

# RESEARCH/INVESTIGACIÓN

## NEMATODES IN TOPOGRAPHICAL MICROHABITATS WITHIN A WET PASTURE

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### ABSTRACT

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A nearly level, wet bahiagrass (*Paspalum notatum* Flugge) pasture in south Florida contained many slight depressions and small ridges, separated by < 30 cm of elevation. Paired soil samples were collected from these microhabitats to determine differences in nematode communities in ridges and depressions. Soil moisture was consistently greater ( $P \leq 0.01$ ) in the depressions on all sampling dates, but moisture was highly correlated ( $P \leq 0.01$ ) with soil organic matter across all microhabitats. The ridges contained more total nematodes, more taxa per sample, and greater numbers of nematodes in most trophic groups and guilds. Similar results were obtained with basal guilds of bacterivores and fungivores and with structured guilds of omnivores and predators. Most nematode genera collected were more abundant in ridges than in depressions. Genera within the Cephalobidae were the most consistently affected, and some plant parasites (e.g. *Hemicriconemoides*) were less affected. The combined higher levels of soil moisture and organic matter were not beneficial to nematodes in this unusual wet pasture site that was poorly drained.

*Key words:* Free-living nematodes, guilds, nematode community, nematode trophic groups, plant-parasitic nematodes, topography.

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### RESUMEN

McSorley, R., 2013. Nemátodos en microhabitats topográficos dentro de un pastizal húmedo. *Nematropica* 43:9-17.

Un pastizal casi plano de zacate de bahía (*Paspalum notatum* Flugge) en el sur de Florida contiene varias ligeras depresiones y pequeñas crestas separadas por menos de 30 cm de elevación. Muestras pareadas de suelo fueron colectadas en estos microhabitats para determinar diferencias en las comunidades de nemátodos tanto en depresiones como en crestas. La humedad del suelo fue consistentemente mayor ( $P \leq 0.01$ ) en las depresiones en todas las fechas del muestreo, pero la humedad estaba altamente correlacionada ( $P \leq 0.01$ ) con materia orgánica en el suelo a lo largo de todos los microhabitats. Las crestas contenían un total más alto de nemátodos, más taxa por muestra así como un mayor número de nemátodos en casi todos los grupos tróficos y agrupaciones o grupos funcionales. Se obtuvieron resultados similares en las agrupaciones de bacterívoros y fungívoros así como omnívoros y depredadores. La mayoría de los géneros de nemátodos fueron más abundantes en las crestas que en las depresiones. Géneros dentro de Cephalobidae fueron los más consistentemente afectados, y algunos fitoparásitos (por ej. *Hemicriconemoides*) fueron menos afectados. La combinación de altos niveles de humedad en el suelo y materia orgánica no fueron benéficos para los nemátodos en este inusual y húmedo pastizal que a la vez tienen pobre drenaje.

*Palabras clave:* Nemátodos de vida libre, grupos funcionales, comunidad de nemátodos, grupos tróficos de nemátodos, nemátodos fitoparasíticos, topografía.

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## INTRODUCTION

The importance of soil moisture for nematode activity and life cycles has been recognized for many years (Norton, 1978; Wallace, 1973). Plant-parasitic and free-living soil nematodes are often positively correlated with rainfall (Caveness and Badra, 1980; Hutton, 1978; McSorley *et al.*, 1997a,b; Yeates, 1981). However, too much water can lead to reduced oxygen levels and other detrimental effects, so that flooding is occasionally used as a nematode management method (Duncan, 1991; Gowen and Queneherve, 1990; Trivedi and Barker, 1986).

In citrus and pasture sites in south Florida, total numbers of nematodes, bacterivores, fungivores, omnivores, and numbers of several different genera were positively correlated with rainfall (McSorley, 1997a). Although many nematodes respond to rainfall and changes in soil moisture, it is possible that some taxa are more affected than others. A recent review (McSorley, 2012) suggests that dorylaimid omnivores such as *Eudorylaimus* and *Aporcelaimellus* are among the nematode taxa most sensitive to moisture. These were the only two genera that consistently increased in response to increased irrigation in a Florida citrus grove (Porazinska *et al.*, 1998).

When an irrigation treatment was applied in a Swedish pine forest, population levels of several genera (e.g., *Tylencholaimus*, *Rhabditis*, *Prismatolaimus*, *Monhystera*, *Achromadora*) increased, numbers of *Wilsonema* decreased, and other genera (e.g., *Acrobeloides*, *Ditylenchus*, *Plectus*) were relatively unaffected (Sohlenius and Wasilewska, 1984). In a recent study in Israel, numbers of plant parasites were positively correlated with soil moisture at one site, while bacterivores and fungivores were negatively correlated with moisture in some instances (Levi *et al.*, 2012).

One objective of this paper was to further investigate the effects of moisture on members of the soil nematode community. The study was carried out in a field site containing slight changes in topography that resulted in low moist areas (depressions) and higher, drier microhabitats (ridges) in close proximity to one another. It was hypothesized that population levels of most nematodes would be greater in the moist microhabitats. The various nematode genera and guilds occurring in this site were examined to determine which were sensitive and which did not respond to the slight differences in topography present.

## MATERIALS AND METHODS

The study was conducted at the MacArthur Agro-ecology Research Center at Buck Island Ranch in Highlands County, Florida (27°9'N, 81°11'W). Historically the area was freshwater marshland (Kushlan, 1991), which had been partially drained and planted to bahiagrass (*Paspalum notatum*

Flugge) pastures. The study site was a 20-ha pasture on Pineda sand (loamy, siliceous, hyperthermic Arenic Glossaqualfs), a wet, poorly drained soil with high water table (Carter *et al.*, 1989). Soil texture consisted of 90% sand, 4% silt, and 6% clay. Although the overall topography of the site was nearly level, the site contained many shallow depressions and small ridges. The vertical change in elevation from the bottom of a depression to the top of a ridge was rarely more than 30 cm, and all locations were covered with bahiagrass. The origin of these depressions and ridges was unclear, although they may have been related to very slight changes in topography, historical water flow, or patterns from previous cattle traffic and grazing. No cattle were present during the course of the current study.

### Sampling

Within the pasture, 4 or 7 replications, each about 10 m x 10 m in area, were designated for sampling. Within each replication, a separate soil sample was collected from depressions (low areas) and from ridges (high areas). Each soil sample consisted of 6 soil cores (2.5-cm diam x 15 cm deep). When a soil core was collected from a depression, a corresponding core was collected from a nearby (<0.5 m away) ridge as well. In every case, the difference in elevation between the bottom of the depression and the top of the ridge was 15-30 cm; this ensured that there was no vertical overlap between cores (15 cm long) from low and high sampling points. The 6 cores from depressions were pooled, as were the 6 cores from ridges, to provide 2 samples (depression and ridge) from each replication. Samples were collected from 4 replications on 1 November 1995 and 20 February 1996. The number of replications was increased to 7 for sampling on 8 May 1996, 2 December 1996, and 6 February 1997.

### Data Collection

The soil cores from each sample were mixed, and a 100-cm<sup>3</sup> subsample removed and extracted by sieving and centrifugation (Jenkins, 1964). Extracted nematodes were identified to genus (except for Rhabditidae and Tylenchidae) and counted under an inverted microscope. Nematodes were classified into five trophic groups (bacterivores, fungivores, herbivores, omnivores, predators) based on reported feeding habits (Yeates *et al.*, 1993), and into guilds based on trophic groups and c-p values (Bongers and Bongers, 1998; Ferris *et al.*, 2001). Tylenchidae (a mix of primarily *Filenchus* with some *Tylenchus*) were classified as fungivores (McSorley and Frederick, 1999; Okada *et al.*, 2005), and accordingly assigned to guild Fu2.

Gravimetric soil moisture was determined by drying a portion of each soil sample at 60-70°C until constant weight was achieved. Soil organic matter was determined by ignition at 500°C for 3 hr in a

muffle furnace (Thermolyne Type 1400 Furnace, Dubuque, IA).

### Statistical Analysis

Data were analyzed by analysis of variance (ANOVA) using SAS software (version 9.2, SAS Institute, Cary, NC) to determine differences between depressions and ridges. Nematode data were log-transformed by  $\log_{10}(x + 1)$  to meet assumptions of ANOVA, but untransformed arithmetic means are presented.

## RESULTS

The nematodes recovered at this site represented 15 different guilds (Table 1). Several guilds contained only a single taxon: Ba4 = *Alaimus*; Fu3 = *Diphtherophora*; P14 = *Paratrichodoros*; Ca2 = *Seinura*; Ca5 = *Nygolaimus*. Guild Om5 included only one specimen that was not *Aporcelaimellus*. More nematode taxa per sample were consistently found in ridges than in depressions (Table 2). Total numbers of nematodes per sample and numbers within all 5 trophic groups were usually greater in the ridges as well. The most notable exception to this pattern was the lack of differences in plant parasites on the last two sampling dates. However,

soil moisture was always greater in depressions, which always averaged >30% soil moisture (Table 2). Soil organic matter averaged 12.4% across all sampling locations, but averaged 4.9% in high areas and 19.8% in low areas (data not shown). Soil moisture and soil organic matter were highly correlated throughout the year ( $r = 0.982$  in May 1996,  $r = 0.948$  in Dec. 1996,  $r = 0.986$  in Feb. 1997;  $P \leq 0.01$ ,  $n = 14$ ).

Patterns observed with nematode trophic groups were evident at the guild level as well, with greater numbers in the ridges for many guilds (Table 3). The trend of greater numbers in the higher, drier ridges was evident with the basal guilds Ba2 and Fu2 and with more structured guilds such as Om4 and Ca5. Guilds Fu3 (*Diphtherophora*) and P15 (*Xiphinema*, *Longidorus*) were never found in the depressions, and guilds P14, Om5, and Ca5 were rare in depressions.

Numbers of selected nematode genera are shown in Table 4. Some genera (e.g., *Alaimus* in guild Ba4, *Paratrichodoros* in P14, *Nygolaimus* in Ca5) are not included because they were the only genus in a particular guild, and so their numbers at genus level and guild level are redundant. Most genera were more common in the ridges (Table 4), and a nematode genus was more abundant in depressions only on two occasions (*Hemicriconemoides* in Dec. 1996, *Tylenchorhynchus* in Feb. 1997). Cephalobidae (*Acrobeles*, *Acrobeloides*,

Table 1. Nematode taxa included in guilds, based on nematodes recovered from pasture samples

Guild <sup>y</sup>	Nematode taxa included in guild <sup>z</sup>
Ba1	<i>Bunonema</i> , <i>Monhystera</i> , <i>Panagrolaimus</i> , Rhabditidae, <i>Turbatrix</i>
Ba2	<i>Acrobeles</i> , <i>Acrobeloides</i> , <i>Cephalobus</i> , <i>Cervidellus</i> , <i>Eucephalobus</i> , <i>Plectus</i> , <i>Tylocephalus</i> , <i>Wilsonema</i> , <i>Zeldia</i>
Ba3	<i>Chronogaster</i> , <i>Odontolaimus</i> , <i>Prismatolaimus</i> , <i>Teratocephalus</i>
Ba4	<i>Alaimus</i>
Fu2	<i>Aphelenchoides</i> , <i>Aphelenchus</i> , <i>Ditylenchus</i> , <i>Ecphyadophora</i> , <i>Filenchus</i> , Neotylenchidae, <i>Nothotylenchus</i> , <i>Psilenchus</i> , Tylenchidae, <i>Tylenchus</i>
Fu3	<i>Diphtherophora</i>
Fu4	<i>Leptonchus</i> , <i>Tylencholaimus</i> , <i>Tylencholaimellus</i>
P13	<i>Criconema</i> , <i>Helicotylenchus</i> , <i>Hemicriconemoides</i> , <i>Hemicycliophora</i> , <i>Heterodera</i> , <i>Hoplolaimus</i> , <i>Mesocriconema</i> , <i>Paratylenchus</i> , <i>Pratylenchus</i> , <i>Tylenchorhynchus</i> , <i>Tylenchulus</i>
P14	<i>Paratrichodoros</i>
P15	<i>Longidorus</i> , <i>Xiphinema</i>
Om4	<i>Crateronema</i> , <i>Eudorylaimus</i> , <i>Mesodorylaimus</i> , <i>Pungentus</i>
Om5	<i>Aporcelaimellus</i> , <i>Dorylaimellus</i>
Ca2	<i>Seinura</i>
Ca4	<i>Iotonchus</i> , <i>Miconchus</i> , <i>Mononchus</i> , <i>Mylonchulus</i>
Ca5	<i>Nygolaimus</i>

<sup>y</sup>See Bongers and Bongers (1998) for definitions of guilds.

<sup>z</sup>Rare taxa represented by only 1-2 specimens: *Bunonema*, *Crateronema*, *Dorylaimellus*, *Hemicycliophora*, *Iotonchus*, *Miconchus*, *Odontolaimus*, *Tylocephalus*.

Table 2. Soil moisture (%), number of taxa per sample, and numbers of nematodes per 100 cm<sup>3</sup> soil in trophic groups on ridges and in depressions within pastures on 5 sampling dates.

	Nov. 1995		Feb. 1996		May 1996		Dec. 1996		Feb. 1997	
	Ridge	Depression	Ridge	Depression	Ridge	Depression	Ridge	Depression	Ridge	Depression
Soil moisture	22.1	39.4**	3.5	33.6*	7.7	36.4**	7.1	31.9**	7.5	35.2**
Taxa per sample	22.5	10.2*	35.0	13.2**	29.9	9.1**	25.9	17.1**	32.3	18.9**
Bacterivores	627.0	56.0*	561.5	48.2*	285.0	14.7**	152.9	52.0*	414.6	131.6**
Fungivores	179.0	15.2*	917.0	14.0**	567.6	7.3**	498.1	133.7 <sup>z</sup>	1082.3	169.3**
Plant parasites	309.0	29.5*	1017.5	64.2*	341.9	36.7**	185.1	218.4	402.3	325.9
Omnivores	0.2	0	23.2	0**	30.1	0.6**	27.1	2.3**	21.4	5.6**
Predators	0.8	0	18.2	0.2*	13.3	1.1*	7.1	0.7**	15.4	4.1*
Total nematodes	1133.8	103.5*	2560.5	131.0**	1255.1	62.7**	878.9	410.9	1951.3	642.6**

\* \*\* indicate significant difference between ridge and depression at  $P \leq 0.05$  and  $P \leq 0.01$ , respectively.

<sup>z</sup>Significant difference between ridge and depression at  $P \leq 0.10$ .

Table 3. Numbers of nematodes per 100 cm<sup>3</sup> soil in guilds on ridges and in depressions within pastures on 5 sampling dates.

Guild <sup>y</sup>	Nov. 1995		Feb. 1996		May 1996		Dec. 1996		Feb. 1997	
	Ridge	Depression	Ridge	Depression	Ridge	Depression	Ridge	Depression	Ridge	Depression
Ba1	396.5	50.0 <sup>z</sup>	130.8	15.2*	68.3	4.6**	30.6	19.9	96.4	39.6**
Ba2	214.0	5.5**	392.5	28.5*	200.6	9.1**	106.9	27.0**	289.4	87.1*
Ba3	15.2	0.5**	28.2	4.5*	10.0	1.0**	7.7	4.1	10.9	3.6 <sup>z</sup>
Ba4	1.2	0	10.0	0 <sup>z</sup>	6.1	0**	7.7	1.0**	17.9	1.3**
Fu2	178.5	15.2 <sup>z</sup>	897.5	13.8**	552.6	7.1**	497.7	133.7 <sup>z</sup>	1075.0	166.1**
Fu3	0.5	0	1.5	0*	1.7	0	0	0	1.1	0**
Fu4	0	0	18.0	0.2**	13.3	0.1**	0.4	0	6.1	3.1
P13	314.8	29.5*	964.2	64.2*	320.0	36.7**	182.0	218.4	392.4	325.7
P14	1.8	0	52.5	0**	21.9	0**	2.9	0*	5.7	0.1**
P15	0	0	0.8	0	0	0	0.6	0	1.1	0
Om4	0.2	0	18.8	0**	29.0	0.3**	26.1	2.1**	21.0	5.34**
Om5	0	0	4.5	0**	1.1	0.3*	1.0	0.1	0.4	0.1
Ca2	0.2	0	0.8	0.2	1.4	1.1	0.3	0	4.0	3.3
Ca4	0.2	0	5.0	0 <sup>z</sup>	3.4	0*	0.6	0.7	1.4	0.3
Ca5	0.2	0	12.5	0 <sup>z</sup>	8.4	0**	6.3	0**	10.0	0.8*

\* \*\* indicate significant difference between ridge and depression at  $P \leq 0.05$  and  $P \leq 0.01$ , respectively.

<sup>y</sup>See Bongers and Bongers (1998) for definitions of guilds.

<sup>z</sup>Significant difference between ridge and depression at  $P \leq 0.10$ .

Table 4. Numbers of nematodes per 100 cm<sup>3</sup> soil on ridges and in depressions within pastures on 5 sampling dates.

Nematode	Nov. 1995		Feb. 1996		May 1996		Dec. 1996		Feb. 1997	
	Ridge	Depression	Ridge	Depression	Ridge	Depression	Ridge	Depression	Ridge	Depression
<i>Acrobelos</i>	9.0	0.2	46.2	0*	25.6	0**	18.0	0**	40.6	0.3**
<i>Acroboloides</i>	81.2	3.2**	231.2	20.8*	108.0	8.3**	51.6	16.4*	142.9	54.0*
<i>Aphelenchoides</i>	23.5	2.5**	20.8	2.5 <sup>z</sup>	14.7	1.1**	11.7	21.7	44.7	41.3
<i>Cervidellus</i>	6.2	0	13.2	0*	13.1	0**	9.1	0**	23.7	0**
<i>Criconema</i>	5.5	0.8	360.2	1.2	6.3	1.9*	1.9	9.3	43.6	16.1
<i>Eucephalobus</i>	104.8	1.5**	80.8	6.2*	38.4	0.9**	21.0	7.7*	56.3	27.3*
<i>Eudorylaimus</i>	0.2	0	6.8	0*	24.1	0.3**	24.6	2.1**	18.1	5.4**
<i>Helicotylenchus</i>	50.0	0.8 <sup>z</sup>	112.2	5.5*	40.3	2.6*	42.0	2.7**	126.0	64.6
<i>Hemicriconemoides</i>	32.2	1.8	71.0	7.2	23.0	4.6*	5.3	28.9 <sup>z</sup>	115.6	31.0
<i>Mesocriconema</i>	121.2	0.8*	600.2	1.0**	141.7	1.0**	86.3	3.9**	29.7	7.9*
<i>Monhystera</i>	2.5	0.2**	6.2	2.2 <sup>z</sup>	5.9	0.4**	4.3	2.4	8.6	4.6
<i>Nothotylenchus</i>	7.5	0.2**	20.5	0.2**	22.9	0.3**	10.0	3.7 <sup>z</sup>	51.0	11.7**
<i>Panagrolaimus</i>	24.2	2.2	9.0	2.2 <sup>z</sup>	9.6	0.3**	3.6	1.3**	5.1	1.4*
<i>Paratylenchus</i>	1.2	0	1.8	0	0.3	0	0	0	6.1	1.6
<i>Prismatolaimus</i>	6.0	0.5	20.2	1.5*	6.7	0.1**	4.6	1.7	3.0	2.4
Rhabditidae	369.5	45.8 <sup>z</sup>	115.5	10.5*	52.6	3.7**	22.3	15.4	82.4	31.6 <sup>z</sup>
<i>Teratocephalus</i>	6.2	0*	5.2	0 <sup>z</sup>	1.7	0.1*	2.0	0.9	5.0	1.6*
<i>Tylencholaimus</i>	0	0	16.0	0 <sup>z</sup>	11.6	0.1**	0.3	0	4.6	3.0
Tylenchidae	144.2	3.5*	845.5	10.8**	508.4	5.6**	472.7	108.3 <sup>z</sup>	976.1	111.0**
<i>Tylenchorhynchus</i>	105.5	11.2*	138.0	48.5 <sup>z</sup>	108.4	14.6**	45.7	81.7	69.1	183.0*
<i>Wilsonema</i>	2.8	0	6.0	1.2	2.3	0**	3.0	2.4	14.4	5.4

\* , \*\* indicate significant difference between ridge and depression at  $P \leq 0.05$  and  $P \leq 0.01$ , respectively.<sup>z</sup>Significant difference between ridge and depression at  $P \leq 0.10$ .

*Cervidellus*, *Eucephalobus*) were most consistent in occurrence in the ridges, and *Cervidellus* was not even found in depressions. On the other hand, genera of Criconeematidae (*Criconema*, *Hemicriconemoides*, *Mesocriconema*) did not show consistent patterns, and numbers fluctuated widely in samples. *Mesocriconema* was more abundant in ridges on every sampling date, whereas numbers of *Criconema* and *Hemicriconemoides* were significantly ( $P \leq 0.10$ ) greater in ridges on only one sampling date.

### DISCUSSION

Despite some exceptions, the majority of nematode genera collected were more abundant in the high, drier ridges than in the low, moist depressions. This main finding contradicts the initial hypothesis that nematode population levels would be greater in the moist microhabitats. In addition, more different taxa were found in ridges (average: 29.1 taxa/sample) than in depressions (average: 13.7 taxa/sample).

The current results are contrary to a number of previous studies. Positive correlation with rainfall was observed in an adjacent pasture site (McSorley, 1997a), although that site was better drained than the

present. Dorylaimid omnivores have been recognized among the most sensitive nematodes to soil moisture (McSorley, 2012) and were increased by irrigation in Florida sandy soils (Porazinska *et al.*, 1998). Omnivore and predator K-strategists also responded in the current study, but in the opposite way. Although uncommon on the first sampling date, *Eudorylaimus* (Om4), *Aporcelaimellus* (Om5), mononchids (Ca4), and *Nyngolaimus* (Ca5) were more common in the drier ridges on most other sampling dates. *Tylencholaimus*, *Monhystera*, and *Prismatolaimus* were favored by increased moisture from irrigation in a previous study (Sohlenius and Wasilewska, 1984), but these 3 genera had lower population levels in the wet depressions on some sampling dates. In pastures in New Zealand, nematode numbers were much higher in a moist site (58.0-65.8% soil moisture) than in a drier site (29.0-31.4% soil moisture) (Yeates, 1982, 1984). Soils in those sites were silt loams with much greater water holding capacity than the sand in the current study. In other pasture sites in New Zealand, total numbers of nematodes and several key taxa such as Rhabditidae and *Helicotylenchus* showed strong positive correlations with soil moisture in several pasture sites (Yeates, 1981). In the current study, both of these taxa were more

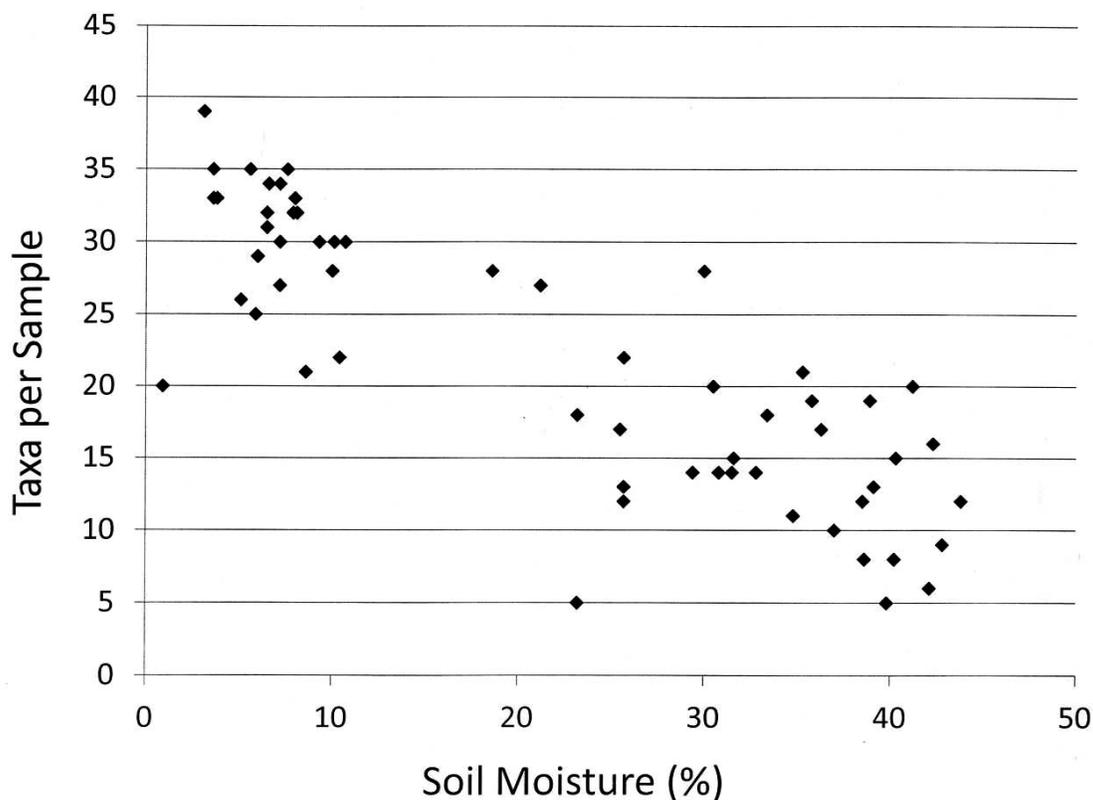


Fig. 1. Relationship between number of taxa per sample and soil moisture for 58 samples.

abundant in the drier ridges on 4 of 5 sampling dates. Such opposite results in contrast with the current study underscore the difficulty in predicting and anticipating relationships between nematodes and soil water, which likely depend on a range of physical factors at the local level.

Other studies report negative or neutral effects of soil moisture. For example, Gowen and Queneherve (1990) mention several instances in which nematode population levels in banana plantations were reduced by flooding. When wetlands were drained and converted into managed pastures in Poland, numbers of K-strategists like *Dorylaimida* increased over time, although this may have resulted more from successional changes than from changes in moisture levels (Wasilewska 2006). In Swedish soils, nematode numbers were increased by irrigation in mineral soil, but decreased in the humus layer (Sohlenius and Wasilewska, 1984). In studies on sandy soils in Florida, numbers of *Eudorylaimus* and *Aporcelaimellus* increased with irrigation in a site where average soil moisture ranged from 2.1-4.9% (Porazinska *et al.*, 1998). However, in a site with higher soil water levels (soil moisture usually around 4-6%), no nematode genera responded to increased irrigation levels (Porazinska *et al.*, 1999).

However, the opposite results discussed in the previous paragraphs may not be in conflict. Organisms typically have an optimum level for physical factors such as soil moisture, and decline when levels are too low or too high (Powers and McSorley, 2000). Preferences of nematodes for intermediate levels of soil moisture are well known (Peacock, 1957; Sultan and Ferris, 1991). An expected relationship between nematodes and soil moisture would be quadratic with the maximum at the optimum moisture level. However, the relationship between taxa per sample ( $y$ ) and soil moisture ( $x$ ) was roughly linear over the range of soil moisture in the current study (Fig. 1), and was given by the regression equation  $y = 33.50 - 0.539x$  ( $P < 0.001$ ;  $n = 58$ ). Numbers of taxa and of many genera consistently declined as soil moisture increased.

A key feature of the current study was the strong correlation between soil moisture and soil organic matter that accumulated in the depressions. The higher levels of organic matter present in the depressions may provide a source of decomposition by-products, such as  $\text{NH}_3$  and organic acids that may be toxic to nematodes (Oka, 2010). Toxic effects from decomposing organic materials may be enhanced in the presence of increased soil moisture and reduced oxygen levels (Butler *et al.*, 2012; Oka, 2010). This synergism among organic amendments, high moisture levels, and low oxygen levels forms the basis of anaerobic soil disinfestation, which has been used for managing nematodes in the field (Butler *et al.*, 2012). A similar mechanism would be consistent with the reductions in nematode numbers as levels of soil moisture (and organic matter) increase in the current study, although measurements of  $\text{O}_2$ ,  $\text{NH}_3$ , and other potentially toxic by-products would be

needed for verification.

Of course, it is possible that unmeasured factors other than soil moisture and organic matter could be responsible for the differences observed in ridges and depressions within the pasture. Oxygen levels, soil porosity, and amount of habitable soil space may affect nematode numbers (Elliott *et al.*, 1980; Yeates, 2002), and moisture tension and other soil factors may affect availability of soil water (Brady, 1974). Although the soil was high in sand content, it is known that sands with different particle sizes have different water holding capacities (Sultan and Ferris, 1991).

Although the current study site was divided into two microhabitats (ridges and depressions), each of these microhabitats could be further subdivided into even smaller microhabitats. At a finer level of resolution, nematode feeding and survival depend on the partitioning and dynamics of water in the soil aggregates and pore spaces (Gorres and Amador, 2010; Neher *et al.*, 1999). As a result, nematode activities including mineralization show patchy distribution and seasonal variation within the soil matrix (Gorres *et al.*, 1999; Neher *et al.*, 1999; Queneherve and Chotte, 1996). Nematode responses to toxins, oxygen, and other soil chemicals are likely partitioned at this level as well. It was impossible to evaluate such mechanisms at the level of resolution used in the current study.

While most nematodes showed a preference for the ridges, plant parasites were somewhat less affected than other groups. Grass and root growth were excellent in both microhabitats, providing a consistent food source for plant parasites, and possibly accounting for fewer differences between microhabitats. Nearly all of the plant parasites recovered from this bahiagrass pasture were ectoparasites, so they are just as exposed to soil environmental factors as the free-living nematodes. While numbers of *Mesocriconema* were lower in depressions on all sampling dates, other genera such as *Criconema* and *Hemicriconemoides* were unaffected on most sampling dates. In contrast, Cephalobidae were among the most affected groups. Observations that Cephalobidae tend to predominate over other bacterivores in drier soils (Yeates *et al.*, 2002) were supported by the current data in which Cephalobidae consistently showed a strong preference for the drier ridges. Yeates *et al.* (2002) suggested that concentration and availability of bacterial food sources may be better in thin films of water than in thick films. It is also possible that some food sources such as bacteria and fungi are affected differentially by moisture (Levi *et al.*, 2012). Possibly such food sources could vary between the ridges and depressions here, affecting nematodes as well.

Many of the free-living nematode genera found in the current study (Table 1) have long been known as common inhabitants of freshwater ecosystems (Ferris *et al.*, 1973; Goodey, 1951), thus they are adapted to both soil and freshwater habitats. Little is known of the nematode fauna of natural wetlands in Florida and

the Everglades but it would be interesting to collect nematode samples from such systems and at the interface of land and freshwater systems to observe the transition and adaptation of these common soil nematodes in a range of soil and aquatic habitats.

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