, Pender, Stokes, Wake, Wayne, Wilson	18
	SC	Aiken, Beaufort, Charleston, Chesterfield, Clarendon, Darlington, Florence, Georgetown, Greenville, Horry, Kershaw, Lexington, Oconee, Pickens, Richland, Spartanburg, Sumter, York	18
Scutellonema brachyurum	NC		0
	SC	Beaufort	1
Meloidogyne graminis	NC	Avery, Brunswick, Burke, Forsyth, Guilford, Mecklenburg, Montgomery, Moore, Nash, New Hanover, Pender, Wake	12
	SC	Aiken, Beaufort, Charleston, Chesterfield, , Clarendon, Darlington, Florence, Georgetown, Greenville, Horry, Kershaw, Laurens, Lexington, Oconee, Pickens, Richland, Spartanburg, Sumter	18
Meloidogyne naasi	NC	Avery, Mecklenburg, Montgomery	3
	SC	Charleston, Greenville, Horry, Kershaw, Pickens, Richland	6
Heterodera sp.	NC		0
	SC	Horry	1
Cactodera sp.	NC	Moore	1
	SC	Florence	1
Tylenchorhynchus claytoni	NC	Alleghany, Avery, Buncombe, Burke, Carteret, Forsyth, Guilford, Mecklenburg, Moore, New Hanover, Stokes, Wake,	12
	SC	Beaufort, Chesterfield, Clarendon, Darlington, Florence, Georgetown, Greenville, Horry, Laurens, Lexington, Pickens, Spartanburg, Sumter, York	14
Pratylenchus penetrans	NC	Guilford, Mecklenburg, Nash, New Hanover, Pender, Stokes, Wake, Wayne, Wilson	9
	SC	Beaufort, Charleston, Chesterfield, Clarendon, Florence, Georgetown, Greenville, Horry, Kershaw, Laurens, Lexington, Oconee, Pickens, Richland, York	15
Hemicycliophora conida	NC	Alleghany, New Hanover	2
	SC	Beaufort, Horry, Lexington	3
Loofia thienemanni	NC		0
	SC	Charleston	1
Hemicaloosia graminis	NC	New Hanover	1
	SC	Beaufort, Charleston	2
Hemicriconemoides wessoni	NC	Carteret, Moore, New Hanover, Pender, Wake	5
	SC	Aiken, Beaufort, Charleston, Chesterfield, Clarendon, Horry, Kershaw, Lexington, Pickens, Richland	10
Mesocriconema xenoplax	NC	Avery, Brunswick, Buncombe, Burke, Carteret, Forsyth, Guilford, Lee, Mecklenburg, Moore, New Hanover, Pender, Wake	13
	SC	Aiken, Beaufort, Charleston, Chesterfield, Chesterfield, Clarendon, Darlington, Florence, Georgetown, Greenville, Horry, Kershaw, Laurens, Lexington, Oconee, Pickens, Richland, Spartanburg, Sumter	19
Mesocriconema curvatum	NC	Mecklenburg, Montgomery, Nash, New Hanover, Wilson	5
	SC	York	1
Mesocriconema sphaerocephala	NC	Montgomery	1
	SC	Beaufort	1
Ogma floridense	NC	Wake	1
	SC	Beaufort	1
Paratrichodorus allius	NC	Avery, Mecklenburg	2
	SC	Charleston, Clarendon, Greenville, Horry, Pickens	5

(*Continued*)

P. minor were not only most prevalent but also the most abundant species, especially in putting greens in both states (Table 1). Similar results were reported in NC (Lucas et al., 1974) and SC(http://www.clemson.edu/extension/horticulture/turf/pest_guidelines/2011_pest_guidelines/nematodes_2011.pdf), Florida (http://edis.ifas.ufl.edu/pdffiles/IN/IN12400.pdf), New York (Murdoch et al., 1978), Kansas (Todd and Tisserat, 1990), and Oklahoma (Walker et al., 2002). This revealed the wide distribution and important role of these

TABLE 3. Continued.

Nematode species	States	Counties	Number of counties
Paratrichodorus minor	NC	Avery, Burke, Carteret, Guilford, Lee, Montgomery, Moore, Nash, New Hanover, Oconee, Pender, Pickens, Stokes, Wake, Wayne, Wilson	16
	SC	Aiken, Beaufort, Charleston, Chesterfield, Clarendon, Darlington, Darlington, Florence, Georgetown, Greenville, Horry, Kershaw, Kershaw, Laurens, Lexington, Richland, Spartanburg, Sumter, York	19
Xiphinema americanum	NC	Avery, Carteret, Mecklenburg, New Hanover	4
	SC	Aiken, Beaufort, Charleston, Chesterfield, Clarendon, Darlington, Horry, Lexington, Sumter	9
Xiphinema bakeri	NC	Lee	1
	SC		0
Longidorus paralongicaudatus	NC		0
	SC	Beaufort	1
Dolichodorus heterocephalus	NC		0
	SC	Beaufort	1

species in the dynamics and structure of the turfgrass nematode community.

Some species with lower relative abundances were found occasionally at high densities, including *Mesocriconema curvatum*, *M. sphaerocephala*, *Hemicycliophora conida*, *X. americanum*, *Pratylenchus penetrans*, *Hemicriconemoides wessoni*, and *Paratrichodorus allius* (Table 1). However, the relationships between nematode density and impact on turfgrass growth are not yet clear even though both NC and SC employ general damage thresholds for the common genera. Further study of these species is necessary to better understand the ecological processes involving plant-parasitic nematodes in turfgrass ecosystems.

Previous studies showed that nematodes from the genera *Belonolaimus, Mesocriconema, Helicotylenchus*, *Hemicycliophora*, *Hoplolaimus*, *Paratrichodorus*, *Pratylenchus, Meloidogyne, Trichodorus*, and *Tylenchorhynchus* were associated with both warm- and cool-season grasses (Lucas et al., 1974; Sikora et al., 2001; Walker et al., 2002). Similar results were found in this study: *Belonolaimus longicaudatus*, *Paratrichodorus minor*, *Mesocriconema xenoplax*, *Helicotylenchus dihystera, Hoplolaimus galeatus, Pratylenchus penetrans, Meloidogyne naasi* and *Tylenchorhynchus claytoni* were found in both bermudagrass and creeping bentgrass. It appears that these most common nematode species are not host specific. In addition, Brodie and Burton (1967) and Nutter and Christie (1958) showed that warm-season hybrid bermudagrass putting greens were susceptible to a number of plant-parasitic nematodes. Findings were similar in this study. The total numbers of species identified were greater in bermudagrass (21 species in SC, 15 in NC) than in creeping bentgrass (10 species in SC, 12 in NC) and zoysiagrass (7 species in SC, 11 in NC) in both states. This result revealed bermudagrass to be a more favorable host than creeping bentgrass and zoysiagrass. In creeping bentgrass, the most prevalent nematodes in NC include *B. longicaudatus, H. dihystera, M. xenoplax, P. minor* and *T. claytoni*. A similar result was observed in SC, but *B. longicaudatus* was less prevalent. This discrepancy could be explained by the fact that very little creeping bentgrass is grown in the southeastern part (Coastal Plain) of SC where temperatures are very warm, making its culture difficult. Most of the bentgrass samples from SC came from the Piedmont or Mountain/Valley regions. The scarcity of sandy soil in those regions could account for the apparent lower prevalence of *B. longicaudatus*.

Most of the plant-parasitic nematodes that damage turfgrasses favor sandy soil (Crow, 2005). The results in the present study confirmed this fact. The total number of species identified in sandy soils was greater than in clay soils in both states. Seven species were prevalent in sandy soils (*B. longicaudatus*, *Paratrichodorus minor*, *Mesocriconema xenoplax*, *Helicotylenchus dihystera, Hoplolaimus galeatus*, *Meloidogyne graminis* and *T. claytoni*), but only three species (*H. dihystera, M. graminis* and *P. penetrans*) were prevalent in clay soils. Particularly, *B. longicaudatus* and *H. galeatus* were only found in sandy soil samples from both states, indicating that they are very sensitive to soil texture. This finding is consistent with a previous report that *B. longicaudatus* is limited to soils with over

TABLE 4. Diversity of plant-parasitic nematodes in North and South Carolina.

Areas (States)	Number of sites	Latitudes of sampling sites	Diversity *H'*	Evenness *J'*	Richness *SR*	Dominance λ	Diversity H_2
SC	63	32°9'-35°8'N	1.36 A ± 0.04	0.75 A ± 0. 02	39.49 A± 1.71	0.33 A ± 0.02	0.97 A ± 0.18
NC	48	35°1'-36°2'N	1.14 B ± 0.05	0.71 A ± 0. 02	30.13 B± 1.96	0.41 B ± 0.02	0.96 A ± 0.21

Differences in the listed items were analyzed by Duncan's multiple range test ($p < 0.05$). Different letters in a column in a group indicate significant differences between samples.

TABLE 5. Effect of soil type on nematode diversity in North and South Carolina.

States	Soil types	Number of samples	Diversity *H'*	Evenness *J'*	Richness *SR*	Dominance λ	Diversity H_2
NC	Sand	53	0.89 A± 0.05	0.73 A± 0.03	16.49 A± 1.33	0.45A ± 0.03	0.95A ± 0.10
	Clay	4	0.41B ± 0.19	0.46B ± 0.12	12.76A± 4.85	0.78 B± 0.10	0.26**B** ± 0.11
SC	Sand	147	1.01A ± 0.03	0.72A ± 0.02	20.42 A± 0.98	0.46 A± 0.02	0.88A ± 0.04
	Clay	5	1.10A ± 0.18	0.71A ± 0.09	25.17A ± 5.32	0.39 A± 0.09	0.99A ± 0.21
NC+SC	Sand	200	0.98A ± 0.03	0.72 A± 0.02	19.38A ± 0.91	0.46 A± 0.02	0.90A ± 0.04
	Clay	9	0.80A ± 0.13	0.60A ± 0.07	19.65A± 3.80	0.56 A± 0.07	0.66A ± 0.18

Differences in the listed items were analyzed by Duncan's multiple range test ($p< 0.05$). Different letters in a column in a group indicate significant differences between samples.

80% sand content (Robbins and Barker, 1974), and it is the dominant and most severely damaging nematode species in golf courses, especially on putting greens that are constructed of over 90% sand content (Crow, 2005).

Indices such as *H', J', SR,* λ and H_2 are useful tools for describing biodiversity and analyzing the impact of certain factors on species distribution. Popvici and Ciobanu (2000) showed that the *H'* of nematode communities did not differ significantly between the different types of grasslands. Similar results were showed by Talavera and Navas (2002). However, clear relationships between the diversity of nematodes and soil texture, climate, plant species, pesticides, and management practices in grasslands were indicated by Yeates and Bongers (1999). Similar results were found in the present study, which revealed effects of different habitats (soil texture, grass species and management zone) on diversity of nematode species in turfgrass ecosystems. *H', J',* λ and H_2 values were significantly different between sand and clay soil in NC, being significantly higher (except for λ) in sandy soils than in clay soils, indicating that a greater diversity and more even distribution of the prevalent species occurred in sandy than in clay soil. However, no significant differences between sandy and clay soil were observed in SC or in pooled data.

With regard to the effects of grass species, there were no significant differences among bermudagrass, bentgrass and zoysiagrass for all indices in SC nor for *J',* λ, *SR* and H_2 either in NC or in pooled data. However, for *H'*, there was significant difference between zoysiagrass and other species in NC and between zoysiagrass and bentgrass in pooled data. *H'* values were greater in zoysiagrass than in other species. There appeared to be higher diversity of species in zoysiagrass than in others.

Concerning the effects of the management zones, there were no significant differences for all indices among the putting green, fairway and tee in NC. However, in SC and pooled data from both states, *H', SR* and H_2 values were significantly higher in fairways and tees than in greens, thus indicating a lower diversity of species in greens.

In turfgrass ecosystems, fluctuations or distribution differences of nematode populations are common (Davis et al., 1994; Peacock et al., 2005; Jordan and Mitkowski, 2006; Settle et al., 2006; Westerdahl and Harivandi, 2007; Giat et al., 2008; McGroary et al., 2009). McGroary et al. (2009) reported that seasonal fluctuations in *B. longicaudatus* and root growth of bermudagrass varied among locations and years. Settle et al. (2006) indicated that populations of *H. galeatus* in a naturally infested experimental putting green of creeping bentgrass increased from late spring through midsummer, declined in August, and increased again in the fall. Jordan and Mitkowski (2006) showed that there was a significant effect of season on population level of *Mesocriconema, Tylenchorynchus* and *Heterodera* juveniles in the sampling year. Such seasonal fluctuations probably lead to changes of nematode structure in the turfgrass community. In this study, soil samples were collected only in the summer of 2011. Further study on

TABLE 6. Effect of management zones on nematode diversity in North and South Carolina.

States	Number of samples	Turf types	Diversity *H'*	Evenness *J'*	Richness *SR*	Dominance λ	Diversity H_2
NC	26	Green	0.89A±0.08	0.74A±0.05	16.36A±1.75	0.50A±0.04	0.77A±0.08
	20	Fairway	0.81A±0.09	0.71A±0.05	13.59A±1.99	0.54A±0.04	0.70A±0.09
	8	Tee	1.01A±0.14	0.80A±0.08	16.46A±3.15	0.43A±0.07	0.89A±0.14
SC	60	Green	0.79A±0.05	0.69A±0.02	14.76A±1.42	0.55A±0.02	0.65A±0.05
	51	Fairway	1.14B±0.05	0.74A±0.03	24.58B±1.54	0.40B±0.02	1.01B±0.06
	57	Tee	1.10B±0.05	0.75A±0.02	22.03B±1.45	0.42B±0.02	0.94B±0.05
NC+SC	86	Green	0.82A±0.07	0.71A±0.04	15.25A±1.99	0.54A±0.02	0.69A±0.05
	71	Fairway	1.05B±0.05	0.73A±0.03	21.48B±1.39	0.44B±0.02	0.92B±0.05
	65	Tee	1.09B±0.04	0.75A±0.02	21.34B±1.24	0.42B±0.03	0.94B±0.08

Differences in the listed items were analyzed by Duncan's multiple range test ($p< 0.05$). Different letters in a column in a group indicate significant differences between samples.

TABLE 7. Effect of grass species on nematode diversity in North and South Carolina.

States	Number of samples	Grass species	Diversity *H'*	Evenness *J'*	Richness *SR*	Dominance λ	Diversity H_2
NC	4	Zoysia	1.23A±0.19	0.76A±0.12	23.37A±4.76	0.36A±0.11	1.08A±0.37
	24	Bermuda	0.85B±0.08	0.71A±0.05	14.85A±1.94	0.49A±0.04	0.85A±0.15
	30	Bentgrass	0.84B±0.07	0.71A±0.04	16.83A±1.74	0.47A±0.04	0.95A±0.14
SC	4	Zoysia	1.07A±0.20	0.69A±0.10	17.37A±5.82	0.42A±0.10	0.91A±0.23
	140	Bermuda	1.02A±0.03	0.71A±0.02	21.15A±0.98	0.46A±0.02	0.88A±0.04
	19	Bentgrass	0.85A±0.09	0.75A±0.04	15.96A±2.67	0.51A±0.04	0.73A±0.11
NC+SC	8	Zoysia	1.15A±0.14	0.73A±0.07	20.37A±3.94	0.39A±0.07	0.99A±0.19
	164	Bermuda	0.99AB±0.04	0.71A±0.02	20.21A±1.23	0.46A±0.02	0.88A±0.06
	49	Bentgrass	0.84B±0.06	0.72A±0.03	16.49A±1.63	0.48A±0.03	0.86A±0.08

Differences in the listed items were analyzed by Duncan's multiple range test ($p < 0.05$). Different letters in a column in a group indicate significant differences between samples.

dynamics of various important nematodes over the course of several seasons or even of several continuous years could prove invaluable for the effective management of turf nematodes. This study provides a baseline of information on species diversity, incidence and distribution of plant-parasitic nematodes associated with golf course turfgrasses in NC and SC.

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