

Nematode Community Composition under Various Irrigation Schemes in a Citrus Soil Ecosystem¹

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Abstract: Interest in the sustainability of farming practices has increased in response to environmental problems associated with conventional agricultural management often adopted for the production of herbaceous crops, ornamentals, and fruit crops. Availability of measures of the status of the soil ecosystem is of immediate importance, particularly for environmental assessment and monitoring programs. This study investigated the effects of various irrigation regimes (an example of an agricultural management practice) on the structure of the nematode fauna in a citrus orchard in the sandy ridge area of Central Florida. Ecological measures such as community structure indices, diversity indices, and maturity indices were assessed and related to irrigation intensity. Maturity index was an effective measure in distinguishing differences between irrigation regimes, whereas other indices of community structure were not. Of various nematode genera and trophic groups, only omnivores and the omnivore genera *Aporcelaimellus* and *Eudorylaimus* responded to irrigation treatments.

Key words: bioindicator, citrus, community structure, diversity, Florida, irrigation regime, maturity index, nematode, soil ecology, sustainable systems.

Conventional agricultural systems have been identified as a significant source of environmental degradation (excessive consumption of nonrenewable resources, groundwater pollution, lake eutrophication, soil erosion, and loss of biodiversity) (Ehrlich, 1988). In recent years, because of environmental and social concerns, more interest has been devoted to developing sustainable systems. Emphasis is placed on conservation of natural resources through reduced inputs of synthetic materials and energy, and through management practices that favor dependence on natural biological ecosystem processes (Elliot and Cole, 1989). Successful transition from current to more sustainable agroecosystems, however, will require detailed information on all components of the ecosystem and appropriate biological measures to evaluate environmental quality.

Nematodes may be useful bioindicators

for estimating environmental quality and disturbance because they are numerous in all environments, where they exhibit diverse life strategies and feeding habits (Freckman, 1988; Yeates et al., 1993). Bongers et al. (1991) related analysis of the nematode community to heavy metal pollution and acidification. Many studies have examined nematode community structure with respect to natural ecosystem succession and environmental disturbance (de Goede et al., 1993; Ettema and Bongers, 1993; Freckman and Ettema, 1993; Wasilewska, 1994; Yeates and Bird, 1994). The effects of management practices on the entire nematode community in agroecosystems also have been investigated (Ferris et al., 1996; Freckman and Ettema, 1993; McSorley and Frederick, 1996; Yeates and Bird, 1994). Environmental disturbance, including agricultural management practices, could be revealed with appropriate diversity and maturity indices. Diversity and maturity indices values were usually less in agricultural fields and greatest in successional or native ecosystems. Within agricultural fields, nematode maturity values (Bongers, 1990) were shown to be greater in rows than between rows of a given crop (McSorley and Frederick, 1996) and lower in organic farming systems, which resulted from an increased density of bacterivorous γ -strategists (Ferris et al., 1996).

There is no information on nematode

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community structure in citrus agroecosystems and on the disturbance to nematode communities produced by agricultural practices in citrus orchards. We hypothesized that as material and energy inputs (fertilizer, water, herbicide) in a citrus agroecosystem were decreased from excessive to more conservative or insufficient levels, nematode community structure would change with values of the input variable. The objectives of this study were to compare nematode communities over a gradient of irrigation in a citrus orchard, and to determine which nematode community measures were effective in differentiating irrigation treatments.

MATERIALS AND METHODS

The experiment was conducted at the University of Florida Citrus Research and Education Center (CREC) in Lake Alfred, Florida. The soil type was Astatula fine sand with pH 6.2 and 0.7% organic matter. The experimental site had been planted to citrus trees (*Citrus* spp.) for the last 50 years. Young citrus trees of 'Hamlin' orange (*Citrus sinensis* (L.) Osbeck) on 'Swingle' citrumelo (*Citrus paradisi* × *Poncirus trifoliata*) rootstock free of endoparasitic nematode pests were planted on 10 April 1991. The experiment was initiated 1 June 1991, and nematode data collection began in 1995. The trees were spaced in rows 6 meters apart, with 3.7 meters between trees in rows. During 1991–1996, nutrient management followed the fertilizer guidelines typical for citrus in Florida (Ferguson et al., 1995). To control weed growth under the tree canopies, plots received glyphosate (N-(phosphonomethyl) glycine, isopropylamine salt) herbicide treatment as needed. Generally, glyphosate was applied 3–4 times per year at approximately 2-month intervals starting in late February.

Trees were watered every fourth day at six different irrigation intensities starting 1 June 1991. Irrigation intensities were expressed as a proportion of the evapotranspiration rate (ET) (0.43 ET, 0.57 ET, 0.85 ET, 1.00 ET, 1.32 ET, and 1.95 ET). These proportions were achieved by using different

size openings of microsprinkler emitters in the irrigation system. To calculate the amount of water required for each month, actual data from the previous 80 years of ET measurements were used. For example, if ET for January of previous years was 0.18 cm of water per day, the treatment 1.00 ET would receive 0.72 (0.18 cm × 4 days) cm of water every fourth day in January. Other treatments would receive an assigned proportion of that amount; for instance, 0.43 ET would receive $0.72 \times 0.43 = 0.31$ cm of water every fourth day. Monthly ET typically varied from a low of 0.18 cm/day of water for January to a high of 0.46 cm/day of water for May.

The experiment was a randomized complete block design with each treatment replicated four times. Data collection started four years after planting to allow nematode community structures sufficient time to reach equilibrium. Soil samples consisting of 16 soil cores (2 cm in diameter and 30 cm in length) taken from under the tree canopy in a diagonal transect pattern were collected on 30 May 1995, 9 September 1996, 10 February 1996, and 16 May 1996. The soil cores were mixed and passed through a sieve (2-mm pores) to separate root tissue from the soil. A soil subsample of approximately 100 cm³ was used immediately to estimate populations of *Phytophthora nicotianae* Breda de Haan (Timmer et al., 1988), a pathogen causing citrus root decay. The remaining soil was stored in sealed plastic bags at 10 °C for up to 15 hours. Nematodes were then extracted from 100-cm³ subsamples by wet sieving followed by centrifugation (Jenkins, 1964). Extracted nematodes were killed with heat, counted, and identified primarily to genus with the aid of an inverted microscope. To determine soil moisture, 4 to 7 g of soil from each soil sample was oven-dried for about 24 hours at 60 °C.

The abundance of each nematode genus, expressed as numbers of specimens of the same genus, total number of nematodes of different genera, and the total number of genera (richness) in each sample, was recorded. Nematode genera were assigned to the following trophic groups: algivores, bac-

terivores, fungivores, omnivores, plant associates, plant parasites, or predators (Yeates et al., 1993), and decomposition associates (bacterivores and fungivores together). The total abundance of nematodes in each trophic group and the percentage of each trophic group within the entire nematode community were determined for each sample.

Based on the genera and trophic group densities, several ecological indices of nematode community structure were calculated. The Shannon-Weaver diversity index (Shannon and Weaver, 1949) was used to compare diversity of either genera or trophic groups:

$$\text{genus (g) or trophic group (t) diversity} = H_g \text{ or } H_t = \sum p_i \log_e p_i \quad (1)$$

where p_i is the proportion of the i th genus or trophic group in the sample. Simpson's (1949) index:

$$\text{genus (g) or trophic group (t) dominance} = \lambda_g \text{ or } \lambda_t = \sum (p_i)^2 \quad (2)$$

was used to compare either generic or trophic group dominance. A reciprocal transformation of the Simpson's dominance index offered an additional measure of diversity either at genus or trophic group (Freckman and Ettema, 1993):

$$\text{Simpson's genus (g) diversity} = 1/\lambda_g \quad (3)$$

Maturity indices *MI* and *PPI* were calculated following Bongers (1990). The *MI* is a weighted mean of the individual *c-p* values:

$$MI = \sum \nu_i \cdot f_i \quad (4)$$

where ν_i is the *c-p* value of taxon i , and f_i is the frequency of that taxon in a sample. *C-p* values, ranging from 1 for colonizers (*c*) to 5 for persisters (*p*), are assigned to nematode families to illustrate their life strategies and, thus, conditions of the surrounding environment (Bongers, 1990). While *MI* relates to the "free-living" component of nematode community (bacterial, fungal, and algal feeders, omnivores, predators, and plant associates, but not plant parasites), the plant parasite index (*PPI*) contains information exclusively on plant-parasitic families. The formula is as for *MI* except that only total abundance of plant-parasitic nematodes is

the basis for calculation of frequencies of plant-parasitic families. To avoid separation of trophic habits, a modified maturity index or total *MI* ($\sum MI$) (Yeates, 1994) was also calculated. $\sum MI$ includes both plant-parasitic and free-living nematodes. Fungivore to bacterivore ratio (*F/B*) (Freckman and Ettema, 1993) and the ratio of fungivores + bacterivores to plant parasites (*F + B/PP*) (Wasilewska, 1994) were determined to illustrate decomposition and nutrient mineralization pathways and primary production. Estimation of primary production was accomplished by harvesting trees in February 1995 and 1996. However, since the trees had not yet reached their productive maturity, the two harvesting seasons were pooled into one crop yield value to better represent tree fruit production.

Effects of irrigation intensity on the above measures of nematode community structure were determined by analysis of variance, single-degree-of-freedom orthogonal contrasts, and correlation analysis with SAS software (SAS Institute, Cary, NC).

RESULTS

The abundances of the most numerous nematode genera are listed in Table 1. The densities of the following rare or occasional genera were not listed in the table but were included in their trophic groups: *Alaimus*, *Bunonema*, *Chronogaster*, *Teratocephalus* (bacterivores); *Diphtherophora* (fungivore); *Mononchus*, *Mylonchulus*, *Prionchulus*, *Carcharolaimus*, *Nygolaimus* (predators); *Mesodorylaimus* (omnivore); *Monochromadora* (algivore). Other Dorylaimida were *Ecumenicus* and *Pungentus* spp., and miscellaneous plant parasites included *Meloidogyne*, *Tylenchulus*, *Trichodorus*, and *Xiphinema* spp. The abundances of most nematode genera did not appear to respond to the irrigation gradient in any predictable manner. However, the abundance of *Aporcelaimellus* and *Eudorylaimus* spp. had patterns with season and irrigation treatments through the year. Irrigation rate was correlated significantly ($P \leq 0.05$) with numbers of *Eudorylaimus* spp. on all sampling occasions ($r = 0.61$ for May

TABLE 1. Nematode abundance per 100 cm³ of soil in samples taken from under the citrus tree canopy.

Feeding habit	Taxonomic unit	<i>c-p</i> value ^a	May 1995	October 1995	February 1996	May 1996
Bacterivores	Monhysterida	1	4 ± 4 ^b	2 ± 2	1 ± 2	2 ± 2
	Rhabditidae	1	40 ± 29	24 ± 14	27 ± 15	21 ± 9
	<i>Acrobelles</i>	2	73 ± 37	48 ± 26	71 ± 44	59 ± 21
	<i>Acrobeloides</i>	2	21 ± 17	3 ± 6	3 ± 4	20 ± 13
	<i>Cephalobus</i>	2	62 ± 30	48 ± 21	78 ± 37	72 ± 28
	<i>Eucephalobus</i>	2	13 ± 7	7 ± 6	8 ± 7	9 ± 7
	<i>Plectus</i>	2	1 ± 2	2 ± 2	1 ± 1	2 ± 3
	<i>Wilsonema</i>	2	5 ± 5	8 ± 7	7 ± 7	3 ± 3
	<i>Zeldia</i>	2	58 ± 30	14 ± 9	30 ± 17	51 ± 24
	<i>Prismatolaimus</i>	3	18 ± 13	8 ± 11	5 ± 6	9 ± 10
	Fungivores	<i>Aphelenchoides</i>	2	4 ± 3	2 ± 2	4 ± 5
<i>Aphelenchus</i>		2	79 ± 38	36 ± 15	75 ± 36	56 ± 23
Predators	<i>Prionchulus</i>	4	4 ± 5	0 ± 1	0 ± 0	0 ± 1
Omnivores	<i>Dorylaimida</i>	5	6 ± 7	10 ± 7	3 ± 3	9 ± 7
Root associates	<i>Tylenchidae</i>	2	32 ± 44	15 ± 15	13 ± 12	15 ± 12
Plant parasites	<i>Belonolaimus</i>	3	4 ± 7	1 ± 1	2 ± 2	3 ± 4
	<i>Criconemoides</i>	3	2 ± 4	1 ± 2	2 ± 5	4 ± 9
	<i>Hoplotaimus</i>	3	2 ± 3	2 ± 3	2 ± 3	3 ± 3
	Miscellaneous ^c	3-5	9 ± 12	5 ± 11	13 ± 23	14 ± 17

^a *c-p* value: colonizer-persister value (Bongers, 1990).

^b Each entry represents an arithmetic mean ± standard deviation of four replicates per treatment pooled across six irrigation treatments (0.43, 0.57, 0.85, 1.00, 1.32, and 1.95 ET) (N = 24). ET: evapotranspiration rate.

^c Miscellaneous plant parasites included: *Meloidogyne*, *Tylenchulus*, *Trichodorus*, and *Xiphinema* spp.

1995, $r = 0.50$ for October 1995, $r = 0.42$ for February, 1996 and $r = 0.36$ for May 1996) and for *Aporcelaimellus* spp. in May ($r = 0.48$) and October ($r = 0.56$) 1995. According to orthogonal contrasts, the genus *Eudorylaimus* was effective in distinguishing treatments with greater (1.95, 1.32 ET) versus lower (1.00, 0.85, 0.57, 0.43 ET) irrigation levels in May and October 1995, and February 1996 ($P \leq 0.05$), and the genus *Aporcelaimellus* was effective in May and October 1995 ($P \leq 0.05$) (Table 2). Some of the bacterivorous genera such as *Acrobelles*, *Eucephalobus*, *Prismatolaimus*, and *Zeldia* seemed to show seasonal patterns with higher densities in May as compared to February 1996 or October 1995, but did not show a significant response to irrigation intensity.

Total abundance of nematodes per 100 cm³ soil was relatively low and ranged from 220 in October 1995 to 572 in May 1995 (Table 3). Total densities were more influenced by the time of sampling than by irrigation rate. Typically, higher numbers of total nematodes were found in May of both years. Of the trophic groups, only omnivores were affected ($P \leq 0.05$) by irrigation intensity (Table 2). A positive correlation of omni-

nivore numbers with irrigation intensity was persistent throughout the entire year of sampling and ranged from $r = 0.40$ in February 1995 to $r = 0.59$ in May 1995. Correlation coefficients were improved when omnivores were expressed as a proportion of the entire nematode community. While the omnivore abundance was a useful measure in differentiating treatments with greater vs. smaller water applications during May and October 1995, and February 1996, omnivores expressed as the percentage of the nematode community differentiated treatments on all sampling dates ($P \leq 0.05$) (Table 2).

Nematode communities were dominated by bacterial feeders, which comprised 54 to 73% of the total nematode community. Fungivores and omnivores were the next most abundant trophic groups. Root associates (*Tylenchidae*) and plant parasites were similarly abundant, and their proportions ranged from 2 to 11%. Predatory and algivorous nematodes were least common and were absent in many samples (Table 3).

Generally, generic richness was usually greatest in May and lowest during February 1995 (Table 4). No response to irrigation

TABLE 2. Nematode numbers and ecological indices showing significant ($P \leq 0.05$) differences between treatments receiving smaller (0.43, 0.57, 0.85, and 1.00 ET) amounts of water and treatments receiving greater (1.35 and 1.97 ET) amounts of water. Irrigation intensity was based on historical data of evapotranspiration rate (ET).

Sampling date	Irrigation Intensity						Contrast P -values ^a
	0.43 ET	0.57 ET	0.85 ET	1.00 ET	1.32 ET	1.97 ET	
Omnivorous genera (numbers/100 cm ³)							
<i>Aporcelaimellus</i> ($c-p5$) ^b							
May 1995	4 ± 3 ^c	4 ± 3	10 ± 4	8 ± 6	13 ± 7	14 ± 11	$P < 0.05$
October 1995	6 ± 2	6 ± 2	9 ± 3	6 ± 2	9 ± 7	16 ± 4	$P < 0.01$
February 1996	5 ± 3	6 ± 7	10 ± 13	6 ± 1	10 ± 11	12 ± 9	ns
May 1996	14 ± 19	10 ± 6	15 ± 7	12 ± 4	23 ± 14	22 ± 11	ns
<i>Eudorylaimus</i> ($c-p4$)							
May 1995	5 ± 2	5 ± 2	4 ± 4	2 ± 2	11 ± 4	17 ± 8	$P < 0.01$
October 1995	4 ± 3	7 ± 4	6 ± 3	5 ± 5	10 ± 8	15 ± 7	$P < 0.01$
February 1996	6 ± 3	6 ± 7	5 ± 3	6 ± 5	10 ± 11	16 ± 10	$P < 0.05$
May 1996	8 ± 6	7 ± 6	9 ± 4	10 ± 3	15 ± 10	13 ± 7	ns
Total omnivorous nematodes (numbers/100 cm ³)							
May 1995	10 ± 7	18 ± 12	21 ± 4	19 ± 12	27 ± 12	40 ± 21	$P < 0.01$
October 1995	18 ± 3	25 ± 9	29 ± 17	15 ± 6	31 ± 16	45 ± 20	$P < 0.05$
February 1996	14 ± 8	13 ± 14	19 ± 16	13 ± 5	24 ± 23	33 ± 18	$P < 0.05$
May 1996	29 ± 25	26 ± 14	35 ± 7	26 ± 4	56 ± 25	46 ± 7	$P < 0.01$
Omnivorous nematodes (as % of total nematodes)							
May 1995	2 ± 1	4 ± 3	4 ± 2	4 ± 3	6 ± 2	11 ± 4	$P < 0.01$
October 1995	7 ± 2	10 ± 4	11 ± 4	7 ± 1	14 ± 7	19 ± 8	$P < 0.01$
February 1996	4 ± 4	3 ± 3	4 ± 3	4 ± 1	6 ± 5	11 ± 5	$P < 0.05$
May 1996	6 ± 4	7 ± 3	9 ± 3	7 ± 2	12 ± 4	15 ± 2	$P < 0.01$
Maturity Index (MI)							
May 1995	2.03 ± 0.06	2.10 ± 0.10	2.10 ± 0.04	2.06 ± 0.14	2.18 ± 0.16	2.29 ± 0.09	$P < 0.01$
October 1995	2.14 ± 0.07	2.18 ± 0.12	2.21 ± 0.09	2.11 ± 0.03	2.24 ± 0.18	2.43 ± 0.24	$P < 0.01$
February 1996	2.06 ± 0.10	2.05 ± 0.07	2.04 ± 0.08	2.00 ± 0.07	2.09 ± 0.16	2.23 ± 0.10	$P < 0.05$
May 1996	2.13 ± 0.11	2.17 ± 0.08	2.22 ± 0.08	2.17 ± 0.05	2.32 ± 0.10	2.37 ± 0.03	$P < 0.01$
Total Maturity Index (ΣMI)							
May 1995	2.05 ± 0.10	2.14 ± 0.13	2.15 ± 0.03	2.05 ± 0.13	2.20 ± 0.19	2.31 ± 0.13	$P < 0.01$
October 1995	2.16 ± 0.06	2.20 ± 0.13	2.25 ± 0.10	2.14 ± 0.04	2.33 ± 0.16	2.45 ± 0.24	$P < 0.01$
February 1996	2.10 ± 0.09	2.09 ± 0.05	2.11 ± 0.06	2.04 ± 0.06	2.20 ± 0.16	2.25 ± 0.09	$P < 0.01$
May 1996	2.19 ± 0.12	2.21 ± 0.09	2.26 ± 0.07	2.22 ± 0.05	2.38 ± 0.13	2.41 ± 0.05	$P < 0.01$

^a P -values for the orthogonal contrast between smaller ET (0.43, 0.57, 0.85, 1.00) and greater ET (1.35, 1.97) treatments.

^b $C-p$ values (colonizer-persister) taken from Bongers (1990).

^c Data represent arithmetic means ± standard deviations. Each entry was estimated from four replicates per treatment.

intensity could be observed. Shannon-Weaver diversity indices for genus and trophic groups did not vary significantly with either season or irrigation rate (Table 4). Genus and trophic group dominance were more variable, but no consistent tendency was present. Simpson's diversity responded only to seasonal change and was always lowest in February 1995 (5.55–7.00) and highest in May 1996 (7.14–9.20). Of all the indices of nematode community structure, only maturity indices were affected by the irrigation treatments. Positive correlations ($P \leq 0.05$) with irrigation intensity were observed on all

sampling dates for MI successively ($r = 0.58, 0.48, 0.39, \text{ and } 0.69$) and for ΣMI successively ($r = 0.48, 0.52, 0.47, \text{ and } 0.66$). Both indices could distinguish treatments receiving greater amounts of water (1.95 and 1.32 ET) (contrast procedure) from treatments with smaller irrigation levels ($P \leq 0.05$) (Table 2). The ratios F/B and $F + B/PP$ varied considerably with respect to season and irrigation rate, but without any consistent pattern (Table 4).

Irrigation treatments were not reflected in either soil moisture or root biomass (Table 4). *Phytophthora nicotianae* levels

TABLE 3. Total abundance and trophic group composition per 100 cm³ of soil in samples taken from under the citrus trees canopy.

Trophic group	May 1995	October 1995	February 1996	May 1996
	Abundance			
Total	461 ± 138 ^a	253 ± 84	362 ± 143	382 ± 108
Bacterivore	296 ± 99	163 ± 73	231 ± 103	248 ± 72
Fungivore	83 ± 39	37 ± 15	79 ± 36	57 ± 24
Algivore	1 ± 3	1 ± 2	0 ± 1	0 ± 2
Predator	6 ± 7	1 ± 1	0 ± 1	1 ± 1
Plant parasite	22 ± 15	9 ± 12	18 ± 23	24 ± 21
Bacterivore and Fungivore	378 ± 117	415 ± 154	310 ± 127	306 ± 86
	Percentage of total numbers			
Bacterivores	64.4 ± 9.0	62.5 ± 11.1	63.6 ± 8.7	65.2 ± 7.0
Fungivores	18.2 ± 6.5	15.8 ± 6.5	22.3 ± 8.0	15.0 ± 5.1
Algivores	0.3 ± 0.6	0.1 ± 0.2	0.1 ± 0.2	0.1 ± 0.4
Predators	1.3 ± 1.5	0.2 ± 0.4	0.1 ± 0.2	0.3 ± 0.4
Root associates	6.1 ± 6.5	6.0 ± 6.3	3.4 ± 2.5	3.8 ± 2.7
Plant parasites	3.8 ± 3.6	3.9 ± 5.7	5.0 ± 4.8	6.0 ± 4.5
Bacterivores and Fungivores	82.6 ± 7.8	78.3 ± 10.0	85.9 ± 6.9	80.2 ± 5.6

^a Data represent arithmetic means ± standard deviations of four replicates per treatments pooled across six irrigation treatments (0.43, 0.57, 0.85, 1.00, 1.32, and 1.95 ET) (N = 24) on four sampling dates. ET: evapotranspiration rate.

tended to increase as the experiment progressed from May 1995 to May 1996, but were not correlated with irrigation intensity. In general, increasing water rate positively affected fruit production (20.8 t/ha for 0.43 ET, 27.5 t/ha for 0.57 ET, 29.8 t/ha for 0.85 ET, 28.6 t/ha for 1.00 ET, 30.9 t/ha for 1.32 ET, and 30 t/ha for 1.95 ET). However, increases higher than 0.85 ET did not result in statistically significant ($P \leq 0.05$) yield improvements.

DISCUSSION

Irrigation is an important management practice in citrus orchards worldwide, as well as in Florida. Higher water application rates usually lead to higher tree growth and fruit yield. Overuse of water, however, may not result in additional yield increase. The wide range of irrigation in this experiment represented various water supply schemes used by citrus growers. In this study, nematode com-

TABLE 4. Soil moisture, *Phytophthora nicotianae* levels, root biomass, and ecological indices obtained from soil samples taken from under the citrus tree canopy.

Ecological Index ^a	May 1995	October 1995	February 1996	May 1996
Soil moisture (%)	2.1 ± 0.6 ^b	4.0 ± 0.7	4.9 ± 0.5	4.4 ± 0.7
<i>P. nicotianae</i> (CFU)	0 ± 0	4.6 ± 6.7	4.7 ± 7.6	11.3 ± 15.7
Root wt. (grams per 100 grams soil)	0.09 ± 0.03	0.1 ± 0.2	nd	nd
Richness	20.1 ± 3.3	18.9 ± 2.4	17.8 ± 2.5	20.6 ± 2.7
F/B	0.30 ± 0.15	0.27 ± 0.15	0.37 ± 0.17	0.24 ± 0.10
F+B/PP	42.7 ± 40.4	56.0 ± 67.2	30.8 ± 32.3	20.0 ± 11.8
H_t	1.03 ± 0.17	1.06 ± 0.17	1.00 ± 0.14	1.04 ± 0.13
λ_t	0.47 ± 0.09	0.46 ± 0.10	0.48 ± 0.09	0.47 ± 0.08
H_g	2.33 ± 0.19	2.30 ± 0.10	2.11 ± 0.16	2.35 ± 0.12
λ_g	0.13 ± 0.03	0.14 ± 0.02	0.17 ± 0.03	0.13 ± 0.02
1/ λ_g	7.98 ± 1.92	7.38 ± 0.83	6.20 ± 1.17	8.03 ± 1.19
PPI	3.09 ± 0.16	3.03 ± 0.11	3.08 ± 0.15	3.04 ± 0.11

^a CFU: colony-forming units (CFU per 10 g dry soil); Root wt: dry root weight (grams per 100 grams dry soil); Richness: number of taxonomic units (genera); F/B: ratio of fungivorous to bacterivorous nematodes; F+B/PP: ratio of fungivorous and bacterivorous nematodes to plant parasites; H_t : Shannon trophic diversity; λ_t : trophic dominance; H_g : Shannon genus diversity; λ_g : genus dominance; 1/ λ_g : Simpson's genus diversity; PPI: plant parasite index.

^b Each entry represents an arithmetic average and its standard deviation of four replicates across six irrigation rates (n = 24); nd = no data.

munity structure was clearly influenced by the water treatments. Of the many nematode genera representing all trophic groups, only omnivores (*Aporcelaimellus* and *Eudorylaimus* spp., in particular) responded strongly to irrigation levels. Their total numbers and relative proportions increased steadily with increased irrigation. The lack of correlation between omnivores and soil moisture suggests that an increase of omnivores can be explained by long-term effects of elevated water supply rather than by the temporary soil water content. The very high sand content in Florida soils exposed to rather high temperatures results in frequent soil water fluctuations through drying. Continuous applications of higher water rates probably stabilize the soil environment and create better opportunities for establishment of nematode communities with a higher proportion of *K*-strategists, which seems to replace some of the bacterial feeders. Of the various trophic groups, only omnivores, particularly when expressed as the proportion of the nematode community, were useful in detecting smaller and greater irrigation regimes on almost all sampling occasions. An increase of omnivorous nematodes in irrigated plots also was observed in a Swedish pine forest (Sohlenius and Wasilewska, 1984). Other *K*-strategists, such as predacious nematodes, were rare in our soil samples, which is rather typical for agroecosystems (Ferris et al., 1996; Freckman and Ettema, 1993; McSorley and Frederick, 1996; Wasilewska, 1994, Yeates and Bird, 1994).

Although bacterivores and plant parasites did not respond to water treatments in this citrus orchard, their abundances differed from other agroecosystems. Bacterial feeders were very abundant in the study soil, comprising 65–72% of the total nematode community compared to about 50% for Florida soybean fields and Polish meadows (McSorley and Frederick, 1996; Wasilewska, 1994), and 20–30% for some south Australian soils (Yeates and Bird, 1994). This predominance of bacterivores may be associated with their particular adaptations to highly variable soil environments with very

low soil organic matter content. Citrus root decay caused by *Phytophthora nicotianae* can also influence the abundance of bacterivores. However, as a result of relatively low *P. nicotianae* population numbers, this relationship was not observed in our study. The densities of plant-parasitic nematodes were unusually low (2–10%), especially when compared to studies mentioned above that reported them comprising 30–50% of the total community. Such a low proportion of plant parasites probably reflects the use of a citrus-nematode-resistant rootstock free of other endoparasitic nematode pests, and effective ground cover management practices under the trees. To minimize the competition for water and nutrients between the citrus tree and other plants (i.e. weeds), the ground directly under the tree is kept free of any vegetation (treated with herbicide). Exclusion of additional roots that could provide food resources for many plant-parasitic nematodes most probably limited their abundance and diversity. Also, the endoparasites typically associated with citrus were not present in this grove. *Belonolaimus* spp. were consistently present in all soil samples since they feed on citrus roots (Duncan and Cohn, 1990) as well as weed hosts. Periodic flushes of weed growth allowed the maintenance of populations of other plant parasites (*Criconemoides* and *Hoplolaimus* spp.), but at much lower numbers. Sporadic appearance of *Meloidogyne*, *Trichodorus*, and *Xiphinema* spp. suggested the weeds were their preferred hosts.

Interpretation of changes in community structure can be based on a direct analysis of the dynamics of all taxa, or on ecological indices derived from taxonomic data. Some of these indices have been used effectively for comparisons of ecosystems with varying degrees of disturbance, succession, productivity, or pollution (Bongers et al., 1991; Bongers and Ettema, 1992; Ferris et al., 1996; Freckman and Ettema, 1993; McSorley and Frederick, 1996, Neher and Campbell, 1994; Wasilewska, 1994; Yeates and Bird, 1994). In the present study, maturity indices were the only measures sensitive to irrigation. Maturity index *sensu* Bongers

(1990) and the total maturity index sensu Yeates (1994) were equally effective in separating low vs. high irrigation management schemes. Higher values of maturity indices with increased irrigation were caused by the higher proportions of omnivores, suggesting that communities are more stable under high irrigation regimes. Maturity indices or omnivorous nematodes could illustrate the water management history, where higher values of *MI* or higher proportions of omnivores would indicate excessive consumption of water. As such, they could be useful indicators of irrigation history in citrus orchards. Whether similar results could be obtained under slightly different experimental conditions (fertilization rates, fertilizer type, pest management, rainfall, etc.) is an important question that requires further investigation. The plant-parasitic index was not useful since predominant parasites were in the $c-p = 3$ group. Subtle deviations from $PPI = 3$ simply illustrated occasional appearances of *Xiphinema* and *Trichodorus* spp.

In terms of nematode community structure, very well irrigated citrus soils in Florida are more sustainable since they promote conditions under which the nematode species most sensitive to environmental stress (omnivorous K-strategists) can exist. Long-lived perennial citrus roots, with limited invasion by weed hosts that promote r-strategists, would support this condition. It has been demonstrated that strong fluctuations of soil moisture in the upper 15 cm negatively affect root life span; thus, soil that is irrigated well on a regular basis would promote more stable root system (Eissenstat and Yanai, 1997). However, conservation of natural resources, including water, is a major goal of sustainable agriculture. What is sustainable for nematodes may not necessarily be sustainable from the agroecosystem management perspective. Indeed, our yield data indicated that irrigation rates above 0.57 ET were wasteful of water and energy. In this scenario, sustainable water management practices probably do not coincide with the stability or sustainability of the soil citrus ecosystem from the nematode community perspective.

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