Nematode Interactions with Weeds and Sugarcane Mosaic Virus in Louisiana Sugarcane¹

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Abstract: Weeds did not appear to serve as reservoirs for phytophagous Louisiana sugarcane nematode populations except for Criconemella spp., Meloidogyne spp., Tylenchorhynchus annulatus, and total phytophagous nematode densities were lower on weed-stressed cane and were accompanied by reduced accumulations of free cysteine, proline, and 13 other free amino acids in sugarcane. A significant weed-virus interaction for sugarcane free cysteine accumulation was detected; T. annulatus populations were highly correlated (r = 0.59, $P \leq 0.001$) with the weed-induced and virus-induced changes in free cysteine. Sugarcane nematodes interacted differently with the weed and virus stresses and changes in host plant stress-related free amino acid concentrations.

Key words: free amino acid, Saccharum hybrid, sugarcane, sugarcane mosaic virus, Tylenchorhynchus annulatus, weed.

Of the 14 plant-parasitic nematode genera reported in Louisiana soils on which sugarcane, interspecific hybrids of Saccharum, is grown, Birchfield (8) identified Trichodorus, Tylenchorhynchus, Meloidogyne, and Pratylenchus spp. as the major pests. Crop loss prediction models are based on initial phytophagous nematode populations (20) but neglect such factors as tillage regimes (14,21), organic soil augmentation (42,47), varietal resistance (3,29,38), number of seasons a cultural practice is implemented (5), size and nutritional quality of available root space (6,41), fungal-nematode (20,28,40) and nematode-nematode (18,23) interactions, insect herbivory (39), and antagonistic plant species (9,26).

Avocado roots were shown to harbor greater nematode populations in weedy systems than do weed-free areas (36). The effects of weed cover on phytophagous nematodes and sugarcane free amino acid (FAA) levels have not been examined. In light of research on the contribution of annual weeds toward sugarcane borer, *Diatraea saccharalis* (F.), control (2,46) and the examination of water stress-induced FAA concentration changes in various plants (7,44,50), it is important to study the interactions among different pest organisms with their environment.

Plant virus stresses also may alter the nematode (13,23,28) and FAA (1,16,17) levels of various crop hosts. Sugarcane mosaic virus (SCMV), a wide-spread Louisiana sugarcane disease (31), was implicated in synergistic and additive yield loss interactions with ratoon stunting disease (30) and *Pythium graminicola* (4). The potential interrelationship of SCMV with nematode abundances and FAA accumulations in sugarcane has not been addressed.

White (50) indicated that host plant stress-induced changes in FAA concentrations may contribute to the proliferation of phytophagous organisms by providing easily assimilated nitrogen. Host plant free proline levels, in particular, have been shown to respond to nematode (15, 19, 24), bacterial (37,45), and viral (16,28) stresses. Lewis and McClure (32) indicated that cotton resistance to Meloidogyne incognita may be related to accumulations of specific FAA. Nematode infestations may be linked with other biotic stress agents, and the relationship is probably mediated through the plant (39,49). The objective of this study was to observe sugarcane nematode interactions

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with common biotic stresses and to delineate relationships associated with sugarcane FAA levels.

MATERIALS AND METHODS

Studies were conducted on a 2.5-ha block of sugarcane (interspecific hybrids of Saccharum, variety CP 74-383) in Assumption Parish, Louisiana, in 1985 and 1986. Moisture content of the unirrigated soil (Commerce loam; 8% sand, 68% silt, 24% clay) varied from saturation to occasional topsoil dessication. The experiment was arranged in a randomized complete block design replicated six times with a 2×2 split plot arrangement of treatments. Each plot was 0.2 ha in area and rows were 1.8 m apart. The four treatments were 1) weeds and virus-infected cane (WV), 2) weed-free and virus-infected cane (WFV), 3) weeds and virus-free or healthy cane (WH), and 4) weed-free and virus-free or control cane (WFH). SCMV-infected sugarcane stools were randomly located within each plot and tagged for future reference in April of each year. In early May, WF plots received a tank mix application of metribuzin (1.3 kg a.i./ha) and dicamba + 2,4-D (1.3 kg a.i./ ha and 1.1 kg a.i./ha, respectively) from a tractor-mounted spray boom. Weeds in weed-free (WF) habitats were spot treated with metribuzin (25.5 g a.i./liter) each season. Weedy (W) plots were spot sprayed with dicamba (9.6 g a.i./liter) to enhance monocot species that were possible alternate hosts of sugarcane nematodes. Johnsongrass, Sorghum halepense L., an unacceptably competitive perennial weed in most agroecosystems, was systematically removed from all habitats by spot spraving with asulam (2% a.i.) and by hand-roguing. Weed samples were collected in June, August, and September of both years. Total weed biomass was determined by taking clipped vegetation from five random 0.5 m² quadrats in each treatment replicate. Two of the five subsamples were recorded by weed species. All samples were oven dried for 48 hours at 94 C and weighed.

Soil samples for nematode assay were collected with an Oakfield soil probe

(2-cm-d) to a depth of 25 cm. Two 18-core subsamples (250 ml each) were taken within 8 cm of 36 randomly selected cane stalks from the W and WF habitats in June, August, and October of both years. In October nematode assay samples were collected at the base of 36 SCMV-infected and 36 SCMV-free plants and along the row tops at least 45 cm from sugarcane stools (interstool gaps). All soil samples were kept in plastic-lined paper bags and transported to the Mississippi State University Plant Pathology Extension Service Laboratory for nematode extraction, by elutriation and sugar flotation centrifugation, and for counting.

In late October 1986 the basal 10 cm of four healthy and four SCMV-infected sugarcane stalks were randomly selected and cut from each W and WF plot, sealed in plastic bags, and placed on ice. Five milliliters of juice was squeezed and combined within each group of four stalks. A 1-ml aliquot was purified from each four-stalk juice sample using 0.45-µm-pore membrane filters mounted on plastic syringes. The filtrate was stored at -100 C until FAA concentrations were measured by HPLC. All FAA were quantified except serine, which was confounded with glucosamine. To determine whether the monocot weeds served as reservoirs for nematodes, comparisons involving gap populations were performed using the Student t-statistic. SAS ANOVA and correlation procedures (27) were employed to delineate relationships among the weed and nematode populations, and FAA accumulations.

RESULTS

Weeds in W plots were broadleaf signalgrass, Brachyaria platyphylla Nash; hairy crabgrass, Digitaria sanguinalis Scop.; Echinochloa spp.; bermudagrass, Cynodon dactylon Pers.; broadleaf panicum, Panicum dichotomiflorum Michx.; and yellow nutsedge, Cyperus esculentis L. Relative biomass of some weed species was higher early in the season, others built up as the season progressed (Table 1). The nematodes most

Month	Total weed biomass $(g/0.5 \text{ m}^2 \pm \text{SE})$	Panicum dichotomiflorum	Brachyaria platyphylla	Digitaria sanguinalis	Echinochloa spp.	Cynodon dactylon
Mav	66 ± 12	0.6	6.0	89.8	2.8	0.6
August	115 ± 32	2.2	3.2	90.1	1.5	3.0
October	41 ± 4	3.8	1.4	70.4	2.4	22.2

TABLE 1. Relative biomass (% of total) of annual monocot weed species in weedy regimes averaged over 1985 and 1986.

Weed biomass was determined using six replicates of two 0.5-m² quadrats/0.02-ha plot.

commonly collected were ring, Criconemella curvata and C. onoensis; root-knot, Meloidogyne incognita and M. javanica; stubby root, Paratrichodorus minor; lesion, Pratylenchus zeae; reniform, Rotylenchus reniformis; and stunt, Tylenchorhynchus annulatus. Lance, Hoplolaimus columbus, and spiral, Helicotylenchus dihystera and H. pseudorobustus, each composed less than 1 % of the total phytophagous nematode populations (Fig. 1).

Tylenchorhynchus annulatus populations were as much as 79% lower on W cane after August 1985 ($P \leq 0.05$), and Criconemella spp. and Meloidogyne spp. followed a similar pattern (Fig. 1). Such weed-related population differences were not observed for P. minor, P. zeae, R. reniformis, or nonphytophagous nematodes (Fig. 1).

Weed effects on nematode populations: Weedy cane harbored 44 and 40% more phytophagous nematodes than WF cane in June and August of 1985, respectively. Thereafter, plant-parasitic nematodes were reduced by as much as 46% ($P \leq 0.03$) on W cane (Fig. 2F).

In 1985 P. minor, T. annulatus, P. zeae, and total phytophagous nematode species were more abundant in W gaps than in WF gaps by 100 ($P \le 0.14$), 57 ($P \le 0.13$), 47, and 49%, respectively. In 1986 these groups were 0, 71 ($P \leq 0.1$), 36, and 41% ($P \leq$ 0.15) lower in the W gaps than WF gaps (Fig. 2). Meloidogyne spp. juvenile numbers were lower (62%) in W gaps only in 1986. Criconemella spp. were 47 and 21% more abundant in W gaps in 1985 and 1986, respectively. Nonphytophagous nematode levels in W gaps were 68% ($P \leq 0.01$) higher in 1985 and 35% ($P \le 0.12$) higher in 1986 than in WF plots (Fig. 2). Relative abundance of the nematode groups (percentage of total plant-parasitic nematodes) were not affected by the weed regimes. Criconemella, the predominant genus, comprised up to 53% of the phytophagous nematodes, but R. reniformis, Meloidogyne spp., and P. minor each accounted for less than 7% in either

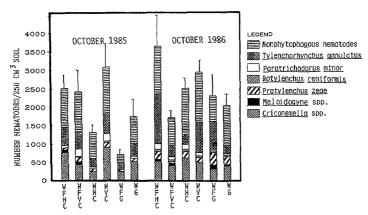


FIG. 1. Mean abundances (\pm SE) of phytophagous nematode species and nonphytophagous nematodes on weed-free healthy cane (WFHC), weed-free sugarcane mosaic-infected cane (WFVC), weedy healthy cane (WHC), weedy sugarcane mosaic virus-infected cane (WVC), weed-free interstool gaps (WFG), and weedy interstool gaps (WG) in a Louisiana sugarcane (CP 74-383) field in October 1985 and 1986.

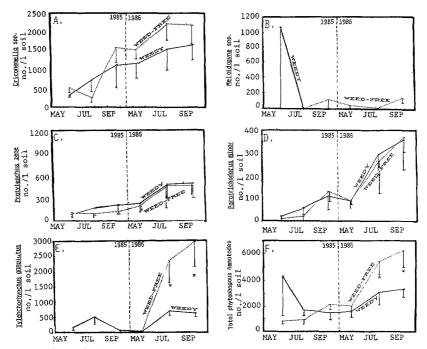


FIG. 2. Mean numbers of phytophagous nematodes $(\pm SE)$ in weedy and weed-free sugarcane rhizospheres in June, August, and October 1985 and 1986. Asterisks indicate significant differences between the two weed regimes. A) Criconemella spp. B) Meloidogyne spp. C) Pratylenchus zeae. D) Paratrichodorus minor. E) Tylenchorhynchus annulatus. F) Total phytophagous nematode populations.

weed regime. Relative abundance of total nonphytophagous and plant-parasitic nematode populations (percentage of total nematodes) was not affected by the presence of weeds.

In W gaps and W cane, Criconemella spp., P. zeae, R. reniformis, P. minor, T. annulatus, and total phytophagous nematode populations were approximately equal. By 1986 Criconemella spp., P. minor, T. annulatus, and total phytophagous nematode densities were 49 ($P \leq 0.08$), 79 ($P \leq 0.05$), 26, and 40% ($P \leq 0.07$) greater, respectively, on W cane than in W gaps. Meloidogyne spp. was found in W gaps but not on the cane (Fig. 2). Pratylenchus zeae was evenly distributed in W cane rows.

Weed-free cane harbored more nematodes than WF gaps in 1985 and 1986, respectively, as follows: 63 ($P \le 0.05$) and 70% ($P \le 0.05$) more Criconemella spp., 100 ($P \le 0.05$) and 79% ($P \le 0.01$) more P. minor, 67 ($P \le 0.05$) and 46% ($P \le 0.05$) more T. annulatus, 49 ($P \le 0.05$) and 45% ($P \le 0.05$) more total phytophagous, and 76 ($P \leq 0.005$) and 46% ($P \leq 0.05$) more nonphytophagous nematodes (Fig. 2). *Meloidogyne* spp. juvenile population trends were similar to those observed in W plots. *R. reniformis* populations were uniform on the sugarcane rows.

Free alanine, arginine, asparagine, cysteine, glycine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, proline, threonine, valine, and total FAA in W cane were lower than in WF cane ($P \leq 0.05$) (Table 2). Asparagine was 29 and 28% of the total measurable FAA in W and WF cane, respectively. Relative amounts of each FAA were unaffected by weed pressure, except that cysteine was 86% ($P \leq$ 0.001) lower in W cane.

Interactions among weeds, SCMV, nematodes, and FAA: Weedy and weed-free plots harbored SCMV infection levels of 11 and 19% in 1985, and 12 and 26% in 1986. WV cane had 44% less free isoleucine and 55% less free phenylalanine ($P \le 0.05$) than WH cane; and 65, 54, 69, 48, 50, 65, 65, 72, 73, 72, 68, 64, and 41% less ($P \le 0.05$)

Free amino acid	WFH	WFV	WH	wv	\pm SD
Alanine	796.5 a	414.4 b	372.6 b	276.4 b	209.0
Arginine	306.3 a	178.8 b	138.4 b	142.4 b	49.1
Asparagine	1,835.5 a	1,580.1 a	1,236.4 b	932.1 Ь	328.8
Cysteine	101.4 a	43.3 b	9.3 с	93.4 a	8.1
Glutamic acid	216.3	208.8	213.8	176.3	44.3
Glycine	1,042.2 a	898.5 ab	681.4 ab	541.3 b	486.2
Histidine	120.2 a	74.6 b	66.1 b	60.2 b	15.2
Isoleucine	117.5 a	88.4 b	73.8 b	41.4 c	26.3
Leucine	66.8 a	43.0 b	39.8 bc	23.1 c	11.5
Lysine	26.6 a	21.1 a	12.9 b	7.5 b	6.7
Methionine	24.7 a	24.4 a	13.8 b	6.7 с	7.1
Phenylalanine	45.5 a	28.4 b	28.0 b	12.6 c	6.8
Proline	1,167.8 a	1,136.0 a	650.2 ь	1,066.3 a	109.2
Serine [†]	1,516.3 a	1,067.3 b	763.6 b	́399.6 с	264.2
Threonine	156.8 a	104.5 b	77.6 bc	49.4 с	40.2
Tyrosine	407.9 bc	455.7 ab	462.4 a	404.8 c	49.8
Valine	244.5 a	198.0 ab	155.8 b	87.0 c	62.5
Total†	8,192.8 a	6,565.5 b	4,996.0 c	4,390.4 c	997.7
Total—serine†	6,676.5 a	5,498.2 b	4,232.3 с	3,920.9 c	841.4

TABLE 2. Free amino acid accumulations (nanomoles per 10 μ l sugarcane juice) in sugarcane mosaic virusstressed and weed-stressed, preharvest basal internodes, 1986.

Means on rows followed by different letters are significantly ($P \le 0.05$) different according to DMRT. Standard deviations were calculated across all treatments for each FAA. WFH = weed-free healthy. WFV = weed-free sugarcane mosaic-infected. WH = weedy healthy. WV = weedy sugarcane mosaic virus-infected.

† Serine was confounded with glucosamine during HPLC analysis so results for serine and total free amino acids may not be accurate.

free alanine, arginine, asparagine, glycine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, threonine, valine, and total FAA, respectively, than WFH cane. WFV cane accumulated 48, 42, 38, 25, 33, and 18% less ($P \leq 0.05$) free alanine, arginine, histidine, isoleucine, threonine, and total FAA, respectively, than WFH cane. WV cane had 41, 53, 46, 64, 73, 53, 56, and 29% lower ($P \le 0.05$) asparagine, isoleucine, leucine, lysine, methionine, threonine, valine, and total FAA levels, respectively, than WFV stalks. FAA accumulations followed the order WFH \geq WFV \geq WH \geq WV (Table 2). *P. zeae* densities on sugarcane were significantly and positively correlated with glutamic acid (r $= 0.52, P \leq 0.05$) and histidine (r = 0.45, $P \leq 0.05$), and *Meloidogyne* spp. numbers with total FAA ($r = 0.44, P \leq 0.05$).

A significant interaction ($P \le 0.001$) between the weed and SCMV stress factors detected for free cysteine levels followed the scheme WFH \ge WH but WFV \le WV, and WV \ge WH but WFV \le WFH (Table 2). *T. annulatus* numbers were correlated with free cysteine (r = 0.59, $P \le 0.0006$) (Fig. 3), and *Criconemella* spp. and total parasitic nematode populations followed a similar trend.

DISCUSSION

Weed effects on nematode populations: Only Criconemella and nonparasitic nematodes from interstool gaps were favored by weed

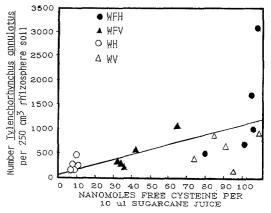


FIG. 3. Correlation of preharvest 1986 Tylenchorhynchus annulatus numbers with free cysteine accumulations in weed-free healthy (WFH), weed-free sugarcane mosaic virus-infected (WFV), weedy healthy (WH), and weedy sugarcane mosaic virus-infected (WV) sugarcane (r = 0.59, $P \le 0.0006$).

growth. Weeds did not appear to act as reservoirs to the other phytophagous species. Weed effects may have been partially obscured, however, because weed biomass declined under cane canopy closure. Criconemella spp., P. minor, P. zeae, and total phytophagous nematode infestations on the sugarcane were greater than WF gap populations. The season-long time lag described by Baird and Bernard (5) for nematode population trends was evident for T. annulatus on W and WF sugarcane and W gap populations of Criconemella spp., R. reniformis, P. minor, P. zeae, T. annulatus, and total phytophagous nematodes.

More Criconemella spp., P. minor, T. annulatus, and nonphytophagus nematodes were found on the ratoon crop than on either the W or WF gaps. Although P. zeae, hosted by many weed species (35), in W plots did not differ between gaps and sugarcane, P. zeae in WF plots was more abundant in the sugarcane rhizosphere than in WF gaps possibly because of weed-induced stress-related reductions of sugarcane FAA.

Interactions among weeds, SCMV, nematodes, and FAA: The weed-virus stress combinations variously affected FAA accumulation. Our results suggest that T. annulatus, Criconemella spp., and total plantparasitic nematode levels may be related to cysteine fluctuations. Information on the role of cysteine in nematodes is sparse. Research has indicated that nematodes orient toward some root exudates (11,12,34). Tomato root exudates, which are attractive to phytophagous nematodes in the soil (10), have been shown to include glutamic acid, alanine, aspartic acid, serine, valine, phenylalanine, and cysteine. Rogers (43) found that, while some phytophagous nematodes excrete cysteine, others may retain it.

Although drought stress has been shown to increase FAA in plants (7,44,50), the competitive effect of weeds in SCMV-free sugarcane resulted in the reduction of FAA levels and nematode populations. Virus-infected plants have been observed to harbor lesser (23,28) or greater (13,48) nematode populations and to reduce (16), increase (1,17,33), or fail to affect (22) FAA accumulation. Nematodes with different feeding habits affect host plant FAA levels differently (19,25). Nematode-induced stress may cause changes in host plant physiology, which subsequently mediates susceptibility to other pests (39). In sugarcane, a significant weed-virus interaction was observed for free cysteine concentrations that were correlated with *T. annulatus* infestations.

Our study showed that weeds did not serve as reservoirs for phytophagous nematodes, with the exception of *Criconemella* spp. Weed-induced and SCMV-induced sugarcane stresses were found to influence FAA accumulations which were positively correlated with phytophagous nematode populations. We conclude that nematode population dynamics were influenced by factors other than initial infestation levels and the direct effects on the crop. These factors involved species-dependent interactions with weed-induced and SCMV-induced stress-related changes in host plant FAA accumulations.

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