10-15-2022

Soil Nematode Trophic Group Composition and Influence on Growth of Amaranthus palmeri and Parthenium hysterophorus

Orlando Garcia

Dana Garibaldi

Krissa Jhaveri

Jake Lanoue

Pushpa G. Soti

Soil Nematode Trophic Group Composition and Influence on Growth of *Amaranthus palmeri* and *Parthenium hysterophorus*

Orlando Garcia[1], Dana Garibaldi[2], Krissa Jhaveri[3], Jake Lanoue[4] & Pushpa Soti[1]

[1] Biology Department, University of Texas Rio Grande Valley, Edinburg, TX, USA

[2] Lamar Academy, McAllen, TX, USA

[3] South Texas High School for Health Professions, Mercedes, TX, USA

[4] UTRGV Mathematics and Science Academy, Edinburg, TX, USA

Correspondence: Pushpa Soti, Biology Department, University of Texas Rio Grande Valley, Edinburg, TX 78539, USA. Tel: 956-665-3131. E-mail: pushpa.soti@utrgv.edu

Abstract

Weeds have a significant impact on agricultural systems. They not only cause a loss in crop yield by competing with them for resources, but they can also serve hosts for several pests and parasties such as plant parasitic nematodes casuing additional crop loss. The aim of this study was to analyze plant-nematode feedback in two major weeds, *Amaranthus palmeri* S Watson and *Parthenium hysterophorus* L. First, a field survey was conducted to determine the rhizosphere nematode trophic groups associated with these two plants in the summer of 2020 and 2021. Then a 6-week greenhouse study was conducted where the two weed species were treated with nematode communities extracted from their respective rhizospheres. Results from this study show that both weeds harbored a high number of herbivore nematodes, followed by fungivore and bacterivore nematodes. Total number of these nematodes were highly influenced by total sol carbon, pH and salinity. Under greenhouse conditions, the nematode treatment did not have any impact on the growth of *P. hysterophorus* but *A. palmeri* plants treated with nematodes had significantly higher above ground biomass. In conclusion, plant-nematode relationships are complex. Given the extent of direct damage caused by these weeds and plant parasitic nematodes in global crop production, the weeds-nematode feedback warrants further detailed studies.

Keywords: soil nematode communities**,** plant-parasitic nematodes, soil carbon, soil pH, soil salinity

1. Introduction

Weeds are important components of terrestrial ecosystems, conserving soil as well as adding species and functional diversity including providing habitats and resources for the associated fauna (including herbivores, pollinators, and browsers) (Marshall et al., 2003). Because of their aggressive growth, high plasticity, and enhanced adaptability compared to crops, weeds pose a significant threat to the productivity of agroecosystems. Since they share the same trophic level as crops, weeds compete with crops for soil nutrients, light, and water (Blackman & Templeman, 1938), making them a major biotic constraint to agricultural production. Weeds as primary producers can attract and host herbivore insects (Capinera, 2005), which can further damage crops. They can also harbor both above-ground and below-ground pests, pathogens, and parasites, including nematodes.

Weeds are reported to serve as reservoirs of several plant-parasitic nematodes (Lopez, Soti, Jagdale, Grewal, & Racelis, 2021; Quénéhervé et al., 2006). They can serve as alternative hosts during the fallow period and promote the persistence of plant-parasitic nematodes in fields which reduces the efficacy of nematode management techniques in controlling plant parasitic nematodes (Thomas, Schroeder, & Murray, 2005). Weeds can suppress soil nematodes through the release of root exudates (Chitwood, 2002) or serve as trap crops, redirecting nematodes from crops to weeds (Datta, 2006). In addition, herbicides in combination with nematodes can increase the effectiveness of weed control and nematicides can reduce weed populations (Gilreath & Santos, 2008). Thus, the interactions between nematodes and weeds are more complex and have significant implications for both weed and nematode management (Thomas et al., 2005).

Impact of nematodes on crops is dependent on the nematode population density, susceptibility of the host, and environmental variables (Trudgill & Phillips, 1997). For example, plant parasitic nematodes at lower density and

in the presence of other free living soil nematodes are known to improve plant growth by stimulating microbial activity and consequently increasing N mineralization in soil benefitting the plants (Gebremikael, Steel, Buchan, Bert, & De Neve, 2016). Most of the past studies on weed-nematode interactions have mostly focused on the few numbers of economically important plant parasitic nematodes, while the interaction between weeds and free-living soil nematodes, which occupy key positions in the soil food-web (bacterivores, fungivores, omnivores, and predators), are not clear.

In this study, the impact of two major weeds, A*maranthus palmeri* S Watson (Palmer amaranth) and *Parthenium hysterophorus* L. (Parthenium, whitetop weed, false ragweed) on the soil nematode community and the influence of soil nematodes on the growth of these two plant species was analyzed. Both *A. palmeri* and *P. hysterophorus* are the most aggressive and herbicide-resistant weeds worldwide (Heap & Duke, 2018; Kistner & Hatfield, 2018). They invade agriculture fields, pastures, roadsides, and natural systems (Adkins & Shabbir, 2014) and cause a significant reduction in crop growth and yield. These weeds are also known to be hosts of root-knot nematodes (*Meloidogyne* spp.) (Chitambo, Haukeland, Fiaboe, & Grundler, 2019; Datta, 2006), which cause a significant decline in crop growth and yield, especially vegetables, and cause serious economic losses (Collange, Navarrete, Peyre, Mateille, & Tchamitchian, 2011). This research builds on the work by (Lopez et al., 2021) who reported high number of plant parasitic nematodes on *P. hysterophorus* and other coexisting weeds in south Texas. In this study, we specifically aimed to answer two questions: 1) How do the two weeds influence the trophic groups of soil nematodes in their rhizosphere? 2) How do the soil nematode trophic groups influence the growth of these two species? To answer these questions, we conducted this study in two phases: 1) field survey of roots and analysis of the rhizosphere soil samples under these two weeds and 2) a greenhouse growth study of the two weed species treated with the soil nematode communities collected from their respective rhizosphere in the field.

2. Method

2.1 Field Study

The field surveys in this study were conducted in 5 different organic vegetable farms in the Lower Rio Grande Valley (LRGV) in south Texas during the summer (June-July) of 2020 and 2021. The LRGV has a semiarid sub-tropical climate with mild winters and hot summers. Vegetable growing season in this region spans from September through May and fields are left fallow (weedy or kept bare with continuous cultivation for weed removal) during summer (June-August).

At each farm we randomly selected 25 plants of each plant species to assess nematode damage symptoms in roots as well as the leaves. We analyzed the plants for aboveground symptoms such as leaf color and plant size and belowground symptoms such as stunted root growth, galls, lesions, and root rotting. We then collected approximately 100 g of rhizosphere soil from five different locations with dense growth *A. palmeri* and *P. hysterophorus* at 0-15 cm depth. The soil samples were placed in plastic bags and transported to the lab in a cooler for further analysis. In the lab, 50 g of soil were stored in the refrigerator until further analysis of soil edaphic properties and 50 g of soil were used to extract and analyze the soil nematode community.

2.2 Nematode Extraction and Analysis

The sucrose-centrifuge method (Jenkins, 1964) was used to extract the nematodes from the soils. To extract nematodes, 50 g of soil was mixed with DI (deionized) water in a beaker and was sieved by placing 106 μm and 38 μm sieves on top of one another. The sediments retained in 38 μm micrometer sieve were poured into a 50 ml centrifuge tube which were centrifuged at 3500 rpm for one minute. The supernatant was then decanted. Sucrose solution was added to the pellet in the 50 ml tube and mixed. The samples were then centrifuged at 3500 rpm for one minute to separate the nematodes from the soil. The supernatant with nematodes was poured into a 32 μm mesh and washed to clean the sucrose from the nematodes. The extracted nematodes were stored overnight in a 4 ºC refrigerator. The nematodes were then viewed under an inverted microscope (Leica DMi1, Buffalo Grove, IL) and counted. The nematodes were identified morphologically and grouped based on their trophic groups: 1) plant-parasitic/herbivores, 2) bacterivores, 3) fungivores, and 4) predators/omnivores.

2.3 Soil Analysis

The soil samples were analyzed for salinity, organic matter (OM%), pH, and total carbon (C) and nitrogen (N). Soil moisture was measured using the gravimetric method. Organic matter was determined by the dry combustion method (500 ºC for 4 hours). Soil pH was measured with a benchtop pH meter (OAKTON ION 700 Thermo fisher scientific, Waltman, MA, USA) in 1:2 (soil:DI water solution). Salinity was measured with an Accumet Conductivity Meter (AB200 Thermo fisher scientific, Waltman, MA, USA) in 1:2 (soil:DI water

solution). Total C and N was measured with a C/N analyzer (928 Series Macro Determinator, LECO, St. Joseph, MI, USA).

2.4 Greenhouse Study

In July 2021, a 6-week greenhouse study was conducted to determine the impact of nematodes on the two weed species, *A. palmeri* and *P. hysterophorus*. A total of 24, one week old seedlings of both weed species (12 each) were randomly selected and transplanted in 1 liter plastic pots filled with soil collected from local farms and sterilized in an autoclave and mixed with perlite (5:1 volume). The soil had 1.32% organic matter, 1.24% total carbon and 0.097% total nitrogen. Six pots of each weed species were treated weekly with nematode communities extracted from the rhizosphere of each weed species in the field. The nematode composition and number of nematodes added to the nematode treatment pots are presented in Table 1. Stomatal conductance and chlorophyll fluorescence were measured weekly using the LI-600 Porometer/ Fluorometer (LI-COR Biosciences, Lincoln NE, USA). After 6 weeks, when the *A. palmeri* plants started producing flowers, they were destructively harvested and dried in an oven to constant weight (70 $^{\circ}$C, 74 hours) to determine the total shoot biomass and biomass allocation pattern in the two weed species.

Table 1. Total number of nematodes that were added to the treatment pots of the two weed species over the six-week study period

	A. palmeri	*P. hysterophorus*
Tylenchus spp.	48	54
Helicotylenchus spp.	300	396
Pratylenchus spp.	60	84
Paratylenchus spp.	24	6
Mesocriconema spp.	0	6
Unknown herbivore	72	96
Bacterivores	60	84
Fungivores	90	24
Predators	24	12
Unidentified	36	30

To determine the nematode host status of the two weeds, 25 g of roots were randomly collected from each of the nematode treatment plants and used to extract root nematodes following the root incubation method in (Hallman & Viaene, 2013). The roots were rinsed with water, cut into small pieces, and sliced by cutting cross sectionally. Roots were then placed (fully submerged) in beakers with 100 ml DI water at 24 $^{\circ}$C for two weeks. During the two-week period, 1 ml water was pipetted from each beaker and observed under the inverted microscope every 3 days. After 2 weeks, the roots were discarded. Since we did not find any nematodes in any of the root samples during the 2 weeks period, no further analysis was done. We also analyzed the soil samples in the pots at the end of the 6-week period to determine the impacts of the weed-nematode associations on the abundance of nematodes in each trophic groups and plant growth. 50 g of soil samples was collected from each treatment pot and the different types of nematodes were extracted and enumerated as outlined above.

2.5 Data Analysis

For the soil nematode community analysis, relative abundance of each trophic group, Shannon diversity index, evenness index, Simpson's index, and nematode channel ratio were calculated as shown in Table A1. Differences in the soil properties between the two years were compared with ANOVA. The relative abundance of different nematode groups was not different between the two years, except for predator nematodes in *A. palmeri*, so the data for the two years were combined and analyzed together. Data on soil nematodes were log transformed (log x + 1). We used forwards stepwise model selection using step AIC to find the best model with which to describe the current dataset. Multiple linear regression analyses (backward elimaination) was performed to evaluate the relative importance and effects of soil variables on the soil nematode trophic groups and community indices. The Akaike information criterion (AIC) was used to identify variables for model selection. Soil variables that were selected by the final RDA models were used to build models.

For the greenhouse study data, canopy cover, plant height, and stomatal conductance were not normally distributed, and thus were log transformed. Student t-test was done to compare the plant measurements in the

nematode and control treatments for each species. Results were considered significant if $P \leq 0.05$. All data was analyzed using JMP Pro statistical software.

3. Results

3.1 Field Survey of A. palmeri and P. hysterophorus

There were some differences in the soil characteristics in the rhizosphere of the two weeds (Table 2). Soil pH was slightly alkaline. While there was no significant difference unde the two weeds in 2020 it was significantly higher under *A. palmeri* in 2021 ($P = 0.015$). Soil salinity was significantly higher under *A. palmeri* in 2020 ($P = 0.001$). There was no significant difference in other soil properties between the two weeds in both the years.

Table 2. Soil characteristics in the rhizosphere of the two weed species, means followed by the standard deviation in parenthesis

Plant	A. palmeri		P. hysterophorus	
Year	2020	2021	2020	2021
pH	7.89 (0.04)	7.34 (0.06)	7.88 (0.04)	7.08 (0.091)
OM%	3.18 (0.09)	3.27 (0.22)	3.20 (0.12)	2.77 (0.18)
Salinity	162.07 (7)	241 (19.84)	260.05 (25.4)	240 (24.91)
Soil moisture (%)	8.12 (0.52)	11.18 (0.69)	7.92 (0.66)	10.19 (0.65)
Total C (%)	0.94 (0.06)	1.67 (0.06)	1.06 (0.05)	1.49 (0.03)
Total N (%)	0.07 (0.003)	0.70 (0.13)	0.08 (0.004)	0.72 (0.14)

A total of 57,910 nematodes of 22 different morphospecies were recorded in the rhizosphere soil samples of the two weeds species. Of which, there were 9 herbivore, 5 fungivore, 3 bacterivore, 1 predator, and 4 unidentified nematode species (features not possible to identify, probably due to damage during extraction). While there was a difference in the relative abundance of the different nematodes in the rhizosphere of the two weed species, herbivores were the most dominant group of nematodes in both the years (Table 3). There was no significant difference in the different nematode types under the two weed species except for the predator nematodes under *A. plameri* in 2020. In 2020, *A plameri* had significantly higher number of predators ($P = 0.018$) and lower number of herbivores, though not statistically significant. Among the different herbivores, *Helicotylenchus* spp., *Tylenchus* spp., and an unknown species of herbivore nematodes were the dominant ones in both weed species (Table 4). *Pratylenchyus* spp., *Paratylenchus* spp., and *Mesocriconema* spp. were also found in the soil samples, but their numbers were relatively low.

Table 3. Relative abundance (%), followed by the standard deviation in parenthesis, of different functional groups of nematodes in the rhizosphere of the two weed species in 2020 and 2021.

Plant	A. palmeri		P. hysterophorus	
Year	2020	2021	2020	2021
Herbivores	42.25 (6.66)	52.11 (8.37)	60.05 (5.03)	51.25 (8.73)
Fungivores	20.95 (4.15)	23.27 (5.70)	21.00 (3.89)	19.34 (3.90)
Bacterivores	22.37 (4.47)	22.48 (4.87)	14.88 (3.04)	26.68 (6.18)
Predators	12.06 (4.37)	0.62 (0.32)	2.78 (1.08)	1.58 (0.55)

Table 4. Relative abundance (%), followed by the standard deviation in parenthesis, of the different herbivore nematodes in the rhizosphere of two weed species in 2020 and 20201

Plant	*A. palmeri*		*P. hysterophorus*	
Year	2020	2021	2020	2021
Helicotylenchus spp.	18.09 (4.12)	30.28 (8.19)	25.97 (4.46)	22.47 (7.44)
Tylenchus spp.	4.73 (1.42)	6.81 (1.59)	8.26 (1.62)	8.69 (2.53)
Pratylenchyus spp.	0.21 (0.21)	0	0.35 (0.16)	0.39 (0.36)
Paratylenchus spp.	0.21 (0.21)	0	0.35 (0.16)	0.39 (0.36)
Mesocriconema spp.	0.31 (0.31)	0	0.49 (0.31)	0
Unknown spp.	16.42 (4.52)	8.62 (3.86)	20.39 (4.41)	13.45 (3.78)

Reuslts form multiple linear regression show that total carbon, salinity, and pH were the most frequently selected variables influencing the abundance of the total number of nematodes and the number of nematodes in each trophic group (Figure 1). Summary of model parameter estimates and p values are presented in Table A2. Total number of neamatodes were influenced by total C ($P < 0.0001$), salinity ($P = 0.005$) and OM ($P = 0.048$). Herbivores were influenced by total soil carbon ($P = 0.0037$). Total number of bacterivores were influenced by the soil pH ($P = 0.002$) and salinity ($P = 0.011$). Fungivores were influenced by total carbon ($P = 0.0002$) and salinity ($P = 0.042$). Predators were influenced by total nitrogen in soil ($P = 0.017$).
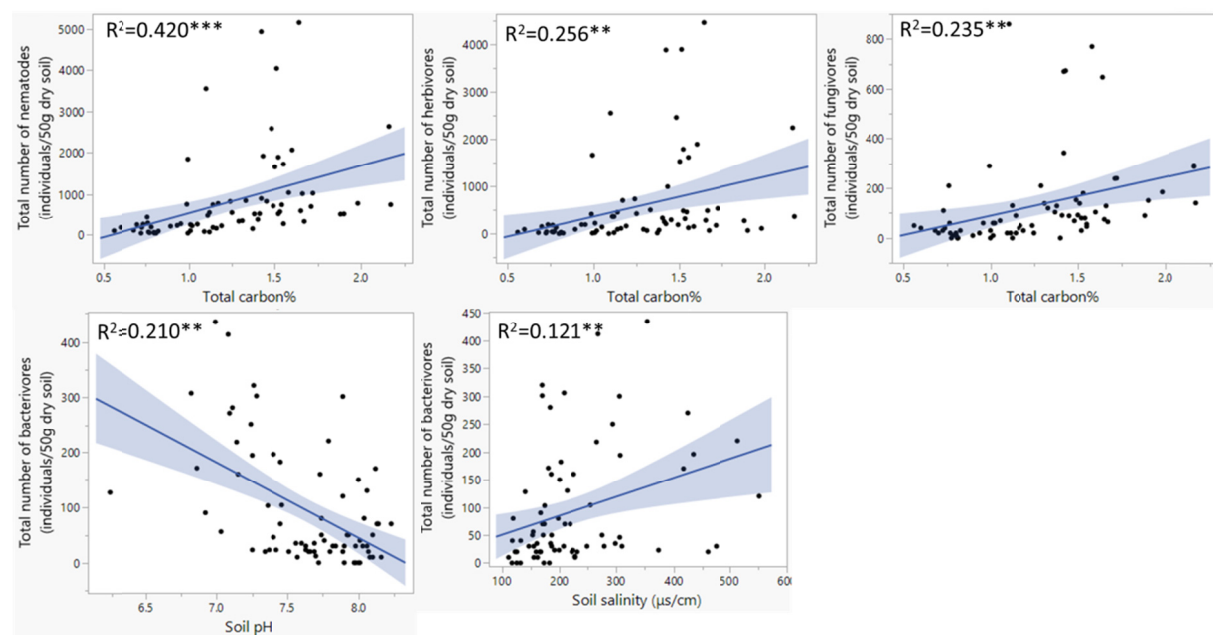

Figure 1. Relationship between soil parameters and nematode trophic groups. Total carbon and total number of nematodes (A); total number of herbivores (B); total number of fungivores (C). Relations between pH and total number of baterivores (D) and salinity and total number of bacterivores (E)

Similarly, the soil variables had a significant influence on the nematode community indices analyzed (Figure 2). Shannon diversity index was significantly influenced by soil salinity ($P = 0.033$) and total carbon ($P = 0.008$). Evenness was influenced by total nitrogen ($P = 0.014$). Nematode channel ratio was influenced by soil pH ($P = 0.015$) and organic matter ($P = 0.012$) while there was no influence on the Simpsons diversity index. Nematode channel ration NCR, used to describe the importance of bacterivore and fungivore nematodes, was slightly over 0.5 in both they years indicating the soil organic matter utilization by bacteria.
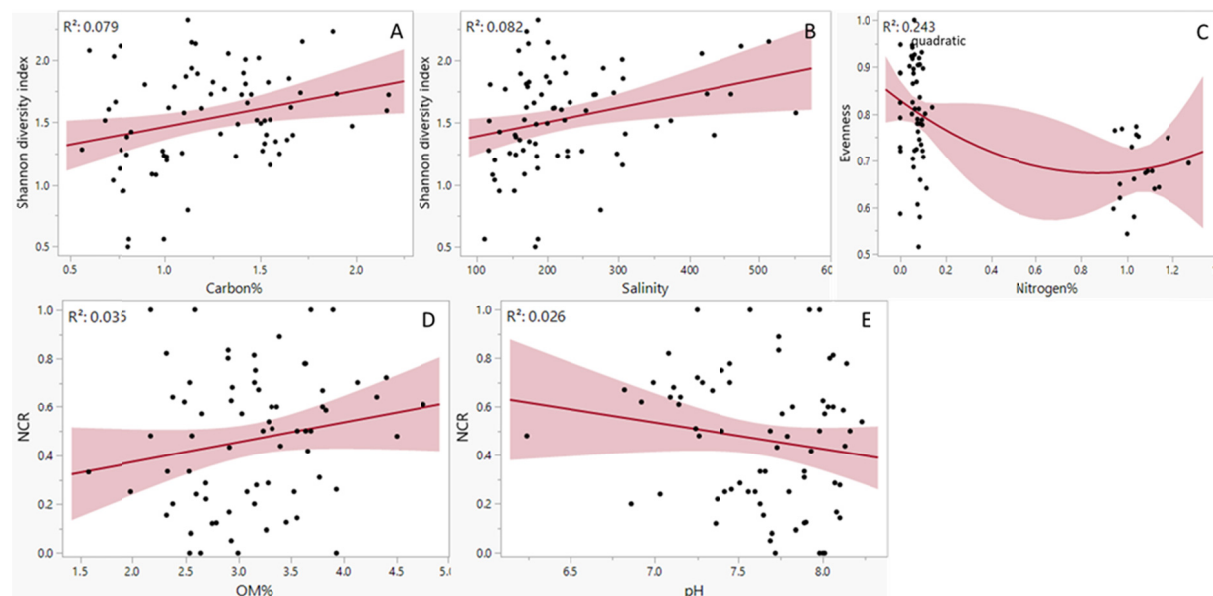
Figure 2. Relationship between soil parameters and nematode community indices. Total carbon and Shanon diversity index (A); salinity and Shannon diversity index (B); total nitrogen and evenness (C); organic matter and nematode channel ratio (NCR) (D); and pH and NCR (E)

3.2 Greenhouse Study

Results from the greenhouse study were similar to the field study results. There were no signs of nematode damage/presence in the root samples of both *A. palmeri* and *P. hysterophorus* under the nematode treatment and control. Soil samples from the pots analyzed for nematodes at the end of 6-week study period showed a shift in the nematode community composition (Table 6). The number of plant parasitic nematodes was lower in both the weed species. While, the total number of bacterivores, fungivores, and predators was higher. While *A. palmeri* had higher number of *Tylenchus* spp., *P hysterphorus* had higher no of *Helicotylenchus* spp. Comparison of the difference in growth of both *A. palmeri* and *P. hysterophorus* treated with nematodes and untreated control show that the two plants responded differently to the nematode treatments (Figure 3). Nematode treatment resulted in increased height in *A. palmeri* compared to control ($P = 0.024$) while there was no difference in *P. hysterophorus*. Similarly, nematode treatment resulted in higher aboveground biomass in *A. palmeri* compared to control ($P = 0.010$) while there was no difference in *P. hysterophorus*. There was no significant difference in the leaf chlorophyll fluorescence and stomatal conductance between the nematode treatment and control in both the plant species durin the study period (data presented in supplementary information).
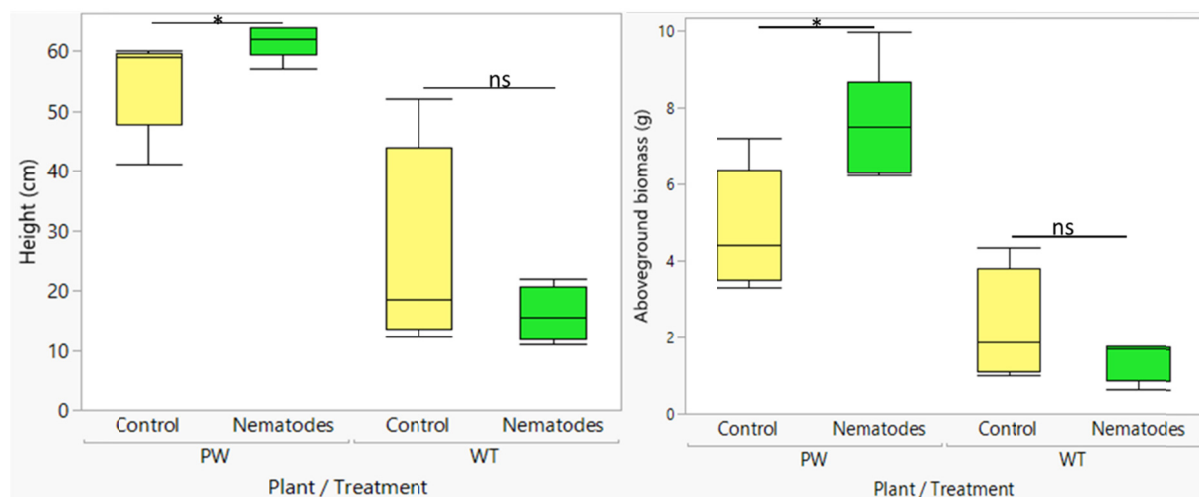
Figure 3. Differences in plant growth (PW: *A. palmeri* and WT: *P. hysterophorus*), plant height at harvest (left) and average aboveground biomass (right)

4. Discussions

4.1 Nematode Trophic Groups Associated With the Two Weeds

Among other factors, high weed infestation is considered one of the major contributing factors for higher numbers of herbivore nematodes (Thomas et al., 2005). Weeds can act as alternate host and enable an increase in nematode populations (Rich, Brito, Kaur, & Ferrell, 2009) directly or by changing the soil nutrient status and influencing the nematode community composition. Results from this study are similar to a previous study that reported a high number of plant parasitic nematodes association with the prominent weeds in the LRGV region (Lopez et al., 2021). While *P. hysterophorus* is reported to have some nematocidal properties suppressing nematodes (S. Datta & Saxena, 2001), *A. palmeri* is reported to be a moderate host for root-knot nematodes, the *Meloidogyne* spp. (Ward, Webster, & Steckel, 2013). However, in this study, there were no signs of root-knot presence in the field root survey and in the analysis of rhizosphere soil samples and recorded a high number of other herbivore nematodes. Nematodes of *Helicotylenchus* spp. were the most prominent grop of nematodes in the rhizosphere of both weeds in this study. (Robinson, Heald, Flanagan, Thames, & Amador, 1987) in their survey of cotton, citrus, and fallow fields in the LRGV, recorded the presence of only three species of plant parasitic nematodes, *Rotylenchulus reniformis*, *Meloidogyne incognita*, and *Tylenchus semipenetrans*. Results from this study show a higher diversity of plant parasitic nematodes in the organic vegetable systems and are similar to a recent study (Lopez et al., 2021) who also did not record the presence of root-knot nematodes in the vegetable farms in the region.

Root-knot nematodes are reported to cause significant damage to vegetables in east Texas, peanut fields (Eisenback, Bernard, Starr, Lee Jr, & Tomaszewski, 2003), and cotton in LRGV (personal communication with growers). Surprisingly, we did not find any root knot nematodes in this 2-years study of the five farms. A reason for this could be the timing of sample collection. The samples were collected during the summer fallow season where the soil moisture levels are very low. Soil moisture is considered be an important factor in development of root knot nematodes (Mohawesh, 2016; Mohawesh & Karajeh, 2014), low soil moisture potentially reduced the egg hatching percentage and presence of root knot nematodes.

High densities of bacterivore and fungivore nematodes were also present in the rhizosphere of both the weeds. Since the bacterivore and fungivore nematodes contribute to soil fertility through the release of nitrogen to the soil (Ferris, 2010), high incidence of these nematodes can recycle the nutrients in crop residues and aid in the growth of the weed species. Species of *Aphelenchoides* were the most dominant fungivores in this study. These nematodes can influence plants indirectly by grazing on beneficial fungi such as mycorrhizal fungi (Ruess, Zapata, & Dighton, 2000). This could aid in the competitive advantage of non-mycorrhizal weeds over mycorrhiza dependent crops. Predator populations were relatively lower compared to others and were different in the rhizosphere of the weed species in both years and we did not record any omnivore nematodes. Overall, these results show that these two weeds host a high number of nematodes and potentially have positive feedback in organic vegetable systems under study leading to direct and indirect loss of crops.

4.2 Influence of Soil Parametres on Nematode Communities

Soil neamtodes are highly influenced by soil biotic and abiotic conditions. They are known to have a narrow range of favorable soi conditions such as moisture, which are highly influenced by soil particle size (Simons, 1973). In this study, soil variables such as total carbon, pH, salinity, organic matter, and total nitrogen in soil had different impact to the different nematode trophic groups and their community indices.

Results from this study show that soil carbon has a significant influence on the soil nematode communities. Increase in soil carbon content resulted in higher numbers of nematodes. Similarly, total number of herbivore and fungivore nematodes also increased linearly with the increase in soil carbon, while we did not see a significant association with the bacterivore nematodes. Bacterivore nematodes declined with the increase in soil pH. Soil pH between 5-7 are reported to be favorable for soil nematodes (Matute, 2013; Warner, 2009). In this study, the average soil pH in the farms was 7.54, this slightly alkaline pH could have reduced bacterivore nematodes. Similarly, bacterivore nematodes also increased linearly with soil salinity. The positive relationship between bacterivores and soil salinity was an unexpected result showing the bacterivore nematodes in this study are tolerant to soil salinity under field conditions. Soil nitrogen enrichment is reported to increase the abundance of of bacterivores and suppressed fungivores and predators (Song et al., 2016), in this study we did not find a strong influence of nitrogen in any of the nematode trophic groups. This could be the result of heavier soil texture or inherently low nitrogen content in these study sites.

Though not very strong, soil variables also had an influenc on the nematode community indices. Shannon diversity index increased the soil carbon content and salinity. Evenness had quadratic relationship with soil nitrogen. NCR value which indicates the organic matter decomposition pathway was around 0.5 which shows that the summer soil conditions (typically hot and dry) are not ideal for the bacterial community. The positive linear relationship between soil carbon and NCR indicates improving soil carbon content can promote the bacterial community. Overall, these resuls show that soil carbon is the key indicator of soil nematode community composition in organic vegetable systems.

4.3 Influence of Nematodes on the Growth of the Two Weeds

Results from the greenhouse study show that herbivore nematodes do not necessarily lead to decline in plant health. Nematode species identity is more critical to plants as suggested by (Brinkman, Duyts, & Van der Putten, 2005b). These results are similar to previous studies reporting no difference in the shoot biomass with nematode treatment (Brinkman, Duyts, & van der Putten, 2005a; Brinkman et al., 2005b). *A. palmeri* plants treated with nematodes had higher shoot biomass. This could be the result of increased number of bacterivores, fungivore, and predator nematodes which aid in nutrient cycling (Ferris, Venette, & Scow, 2004). The total number of plant parasitic nematodes declined in both weed species while the beneficial nematodes bacterivores and fungivores increased in number in the pot experiments at the end of the study period. Lower number of herbivores in soil along with the absence of nematodes in the roots indicate that the two weed species do not serve as direct hosts of the plant parasitic nematodes recorded in this study. A possible explanation for the high number of plant parasitic nematodes in the rhizosphere of the two weed species in the field could be the presence of other smaller weeds in the understory of these two weed species. The other possibility is the release of volatiles by these two weed species which attract plant parasitic nematodes (Reynolds et al., 2011), but this weeds-volatile-nematode interaction in *A. palmeri* and *P. hysterophorus* requires further research.

In conclusion, results form this study show that the two weeds *A. palmeri* and *P. hysterophorus* harbor a high number of herbivore nematodes to whom they do not directly serve as hosts. In addition, abundance of soil nematodes was highly dependent on the soil conditions, particularly soil carbon and pH. *A. palmeri*, which is described as "one of the most widespread, troublesome, and economically damaging agronomic weeds in the southeastern U.S." (Ward et al., 2013), can potentially attract high number of plant parasitic nematodes. Thus, identifying nematode species is crucial in adopting a both weed and nematode management technique in agricultural fields. With the increased research interest in manipulating the plant microbiomes as an invasive plant/weed management tool (Shahrtash & Brown, 2021), more research is needed on the plant-soil feed back in both *A. palmeri* and *P. hysterophorus* and their role in shaping the soil nematode community. In addition, the morphological identification of the nematodes used in this study does not provide full information on the nematode species, thus there is a need for further research in weed mediated plant-soil feedback using molecular techniques for proper identification of plant parasitic nematodes and effective management of both weeds and nematodes in agricultural systems.

Acknowledgements

References

Adkins, S., & Shabbir, A. (2014). Biology, ecology and management of the invasive parthenium weed (*Parthenium hysterophorus* L.). *Pest Management Science, 70*(7), 1023-1029. https://doi.org/10.1002/ps.3708

Blackman, G., & Templeman, W. G. (1938). The nature of the competition between cereal crops and annual weeds. *The Journal of Agricultural Science, 28*(2), 247-271. https://doi.org/10.1017/S0021859600050656

Brinkman, E. P., Duyts, H., & van der Putten, W. H. (2005a). Competition between endoparasitic nematodes and effect on biomass of *Ammophila arenaria* (marram grass) as affected by timing of inoculation and plant age. *Nematology, 7*(2), 169-178. https://doi.org/10.1163/1568541054879647

Brinkman, E. P., Duyts, H., & Van der Putten, W. H. (2005b). Consequences of variation in species diversity in a community of root-feeding herbivores for nematode dynamics and host plant biomass. *Oikos, 110*(3), 417-427. https://doi.org/10.1111/j.0030-1299.2005.13659.x

Capinera, J. L. (2005). Relationships between insect pests and weeds: an evolutionary perspective. *Weed science, 53*(6), 892-901. https://doi.org/10.1614/WS-04-049R.1

Chitambo, O., Haukeland, S., Fiaboe, K., & Grundler, F. (2019). First Report of *Meloidogyne hapla* and *M. javanica* Coinfection on *Parthenium hysterophorus* in Kenya. *Plant Disease, 103*(1), 162-162. https://doi.org/10.1094/PDIS-06-18-0964-PDN

Chitwood, D. J. (2002). Phytochemical based strategies for nematode control. *Annual Review of Phytopathology, 40*(1), 221-249. https://doi.org/10.1146/annurev.phyto.40.032602.130045

Collange, B., Navarrete, M., Peyre, G., Mateille, T., & Tchamitchian, M. (2011). Root-knot nematode (Meloidogyne) management in vegetable crop production: The challenge of an agronomic system analysis. *Crop protection, 30*(10), 1251-1262. https://doi.org/10.1016/j.cropro.2011.04.016

Datta, S. C. (2006). Possible use of amaranth as catch crop for root-knot nematodes intercropped with okra. *Phytomorphology, 56*(3), 113.

Datta, S., & Saxena, D. B. (2001). Pesticidal properties of parthenin (from *Parthenium hysterophorus*) and related compounds. *Pest Management Science: formerly Pesticide Science, 57*(1), 95-101. https://doi.org/10.1002/1526-4998(200101)57:1%3C95::AID-PS248%3E3.0.CO;2-J

Eisenback, J., Bernard, E., Starr, J., Lee Jr, T., & Tomaszewski, E. (2003). *Meloidogyne haplanaria* n. sp. (Nematoda: Meloidogynidae), a root-knot nematode parasitizing peanut in Texas. *Journal of Nematology, 35*(4), 395. https://doi.org/10.1163/15685410260438926

Ferris, H. (2010). Contribution of nematodes to the structure and function of the soil food web. *Journal of Nematology, 42*(1), 63.

Ferris, H., Venette, R., & Scow, K. (2004). Soil management to enhance bacterivore and fungivore nematode populations and their nitrogen mineralisation function. *Applied Soil Ecology, 25*(1), 19-35. https://doi.org/10.1016/j.apsoil.2003.07.001

Gebremikael, M. T., Steel, H., Buchan, D., Bert, W., & De Neve, S. (2016). Nematodes enhance plant growth and nutrient uptake under C and N-rich conditions. *Scientific Reports, 6*(1), 1-10. https://doi.org/10.1038/srep32862

Gilreath, J. P., & Santos, B. M. (2008). Managing weeds and nematodes with combinations of methyl bromide alternatives in tomato. *Crop Protection, 27*(3-5), 648-652. https://doi.org/10.1016/j.cropro.2007.09.008

Hallman, J., & Viaene, N. (2013). PM 7/119 (1) Nematode extraction. *EPPO Bulletin, 43*(3), 471-495. https://doi.org/10.1111/epp.12077

Heap, I., & Duke, S. O. (2018). Overview of glyphosate-resistant weeds worldwide. *Pest Management Science, 74*(5), 1040-1049. https://doi.org/10.1002/ps.4760

Jenkins, W. (1964). A rapid centrifugal-flotation technique for separating nematodes from soil. *Plant Disease Reporter, 48*(9).

Kistner, E. J., & Hatfield, J. L. (2018). Potential geographic distribution of Palmer amaranth under current and future climates. *Agricultural & Environmental Letters, 3*(1), 170044. https://doi.org/10.2134/ael2017.12.0044

Lopez, H. F., Soti, P., Jagdale, G. B., Grewal, P., & Racelis, A. (2021). Weeds as Hosts of Plant Parasitic Nematodes in Subtropical Agri-culture Systems. *Subtropical Agriculture and Environments*.

Marshall, E., Brown, V., Boatman, N., Lutman, P., Squire, G., & Ward, L. (2003). The role of weeds in supporting biological diversity within crop fields. *Weed Research, 43*(2), 77-89. https://doi.org/10.1046/j.1365-3180.2003.00326.x

Matute, M. M. (2013). Soil nematodes of Brassica rapa: Influence of temperature and pH. *Advances in Natural Science, 6*(4), 20-26.

Mohawesh, O. (2016). Utilizing deficit irrigation to enhance growth performance and water-use efficiency of eggplant in arid environments. *Journal of Agricultural Science and Technology, 18*(1), 265-276.

Mohawesh, O., & Karajeh, M. (2014). Effects of deficit irrigation on tomato and eggplant and their infection with the root-knot nematode under controlled environmental conditions. *Archives of Agronomy and Soil Science, 60*(8), 1091-1102. https://doi.org/10.1080/03650340.2013.871385

Quénéhervé, P., Chabrier, C., Auwerkerken, A., Topart, P., Martiny, B., & Marie-Luce, S. (2006). Status of weeds as reservoirs of plant parasitic nematodes in banana fields in Martinique. *Crop Protection, 25*(8), 860-867. https://doi.org/10.1016/j.cropro.2005.11.009

Reynolds, A. M., Dutta, T. K., Curtis, R. H., Powers, S. J., Gaur, H. S., & Kerry, B. R. (2011). Chemotaxis can take plant-parasitic nematodes to the source of a chemo-attractant via the shortest possible routes. *Journal of the Royal Society Interface, 8*(57), 568-577. https://doi.org/10.1098/rsif.2010.0417

Rich, J., Brito, J., Kaur, R., & Ferrell, J. (2009). Weed species as hosts of *Meloidogyne*: A review. *Nematropica*, 157-185.

Robinson, A., Heald, C., Flanagan, S., Thames, W., & Amador, J. (1987). Geographical distributions of Rotylenchulus reniformis, *Meloidogyne incognita*, and *Tylenchulus semipenetrans* in the Lower Rio Grande Valley as related to soil texture and land use. *Journal of Nematology, 19*(1), 20.

Ruess, L., Zapata, E. J. G., & Dighton, J. (2000). Food preferences of a fungal-feeding *Aphelenchoides* species. *Nematology, 2*(2), 223-230. https://doi.org/10.1163/156854100508962

Shahrtash, M., & Brown, S. P. (2021). A Path Forward: Promoting Microbial-Based Methods in the Control of Invasive Plant Species. *Plants, 10*(5), 943. https://doi.org/10.3390/plants10050943

Simons, W. R. (1973). *Nematode survival in relation to soil moisture*. Veenman.

Song, M., Li, X., Jing, S., Lei, L., Wang, J., & Wan, S. (2016). Responses of soil nematodes to water and nitrogen additions in an old-field grassland. *Applied Soil Ecology, 102*, 53-60. https://doi.org/10.1016/j.apsoil.2016.02.011

Thomas, S. H., Schroeder, J., & Murray, L. W. (2005). The role of weeds in nematode management. *Weed Science, 53*(6), 923-928. https://doi.org/10.1614/WS-04-053R.1

Trudgill, D., & Phillips, M. (1997). Nematode population dynamics, threshold levels and estimation of crop losses. *Plant nematode problems and their control in the Near East region* (p. 144). FAO: Plant Production and Protection Paper.

Ward, S. M., Webster, T. M., & Steckel, L. E. (2013). Palmer amaranth (*Amaranthus palmeri*): A review. *Weed Technology, 27*(1), 12-27. https://doi.org/10.1614/WT-D-12-00113.1

Warner, F. (2009). Soil fertility, pH, texture and nematodes. *Diagnostic Services, 13*, 21.

Appendix A

Table A1. Soil nematode community indices and formulas

Community index	Formula used
Relative abundance	$pi = ni/N$
Shannon Diversity Index	$H' = -\Sigma pi(\text{Ln}Pi)$
Evenness Index	$H' = H'/\text{Ln}(S)$
Simpsons Index	$D = 1 - \frac{\Sigma n(n-1)}{N(N-1)}$
Nematode Channel Ratio (NCR)	$NCR = 1 - \frac{Ba}{Fu+Ba}$

Copyrights