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ORIGINAL ARTICLE

Pest Interactions in Agronomic Systems

Crop rotation for management of plant-parasitic nematodes in forage corn production

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Abstract

Corn (*Zea mays* L.) is an important silage source for dairy cattle production in the southeastern United States. Silage corn is often grown continuously, which frequently results in severe pressure from plant-parasitic nematodes such as sting nematode (*Belonolaimus longicaudatus*). Crop rotation is one of the few nematode management options available in forage production. The research objective was to assess summer-planted rotation crops, preceding spring silage corn, for management of plant-parasitic nematodes. Rotation crops included field corn, pearl millet [*Cenchrus americanus* (L.) Morrone]—with or without fertilizer—, sorghum-sudangrass [*Sorghum bicolor* (L.) Moench × *Sorghum sudanense* Piper], and sunn hemp (*Crotalaria juncea* L.), which was either incorporated into soil or harvested. Rotation crops were assessed in a 3-year field study in central Florida. Sunn hemp treatments significantly reduced sting nematode soil abundances relative to corn by 84%, 90%, and 84% before spring corn planting in 2019–2020 and 2020–2021 and at rotation crop termination in 2021–2022, respectively. Abundances of other plant-parasitic nematodes were not consistently influenced by rotation. Biomass of winter rye (*Secale cereale* L.)—a bridge cover crop between summer and spring crops—was consistently increased following sunn hemp with significant increases of 87%, 106%, and 186% relative to following corn in 2019–2020, 2020–2021, and 2021–2022, respectively. Similarly, sunn hemp significantly increased spring corn yield by 70% and 136% relative to double-cropped corn in 2020–2021 and 2021–2022, respectively. Overall, rotation with sunn hemp improved plant-parasitic nematode management in forage corn production relative to rotations with only gramineous crops.

1 | INTRODUCTION

Corn (*Zea mays* L.) silage is one of the most popular forages for dairy cattle given the high production capacity and nutritive value of corn (Wilkinson & Rinne, 2018). Additionally, due to its high nitrogen demand (Lindquist et al., 2007), corn becomes an essential sink for nutrients from manure application, regularly cycling nutrients between plants and animals. In the southeastern United States, given the long warm-season period, it is possible to grow two warm-season crops

Abbreviations: ANOVA, analysis of variance; LSD, least significant difference.

(i.e., double cropping) in 1 year. Silage corn, planted between February and April depending on the latitude, is often followed by a second, continuous, crop of corn or in rotation with other annual grass crops (generally sorghum [*Sorghum bicolor* (L.) Moench]) of similar silage or green chop value. These continuous corn or grass-heavy rotations often lead to an increase in plant-parasitic nematode levels and crop damage by these nematodes, particularly on the sandy soils predominant in the region (Koenning et al., 1996; Mashela et al., 1991).

Soil-borne plant-parasitic nematodes infect crop roots, impairing root function and leading to a decrease in plant growth and yield (Crow et al., 2000; Todd, 1989). A number of plant-parasitic nematodes are associated with corn. Sting nematode (*Belonolaimus longicaudatus*) and stubby-root nematodes (primarily *Nanidorus minor* and *Trichodorus obtusus*) are acutely damaging even at low abundances and are the most problematic nematodes in Southeast corn (Rhoades, 1985a, 1985b; Timper et al., 2007). Southern root-knot (*Meloidogyne incognita*) and lesion nematodes (*Pratylenchus* spp.) can decrease corn yield when present in high enough abundances (Bowen et al., 2008; MacGuidwin & Bender, 2016; Todd & Oakley, 1996). Other nematodes, such as ring (*Mesocriconema* spp.) are common, and may infect corn, but are thought to have minor, if any impacts on yield (Windham, 1998).

There are few practical strategies available to manage plant-parasitic nematodes in silage corn, with nematicide application and crop rotation being the main options. Crop rotation relies on selecting a crop that is poor or nonhost of the particular plant-parasitic nematodes in a field (Grabau & Chen, 2016a). This decreases plant-parasitic nematode populations before the susceptible corn crop is planted, reducing nematode-induced damage (Grabau & Chen, 2016a; Schumacher et al., 2020). In double-cropping forage production systems, midsummer planting is a good time to introduce a rotational crop, with a few options available. For example, summer cover crops, such as sorghum-sudangrass and sunn hemp (*Crotalaria juncea* L.), are already established in the Southeast in vegetable rotations and would also fit in a forage rotation (Crow et al., 2001; Van Biljon et al., 2015). Sunn hemp is a common choice for nematode management because it is a nonhost for various root-knot nematode species (Bhan et al., 2010; McSorley, 1999; K. H. Wang, Sipes, et al., 2002) and may also enhance nematode management by stimulating antagonistic microorganisms (K. H. Wang et al., 2001, 2003a) and producing toxic compounds (K. H. Wang et al., 2001).

In addition to plant-parasitic nematodes, free-living nematodes are increasingly considered when developing and selecting nematode management tactics. Free-living nematodes are non-plant-parasitic nematodes that feed primarily on microbes or mesofauna (Grabau & Chen, 2016b; Yeates et al., 1993). They are involved in nutrient cycling (Holajjer et al., 2016; Trap et al., 2016), microbe colonization (Jiang et al., 2018), and may even help with pest management (Khan & Kim, 2005). Thus, they are considered a net benefit to the cropping system, and plant-parasitic nematode management strategies that increase, or at least do not affect, free-living nematodes are desired. Application of most nematicides decreases nontarget, free-living nematodes (Grabau et al., 2020; Grabau & Chen, 2016b; Waldo et al., 2019). Choice of crop rotation can also influence free-living nematodes (Briar et al., 2012; Grabau et al., 2018; Grabau & Chen, 2016b), likely due to factors such as root structure, and crop residue biomass and composition.

Despite these benefits, how well sunn hemp and other forage rotation crops can manage the most important plant-parasitic nematodes of corn—sting and stubby-root nematodes—is not well-established. In greenhouse tests, sunn hemp has been a poor host for sting nematode as sting nematode does not grow on most sunn hemp cultivars (Braz et al., 2016; Grabau et al., 2022). Field testing of sunn hemp against sting nematode is not extensive and has been conducted in vegetable, but not in forage systems (K. H. Wang et al., 2004). Similarly, information on the relationship between sunn hemp and stubby-root nematodes, and thus, whether it can be useful in managing this pest is needed. Graminaceous crops, such as sorghum-sudangrass, are typically hosts that increase populations of sting nematode and stubby-root nematodes (Crow et al., 2001; Perez et al., 2000). The objective of this study was to investigate the efficacy of rotation crops to (1) manage plant-parasitic nematodes and their damage to corn and (2) influence free-living nematodes in a forage production system.

Core Ideas

- Summer rotation with sunn hemp manages sting nematode populations before spring silage corn better than grasses.
- Nematode management by sunn hemp leads to improved spring silage corn yield and winter rye growth.
- Diversifying forage rotations by including sunn hemp improves forage production systems.

2 | MATERIALS AND METHODS

2.1 | Field site

The study was conducted at the Plant Science Research and Education Unit of the University of Florida in Citra, Florida

TABLE 1 Summer rotation crop treatments and planting parameters.

Rotation crop treatment	Variety	Planting rate	Row spacing (cm)
Corn	NK1808-3111[a]	75,615 seeds ha^{-1}	76
Sorghum-sudangrass	Unknown[b]	302,733 seeds ha^{-1}	76
Pearl millet	TIFLEAF 3[c]	16.8 kg ha^{-1}	18
Pearl millet unfertilized	TIFLEAF 3	16.8 kg ha^{-1}	18
Sunn hemp	Crescent Sun[d]	28 kg ha^{-1}	18
Sunn hemp incorporated	Crescent Sun	28 kg ha^{-1}	18

[a]NK1308-3111 from Syngenta Corporation.
[b]Variety not specified, from Hancock Seeds.
[c]TIFLEAF 3 from Hancock Seeds.
[d]Crescent Sun from Tropical Seeds LLC.

(29.2425 N, 82.9445 W) between spring 2019 and summer 2022. The soil at the site was Arrendondo sand (Loamy, siliceous, semiactive, hyperthermic Grossarenic Paleudults). In spring 2019, the whole site was planted with corn to enhance the buildup of nematodes in the area before treatments were established in summer 2019. From 2016 to 2018, the site was either weedy fallow or a weedy stand of bahiagrass (*Paspalum notatum* Flugge).

2.2 | Experimental design

The study employed a randomized complete block design with four replicates, six treatments, and a single factor—summer rotation crop (planted in mid-summer and harvested in fall). Rotation crop treatments included: (1) silage corn, (2) sorghum-sudangrass, (3) sunn hemp harvested and removed, (4) sunn hemp incorporated into soil, (5) fertilized pearl millet [*Cenchrus americanus* (L.) Morrone], and (6) pearl millet without nitrogen fertilizer. The experimental units (plots) consisted of four rows on 75-cm centers (3 m total) by 6-m long. Plot identity (i.e., rotation crop treatments) was maintained throughout the study. Variety and planting rates are described in Table 1. Commercial corn seeds were used and came pre-treated with abamectin {Spiro[11,15-methano-2H,13*H*,17*H*-furo(4,3,2-pq)(2,6)benzodioxacyclooctadecin-13,2′-(2*H*)pyran]} nematicide (Avicta Complete Corn with Vibrance, Syngenta). All other crop seeds had no insecticide or nematicide pre-treatment. Except for the sunn hemp incorporated treatment, biomass from all crops was harvested and removed as described in the next section. The pearl millet treatment without nitrogen fertilizer was included to estimate nitrogen fixation by sunn hemp in a separate experiment. The experiment was repeated in the same location for three cropping cycles (2019–2020, 2020–2021, and 2021–2022). Treatment locations were not changed between cropping cycles, so each plot received the same treatment in all three cycles.

2.3 | Crop termination

Prior to trial initiation, the entire trial area had been planted with corn in 2019. Rotation crops were initially planted in late summer 2019 after corn harvest, harvested in the fall, and planted again in the same area in 2020 and 2021. Exact dates of these and other production practices are provided in Table 2. For each cropping cycle, following summer rotation crop treatments, all plots were planted with rye (Kellygrazer III, Kelly Seeds), which was then terminated by paraquat (*N*,*N*-dimethyl-4,4 -bipyridinium dichloride) herbicide application. Throughout the trial, all pesticide applications were made at labeled rates for each product. Following rye termination, each spring (2020, 2021, and 2022), all plots were planted with silage corn using the same variety and planting density as described for the summer rotation. Bifenthrin [2-methylbiphenyl-3-ylmethyl (Z)-(1RS,3RS)−3-(2-chloro-3,3,3-trifluoroprop-l-enyl)- 2,2-dimethylcyclopropanecarboxylate] insecticide was applied in-furrow for corn (spring and summer plantings) and sorghum (summer).

All summer rotation crops and the spring corn were seeded directly over residue (no-till). The winter rye was also no-till, except for the rye following the sunn hemp incorporated treatment, as the sunn hemp was roto-tilled to incorporate (Maletti 6-ft cultivator, Oliver & Dahlman Equipment Co.). Corn and sorghum were planted with a John Deere MaxEmerge Plus vacuum seeder (John Deere), modified to apply starter fertilizer, at 5-cm deep and 5 cm off the row, and in-furrow bifenthrin. All other crops were planted with a Great Plains no-till drill (Great Plains AG) fitted with a cone seed spreader for precise plot seeding. Spring silage corn was planted at 75,615 plants ha^{-1} around mid-March and harvested in late June (Table 2).

2.4 | Fertilizer and pest management

For summer rotation crops, fertilizer, herbicide, and other pest management regimes varied by rotation crop based on production practices typical for the given crop. Fertilizer and in-season herbicide regimes are described in Table 3. Pesticide applications for fungal disease and insect control were tailored to protect corn and sorghum-sudangrass, but were broadcast throughout the trial during the growing season. For both spring and summer crops, post-plant fungicide applications were done throughout the season and included pyrasclostrobin {methyl *N*-[2-[[1-(4-chlorophenyl)pyrazol-3-yl]oxymethyl]phenyl]-*N*-methoxycarbamate}, pyraclostrobin + metconazole {5-[(4-chlorophenyl)methyl]−2,2-dimethyl-1-(1*H*-1,2,4-triazol-1-ylmethyl)cyclopentanol}, and/or tebuconazole {1*H*-1,2,4-Triazole-1-ethanol, *α*-[2-(4-chlorophenyl)ethyl]-*α*-(1,1-dimethylethyl)-}. Insecticides were applied as needed in both spring and summer crops and included flubendiamide {*N*2-[1,1-dimethyl-2-(methylsulfonyl)ethyl]−3-iodo-*N*1-[2-methyl-4-(1,2,2,2-tetrafluoro-1-(trifluoromethyl)ethyl)phenyl]−1,2-benzenedicarboxamide}, spinetoram {(2R,5R,9R,10S,14R,15S,19S)−15-[(2R,5S,6R)−5-(dimethylamino)−6-methyloxan-2-yl]oxy-7-[(2R,3R,4R,5S,6S)−4-ethoxy-3,5-dimethoxy-6-methyloxan-2-yl]oxy-19-ethyl-14-methyl-20-oxatetracyclo[10.10.0.0^{2,10}.0^{5,9}]docos-11-ene-13,21-dione}, and sulfoxaflor (methyl(oxido){1-[6-(trifluoromethyl)pyridin-3-yl]ethyl}-lambda(6)-sulfanylidene]cyanamide) or permethrin [3-Phenoxybenzyl (1RS)-cis,trans-3-(2,2-dichlorovinyl)−2,2-dimethylcyclopropanecarboxylate]. The winter rye and spring silage corn crops were maintained uniformly across the trial based on standard practices for the region (Table 3).

2.5 | Nematode soil abundance assessments

Soil samples were collected for nematode extraction and analysis four times during each growing cycle: (1) at termination of rotational crops in October or November, (2) before planting spring corn (after winter rye cover crop harvest), (3) at midseason during spring corn production (45 days after planting), and (4) around spring corn harvest (Table 2). From each plot, 12 soil cores at a depth of 30 cm and 2 cm diameter were collected using an Oakfield sampling probe. The cores were collected from the center two rows in each plot. Soil cores were collected close to the plant roots when plants were present. Samples were homogenized in plastic bags and nematodes were extracted from 100 cm^3 soil per plot. Nematodes were extracted by the sucrose floatation and centrifugation method (Jenkins, 1964). After nematodes were extracted, they were fixed by 2% formalin to halt their motility and quantified under a microscope. Plant parasitic nematodes were identified to the genera level and quantified, and total free-living nematodes were quantified using an inverted, light microscope. Sting nematode, stubby-root nematode (*Nanidorus* spp.), ring nematode, root lesion nematode, and southern root-knot nematode (*Meloidogyne incognita*) were present at the site. Initial nematode soil abundances when establishing the trial were nine sting nematodes, six stubby-root nematodes, 19 lesion nematodes, 77 ring nematodes, and 33 root-knot nematodes 100 cm^{-3} soil averaged across the trial site.

2.6 | Spring corn root weight and nematode damage assessment

In 2021 and 2022, spring corn root samples were collected around harvest (Table 2) to assess nematode damage because qualitative observations in 2020 suggested that there were differences among plots. From each plot, six corn root systems were dug from the first and fourth rows of each plot to avoid compromising central yield rows. Soil and debris were removed from root systems by gentle shaking and washing. After patting roots dry, total root weight for each plot was recorded and average plant root weight was calculated. Each root system was visually assessed to estimate the percentage of the root system that had symptoms characteristic of sting or stubby-root nematode damage, namely, "bearding" of the root system due to proliferation of stunted lateral roots with necrotic root tips (Rhoades, 1985b; Timper et al., 2007).

In fall 2019, yield for sunn hemp and pearl millet was estimated by hand harvesting from two quadrats (0.25 m^2 each) because they matured earlier than corn or sorghum-sudangrass that year (Table 2). Samples were harvested using hand shears, cut to approximately 5-cm height, then dried to a constant weight at 60°C, and weighed for an estimate of biomass production in kg DM ha^{-1}. Yield for corn and pearl millet in 2019, all rotation crops in 2020 and 2021, and spring silage corn each year was estimated by harvesting silage mechanically. Yield of these crops was sampled from each plot (6.1-m long) using a Wintersteiger Cibus harvester with a Kemper Champion 1200 head (Wintersteiger) in a 1.52-m band. Fresh biomass was calculated using an internal scale in the harvester. Dry biomass (kg dry matter [DM] ha^{-1}) was estimated by collecting and weighing a fresh biomass subsample, which was dried to constant weight (approximately 5 days at 60°C) and re-weighed. Rye biomass was estimated manually prior to harvest, as described for early harvest of rotation crops in 2019. For each crop, yield is reported as dry biomass.

2.7 | Statistical analysis

Initially, data were analyzed across time points (year for crop yield and season for nematode abundances) using repeated

TABLE 2 Timeline of data collection and important trial management events.

Task	Cycle 1 (2019–2020)	Cycle 2 (2020–2021)	Cycle 3 (2021–2022)
Rotation crop planted	August 7, 2019	July 8, 2020	August 4, 2021[a]
Rotation crop harvested	October 3, 2019[b]–October 29, 2019	October 6, 2020	October 26, 2021
Nematode soil samples	November 13, 2019	October 6, 2020	October 12, 2021
Rye planted	November 6, 2019	October 26, 2020	November 3, 2021
Rye harvest	March 6, 2019	March 4, 2021	March 10, 2022
Nematode soil samples	March 10, 2020	March 4, 2021	March 14, 2022
Spring corn planted	March 11, 2020	March 18, 2021	March 18, 2022
Nematode soil samples	May 20, 2020	May 17, 2021	April 19, 2022
Nematode soil samples	June 24, 2020	June 30, 2021[c]	June 20, 2022[c]
Spring corn harvested	June 24, 2020	July 9, 2021	July 7, 2022

[a]In 2021, sorghum-sudangrass was replanted on August 18 due to poor stand.
[b]In 2019, sunn hemp and pearl millet were harvested earlier than corn and sorghum-sudangrass due to maturity.
[c]In 2021 and 2022, root samples for biomass and nematode damage assessment were collected on the same dates as these nematode soil samples.

measures mixed model (Littell et al., 1998). However, because there were time-by-rotation treatment interactions and rotation effects on nematodes at individual time points were of biological interest, the final analysis was done separately for each season (nematode abundances) or year (crop parameters). Variables were analyzed by analysis of variance (ANOVA). The analysis software used in this study was R version 3.6 (The R Foundation for Statistical Computing). The ANOVA statistical models of each test of the variables taken were assessed by Levene's test for homogeneity of variance and graphically for normality of residuals (Cook & Weisburg, 1999; Levene, 1960). Response variables were transformed when necessary to meet assumptions of linear statistical models. For variables with significant ($p \leq 0.1$) nematicide treatment effects in ANOVA, treatment means were separated using Fisher's protected least significant difference (LSD) test ($\alpha = 0.05$).

3 | RESULTS

3.1 | Soil nematode abundances

Sting nematode soil abundances were significantly affected by rotation crops before spring corn in 2020 and 2021 (ANOVA, $p < 0.05$) and at summer crop termination in 2021 (ANOVA, $p < 0.1$; Figure 1). In each of those seasons, sting nematode abundances tended to be greater following corn and fertilized millet than sunn hemp treatments. Specifically, for those seasons, sting nematode soil abundances were reduced by 84%, 90%, and 84%, respectively, following sunn hemp treatments relative to corn. Sting nematode populations following unfertilized millet and sorghum-sudangrass were typically intermediate relative to other rotation crops. Sting nematode

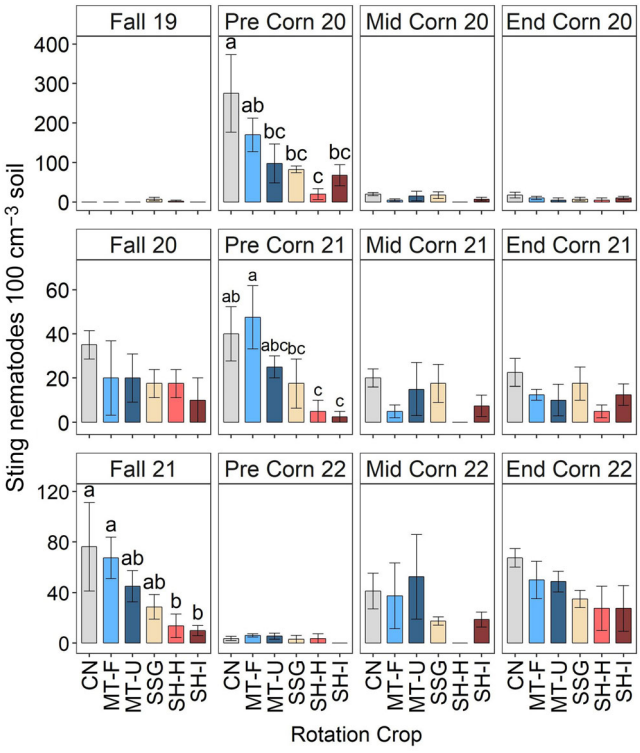

FIGURE 1 Sting nematode soil abundances as influenced by rotation crop across seasons. Values are means ($n = 4$) ± standard errors. Within seasons, different letters indicate significantly different values according to protected (analysis of variance [ANOVA], $\alpha = 0.1$) Fisher's least significant difference (LSD; $\alpha = 0.05$). In subfigure titles, "fall," "pre corn," and "end corn" indicate sampling in fall after rotation crop termination, before planting spring corn, midseason of spring corn (1–2 months after planting), and at spring corn harvest, respectively. In subfigure titles, "19," "20," and "21" indicate 2019, 2020, and 2021 sampling dates, respectively. "CN," "MT-F," "MT-U," "SSG," "SH-H," and "SH-I" indicate corn, fertilized pearl millet, unfertilized pearl millet, sorghum-sudangrass, harvested sunn hemp, and incorporated sunn hemp rotation crop treatments, respectively.

TABLE 3 Fertilizer and herbicide practices for each crop.

Crop	NPK fertilizer rates (elemental in kg ha^{-1})	NPK application timing/methods	Micronutrients	Herbicide[a,b]
Spring corn	303–28–195	Starter fertilizer[c], three side dress, and one through overhead irrigation	S at 31 kg ha^{-1} Mg at 30 kg ha^{-1} Mn at 11 kg ha^{-1} Zn at 4 kg ha^{-1}	Pendimethalin[c], atrazine[d], and s-metolachlor[e] at spike
Summer corn	238–28–195	Starter fertilizer plus three side dress	S at 31 kg ha^{-1} Mg at 30 kg ha^{-1} Mn at 11 kg ha^{-1} Zn at 4 kg ha^{-1}	Pendimethalin, atrazine, and s-metolachlor at spike
Sorghum-sudangrass	159–28–112	Starter fertilizer plus two side dress (Micronutrients with first two applications)	S at 18 kg ha^{-1} Mg at 4 kg ha^{-1} Mn at 11 kg ha^{-1} Zn at 4 kg ha^{-1}	s-Metolachlor and pendimethalin at spike; atrazine when plants taller than 15 cm
Pearl millet	45–10–37	Side dress 14–21 DAP	None	None
Unfertilized pearl millet	0–10–37	Side dress 14–21 DAP	None	None
Sunn hemp (harvested or incorporated)	0–10–37	Side dress 14–21 DAP	None	Paraquat 1 DAP (2020) Glyphosate[f] before planting (2021); Fluasifop[g] 7–10 DAP
Rye (winter)	60–0–0	Broadcast 42–56 DAP	None	None

Abbreviations: DAP, days after planting; NPK, nitrogen–phosphorus–potassium.

[a]For summer rotational crops, herbicide was applied at plot level using a backpack sprayer at labeled rates. For spring corn, herbicide broadcast was applied across the whole trial using a commercial sprayer.

[b]Pendimethalin [*N*-(1-ethylpropyl)−2,6-dinitro-3,4-xylidine].

[c]Starter fertilizer was applied as liquid dribble on the soil surface at planting.

[d]Atrazine [6-chloro-*N*-ethyl-*N*′-(1-methylethyl)−1,3,5-triazine-2,4-diamine].

[e]s-metolachlor [(RS)−2-Chloro-*N*-(2-ethyl-6-methyl-phenyl)-*N*-(1-methoxypropan-2-yl)acetamide].

[f]Glyphosate [*N*-(phosphonomethyl)glycine].

[g]Fluasifop {(R)−2-[4-(5-trifluoromethyl-2-pyridyloxy)phenoxy]propionic acid}.

soil abundances were not significantly affected by rotation crops in other seasons (ANOVA, $p > 0.1$).

Stubby-root nematode soil abundances were significantly affected by rotation crops only in fall 2019 (ANOVA, $p < 0.01$) and at spring corn harvest in 2020 (ANOVA, $p < 0.05$; Figure 2). In all other seasons, rotation crops did not significantly affect stubby-root nematode soil abundances (ANOVA, $p > 0.1$). In fall 2019, stubby-root nematode abundances were significantly greater (Fisher's LSD, $\alpha = 0.05$) following sorghum-sudangrass than any other treatment and greater for fertilized millet than either sunn hemp treatment. At spring corn harvest in 2020, stubby-root nematode abundances were significantly greater (Fisher's LSD, $\alpha = 0.05$) following incorporated sunn hemp than any other treatment.

Lesion nematode soil abundances were significantly affected by rotation crops in fall 2021, preplant spring corn 2022, and midseason corn 2022 (ANOVA, $p < 0.01$; Figure 3). Lesion nematode soil abundances were not significantly affected by rotation crops at corn harvest in 2022 or the 2019–2020 or 2020–2021 rotation cycles (ANOVA, $p > 0.1$). In fall 2021 and preplant spring corn 2022, lesion nematode soil abundances were significantly greater (Fisher's LSD,

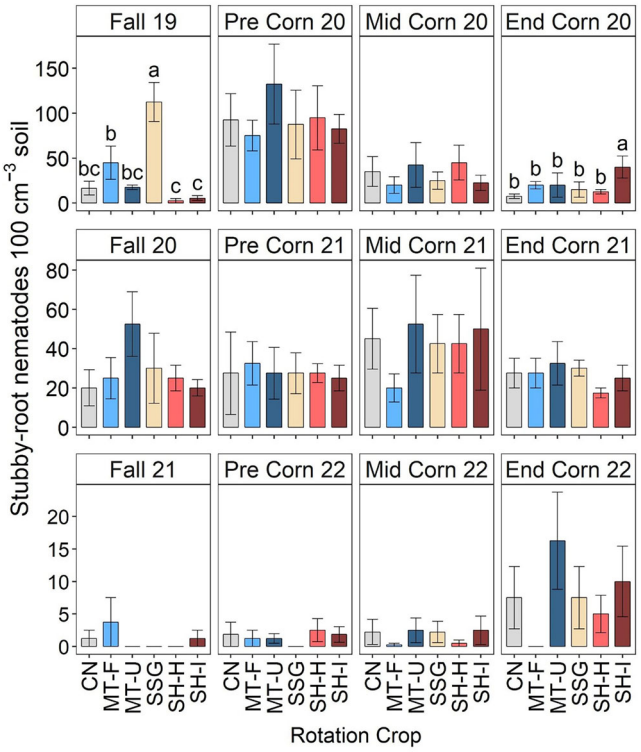

FIGURE 2 Stubby-root nematode soil abundances as influenced by rotation crop across seasons. Values are means ($n = 4$) ± standard errors. Within seasons, different letters indicate significantly different values according to protected (analysis of variance [ANOVA], $\alpha = 0.1$) Fisher's least significant difference (LSD; $\alpha = 0.05$). In subfigure titles, "fall," "pre corn," and "end corn" indicate sampling in fall after rotation crop termination, before planting spring corn, midseason of spring corn (1–2 months after planting), and at spring corn harvest, respectively. In subfigure titles, "19," "20," and "21" indicate 2019, 2020, and 2021 sampling dates, respectively. "CN," "MT-F," "MT-U," "SSG," "SH-H," and "SH-I" indicate corn, fertilized pearl millet, unfertilized pearl millet, sorghum-sudangrass, harvested sunn hemp, and incorporated sunn hemp rotation crop treatments, respectively.

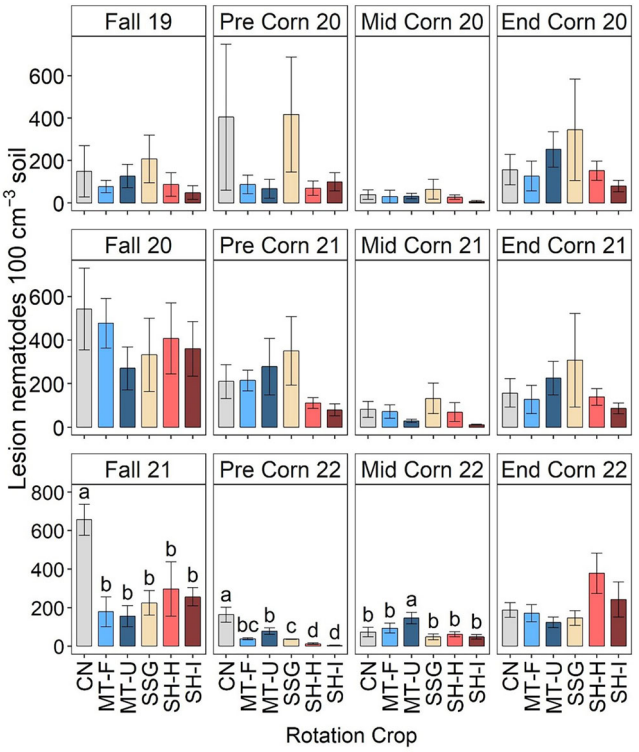

FIGURE 3 Lesion nematode soil abundances as influenced by rotation crop across seasons. Values are means ($n = 4$) ± standard errors. Within seasons, different letters indicate significantly different values according to protected (analysis of variance [ANOVA], $\alpha = 0.1$) Fisher's least significant difference (LSD; $\alpha = 0.05$). In subfigure titles, "fall," "pre corn," and "end corn" indicate sampling in fall after rotation crop termination, before planting spring corn, midseason of spring corn (1–2 months after planting), and at spring corn harvest, respectively. In subfigure titles, "19," "20," and "21" indicate 2019, 2020, and 2021 sampling dates, respectively. "CN," "MT-F," "MT-U," "SSG," "SH-H," and "SH-I" indicate corn, fertilized pearl millet, unfertilized pearl millet, sorghum-sudangrass, harvested sunn hemp, and incorporated sunn hemp rotation crop treatments, respectively.

$\alpha = 0.05$) following corn than any other rotation crop. Also, at preplant spring corn 2022, lesion nematode abundances were significantly less (Fisher's LSD, $\alpha = 0.05$) for either sunn hemp crop than any other rotation crop. In midseason 2022 of spring corn production, lesion nematode abundances were significantly greater (Fisher's LSD, $\alpha = 0.05$) following unfertilized millet than any other rotation crop.

Ring nematode soil abundances were significantly affected by rotation crop treatments in midseason spring corn 2020 (ANOVA, $p < 0.01$), preplant spring corn 2021 (ANOVA, $p < 0.1$), and midseason spring corn 2021 (ANOVA, $p < 0.01$; Figure 4). In seasons with significant treatment effects, ring nematode abundances were always significantly greater (Fisher's LSD, $\alpha = 0.05$) following sorghum-sudangrass than incorporated sunn hemp, but trends for other crops varied from season to season.

Root-knot nematode soil abundances were highly variable, averaging 70 root-knot nematodes 100 cm^{-3} (standard deviation 366) across time points and treatments (data not shown). Before spring corn planting in 2020, root-knot nematode soil abundances were affected by crop (ANOVA, $p < 0.1$) and were significantly greater (Fisher's LSD, $\alpha = 0.05$) following corn (418 root-knot nematodes 100 cm^{-3} soil) than any other treatment (12 root-knot nematodes 100 cm^{-3} soil). At corn harvest in 2022, root-knot nematode soil abundances were significantly affected by crop (ANOVA, $p < 0.1$) and were significantly greater (Fisher's LSD, $\alpha = 0.05$) following sunn hemp incorporated or harvested (24 and 35 root-knot nematodes 100 cm^{-3} soil, respectively) than fertilized pearl millet or sorghum-sudangrass (0 root-knot nematodes 100 cm^{-3} soil). There were no significant treatment effects in any other season (ANOVA, $p > 0.1$) with mean root-knot nematode soil

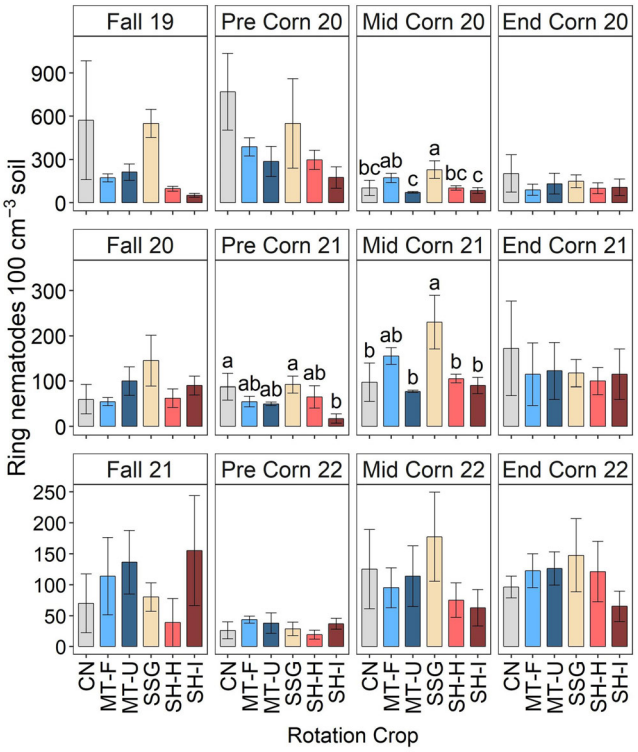

FIGURE 4 Ring nematode soil abundances as influenced by rotation crop across seasons. Values are means ($n = 4$) ± standard errors. Within seasons, different letters indicate significantly different values according to protected (analysis of variance [ANOVA], $\alpha = 0.1$) Fisher's least significant difference (LSD; $\alpha = 0.05$). In subfigure titles, "fall," "pre corn," and "end corn" indicate sampling in fall after rotation crop termination, before planting spring corn, midseason of spring corn (1–2 months after planting), and at spring corn harvest, respectively. In subfigure titles, "19," "20," and "21" indicate 2019, 2020, and 2021 sampling dates, respectively. "CN," "MT-F," "MT-U," "SSG," "SH-H," and "SH-I" indicate corn, fertilized pearl millet, unfertilized pearl millet, sorghum-sudangrass, harvested sunn hemp, and incorporated sunn hemp rotation crop treatments, respectively.

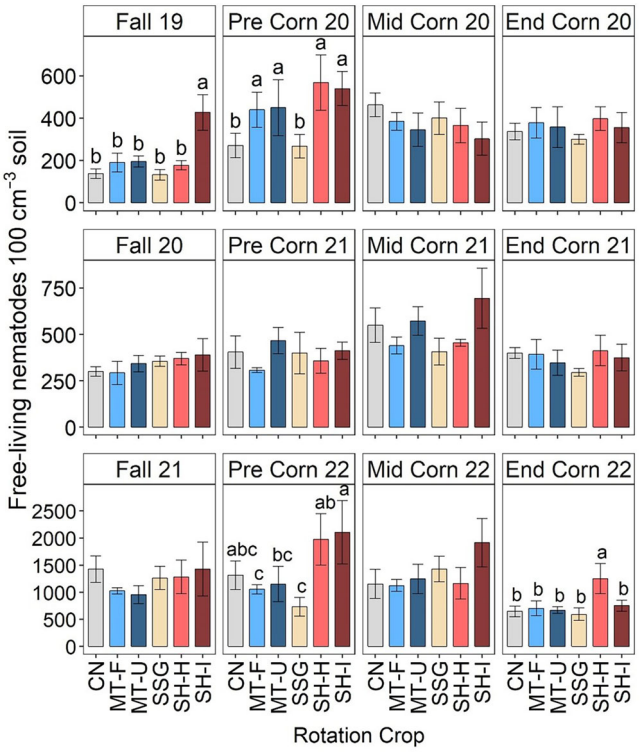

FIGURE 5 Free-living nematode soil abundances as influenced by rotation crop across seasons. Values are means ($n = 4$) ± standard errors. Within seasons, different letters indicate significantly different values according to protected (analysis of variance [ANOVA], $\alpha = 0.1$) Fisher's least significant difference (LSD; $\alpha = 0.05$). In subfigure titles, "fall," "pre corn," and "end corn" indicate sampling in fall after rotation crop termination, before planting spring corn, midseason of spring corn (1–2 months after planting), and at spring corn harvest, respectively. In subfigure titles, "19," "20," and "21" indicate 2019, 2020, and 2021 sampling dates, respectively. "CN," "MT-F," "MT-U," "SSG," "SH-H," and "SH-I" indicate corn, fertilized pearl millet, unfertilized pearl millet, sorghum-sudangrass, harvested sunn hemp, and incorporated sunn hemp rotation crop treatments, respectively.

abundances (per 100 cm^3 soil) of 300 at rotation crop termination in 2019, 10 at midseason in 2020 spring corn, 144 at spring corn harvest in 2020, 86 at rotation crop termination in 2020, 16 before spring corn planting in 2021, 58 at midseason in 2021 spring corn, 139 at spring corn harvest in 2021, 31 at rotation crop termination in 2021, and two before spring corn planting in 2022.

Free-living nematode soil abundances were significantly affected by rotation crops only in fall 2019 (ANOVA, $p < 0.01$), preplant spring corn 2020 (ANOVA, $p < 0.01$), preplant spring corn 2022 (ANOVA, $p < 0.05$), and corn harvest 2022 (ANOVA, $p < 0.1$; Figure 5). In those seasons, free-living nematodes tended to be most abundant following sunn hemp (Figure 5).

3.2 | Crop yield and nematode damage

Summer rotation crop yield was significantly affected by crop in 2019-2020 (ANOVA, $p < 0.01$), being greatest for sorghum-sudangrass and least for unfertilized pearl millet or sunn hemp treatments (Fisher's LSD, $\alpha = 0.05$; Figure 6.). However, rotation crop yield did not vary significantly among crops in 2020-2021 or 2021-2022 (ANOVA, $p > 0.1$; Figure 6). Dry biomass of winter rye was significantly affected by previous rotation crop in each season ($p < 0.01$; Figure 7), being significantly greater (Fisher's LSD, $\alpha = 0.05$) following either sunn hemp treatment than corn or sorghum-sudangrass in each season, especially when incorporated (for 2020-2021 and 2021-2022). Rye biomass was increased by

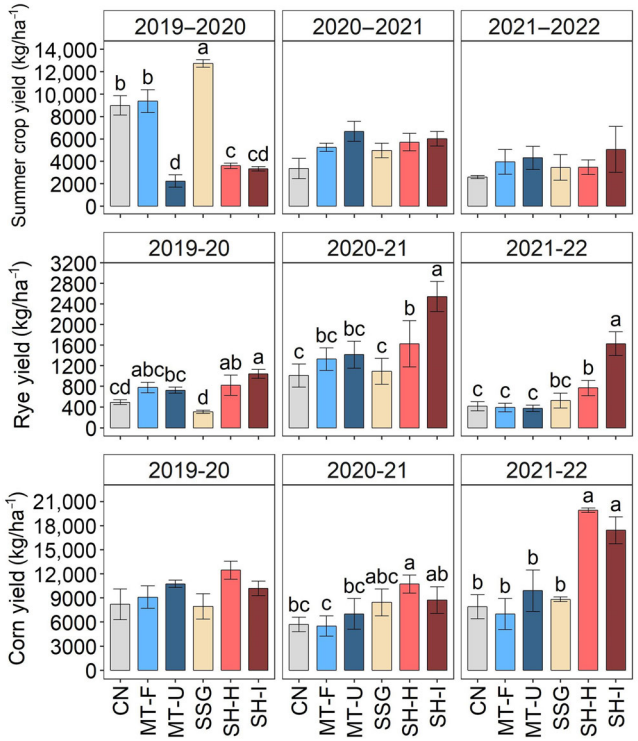

FIGURE 6 Summer rotation crop dry yield (top), winter rye biomass (middle), and spring corn dry yield (bottom) as affected by prior rotation crop treatments in 2019–2020, 2020–2021, and 2021–2022. Values are means ($n = 4$) ± standard errors. Within seasons, different letters indicate significantly different values according to protected (analysis of variance [ANOVA], $\alpha = 0.1$) Fisher's least significant difference (LSD; $\alpha = 0.05$). "CN," "MT-F," "MT-U," "SSG," "SH-H," and "SH-I" indicate corn, fertilized pearl millet, unfertilized pearl millet, sorghum-sudangrass, harvested sunn hemp, and incorporated sunn hemp summer rotation crop treatments, respectively.

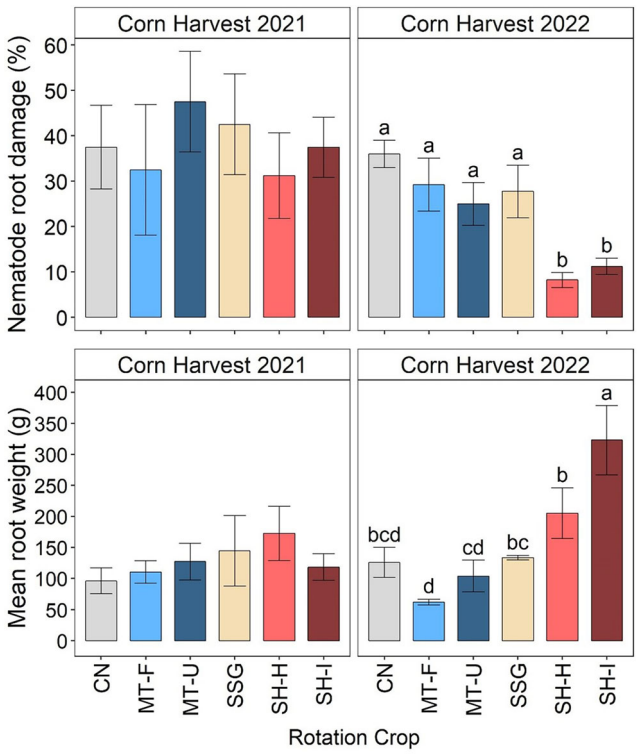

FIGURE 7 Nematode damage symptoms on spring corn roots (percentage of root system damaged as visually assessed, average of six plants per plot) and spring corn root weight at harvest in 2021 and 2022. Values are means ($n = 4$) ± standard errors. Within seasons, different letters indicate significantly different values according to protected (analysis of variance [ANOVA], $\alpha = 0.1$) Fisher's least significant difference (LSD; $\alpha = 0.05$). "CN," "MT-F," "MT-U," "SSG," "SH-H," and "SH-I" indicate corn, fertilized pearl millet, unfertilized pearl millet, sorghum-sudangrass, harvested sunn hemp, and incorporated sunn hemp rotation crop treatments, respectively.

87%, 106%, and 186% following sunn hemp treatments relative to corn in 2019, 2020, and 2021, respectively. Spring corn silage yield (dry biomass) was not significantly affected by rotation crops in 2020 (ANOVA, $p > 0.1$), but as rotation cycles evolved, there were significant distinctions among treatments in 2021 and 2022 (ANOVA, $p < 0.01$), especially for sunn hemp (Figure 6). At the end of three cycles (2022), spring corn following sunn hemp had doubled the yield of either of the grass treatments. Sunn hemp increased spring corn yield by 70% and 136% relative to double-cropped corn in 2021 and 2022, respectively.

In 2021, neither percentage nematode damage symptoms on spring corn roots nor spring corn root weight was significantly affected by rotation crops (Figure 7). In 2022, there was less nematode damage to spring corn roots following either sunn hemp treatment than any other rotation crop. Similarly, in 2022, mean spring corn root weight was significantly greater following incorporated sunn hemp than other treatments and significantly greater following harvest sunn hemp than either millet treatment.

4 | DISCUSSION

Considering all factors—nematode populations, crop yield, and nematode symptoms on crops—sunn hemp as a rotational crop improved plant-parasitic nematode management relative to double-cropping corn or following spring corn with any of the grasses tested. Despite the variations within and across seasons, in general, plant-parasitic nematode populations tended to be less for sunn hemp treatments than grasses while increasing free-living nematodes. After three cycles, the use of sunn hemp in rotation to corn improved system productivity and resulted in less root damage and greater root weight for spring corn.

In particular, either sunn hemp treatment (harvested or incorporated) was better for managing sting nematode than

a second crop of corn or fertilized pearl millet, although differences were only detected before planting spring corn or at cover crop harvest. Despite the seasonality of these results, among plant-parasitic nematodes in this study, sting nematode was most consistently influenced by rotation crop treatments. Those results are consistent with prior literature as sunn hemp is reported to be a poor host to sting nematode (Braz et al., 2016; K. H. Wang et al., 2004). Although corn is well-known to be a good host of sting nematode (Rhoades, 1985b; Timper & Hanna, 2005), there is less prior information on pearl millet. Pearl millet was a host for sting nematodes in previous greenhouse studies (Robbins & Barker, 1973), but there are reported differences in tolerance between genetic materials (Timper & Hanna, 2005).

In this study, sting nematode soil abundances were typically intermediate for unfertilized pearl millet and sorghum-sudangrass. The somewhat lower sting nematode abundances under unfertilized pearl millet than the most susceptible treatments (corn and fertilized millet) may be due to less overall crop growth (2019) or slower initial crop growth (not measured) without fertilizer, resulting in less roots for nematodes to feed on. It is somewhat unexpected that sorghum-sudangrass did not support more sting nematode reproduction as it is previously reported as a good host for sting nematode under field conditions (Crow et al., 2001; Perez et al., 2000). As is typical for sting nematode, soil abundances were variable from season to season and were typically numerically most abundant during cooler seasons, particularly after rye, which is known as a maintenance or good host for sting nematode (McSorley & Dickson, 1989). These low abundances in warmer seasons, along with the natural evening out of abundances across treatments as time increases, help explain the seasonality of treatment effects. Seasonal variation in sting nematode abundances has also been observed in other cropping systems, such as potato and cabbage (Perez et al., 2000). If winter rye was replaced with a poor host (for sting nematode and other targets) or clean fallow, nematode management may be improved further. Given the low production cost of rye or other small grains and the wide host range of sting nematode, research is needed to identify cost-effective alternatives.

Stubby-root nematode abundance was overall low, variable across seasons, and was not consistently managed by any crop. Most grasses, including corn (Timper et al., 2007), pearl millet (Cram & Fraedrich, 2009; Timper & Hanna, 2005), and sorghum-sudangrass (Crow et al., 2001; Perez et al., 2000) are reported to increase abundances of stubby-root nematode. Similar to the mixed results from this study, there are prior reports of sunn hemp either providing some field suppression (K. H. Wang, McSorley, et al., 2002) or having no effect on stubby-root nematodes (K. H. Wang et al., 2004).

Similarly, lesion and ring nematode soil abundances were not consistently affected by rotation crops. Sunn hemp tended to manage lesion nematode better than grasses, particularly corn, although this was only statistically significant in the 2021–2022 cycle. The relationship between sunn hemp and lesion nematodes is not well-established, although grasses such as sorghum-sudangrass (Bhan et al., 2010) and corn (Grabau & Chen, 2016a; MacGuidwin & Bender, 2016) are known to be hosts. Pearl millet cultivars, on the other hand, have been reported as relatively poor hosts of lesion nematode (Belair et al., 2005; Timper & Hanna, 2005). Ring nematode population management during spring corn production was generally (2 of 3 years) improved by sunn hemp or unfertilized pearl millet, but sorghum-sudangrass was counterproductive. Regardless, the influence of lesion and ring nematodes on corn production is thought to be much less substantial than sting, stubby-root, and south root-knot nematodes (Bowen et al., 2008; Rhoades, 1978).

Sunn hemp was also relatively consistent (2 of 3 years) in enhancing abundances of beneficial, free-living nematodes, similar to results found by McSorley et al. (2009) and K. H. Wang et al. (2003b), but in contrast to K. Wang et al. (2008). Although biomass of sunn hemp per se did not differ from the other crops, subsequent rye and corn following sunn hemp outperformed those following grass crops and greater organic matter inputs from crop residue may have contributed to increased free-living nematode abundances. This study did not include an evaluation of soil organic matter, which is not expected to change in such a short period. However, differences in crop residue composition may also be driving these results, such as observed in the Midwest on legume-grass systems (soybean and corn) where soybean promoted bacteria-feeding free-living nematodes, whereas corn promoted fungal-feeding nematodes (Grabau & Chen, 2016b). In this study, free-living nematodes were not differentiated by feeding type, so future research would be needed to more accurately determine the influence of sunn hemp—relative to grasses—on nematode community composition in this production system.

Crop yield and nematode damage parameters helped provide a more complete picture of the efficacy of rotational crops for plant-parasitic nematode management. Crop growth roughly corresponded to the level of sting nematode management with sunn hemp treatments enhancing crop growth (winter rye and spring corn) relative to rotation with grasses, particularly corn or sorghum-sudangrass. Rye yield was somewhat more responsive to rotation treatments than spring corn (affected all 3 years vs. only 2 years), potentially, as it was planted right after harvest of summer rotation crops. Yield improvement of winter rye and spring corn by sunn hemp was likely driven primarily by improved management of sting nematode based on population trends (Rhoades, 1978, 1985b), but improvements in soil fertility (especially N) could have played an important role (Mansoer et al., 1997). Incorporated sunn hemp improved rye yield compared

with harvested sunn hemp (2 of 3 years), and this minor increase in system productivity was likely due to short-term improved soil quality from rototilling (Vazquez et al., 1989) or greater nutrient credits from retaining residues as nematode control was similar between the sunn hemp treatments. Despite differences among treatments, anecdotally, none of the treatments approached yield potential for corn or rye in this system based on other simultaneous trials at the same research station with similar management (fertility and pest control) protocols (authors' observations). As discussed above, replacing winter rye with a crop that is less susceptible to plant-parasitic nematodes—especially sting nematode—may improve nematode management and thus crop productivity.

In summary, this showed that growers can improve corn productivity under sting nematode pressure by incorporating sunn hemp into a rotation scheme. The diversification of crop production, especially with inclusion of legumes, has multiple other benefits for nutrient cycling, soil conservation, and forage production compared to monoculture or grass-based systems. Given the shortage of nematode management options in forage cropping systems, sunn hemp provides growers with an important tool. Additionally, it has been shown to have good forage nutritive value (Garzon et al., 2021), providing an alternative use of the crop as animal feed, although the practice is not widely adopted yet. More research is needed on secondary compounds of sunn hemp and ways to use it as forage, including optimizing harvesting practices and technologies to improve its conservation as silage.

AUTHOR CONTRIBUTIONS

Mussie Wolday Tsegay: Data curation; formal analysis; investigation; methodology; writing—original draft; writing—review and editing. **Marcelo O. Wallau**: Conceptualization; data curation; funding acquisition; investigation; methodology; supervision; writing—review and editing. **Chang Liu**: Data curation; investigation; writing—review and editing. **José C. Dubeux Jr.**: Conceptualization; funding acquisition; investigation; methodology; supervision; writing—review and editing. **Zane Joseph Grabau**: Conceptualization; formal analysis; funding acquisition; investigation; methodology; supervision; writing—original draft.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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