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Characterization of Soil Nematode Community as Influenced by Weedy Plants and Edaphic Properties

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CHARACTERIZATION OF SOIL NEMATODE COMMUNITY AS INFLUENCED BY
WEEDY PLANTS AND EDAPHIC PROPERTIES

A Thesis

by

ORLANDO GARCIA

Submitted in Partial Fulfillment of the
Requirements of the Degree of
MASTER OF SCIENCE

Major Subject: Biology

The University of Texas Rio Grande Valley

December 2021

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WEEDY PLANTS AND EDAPHIC PROPERTIES

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December 2021

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ABSTRACT

Garcia, Orlando, Characterization of soil nematode community as influenced by weedy plants and edaphic properties. Master of Science (MS), December 2021, 42 pp., 6 tables, 6 figures, references, 69 titles.

Nematodes are an important component of soil food web. They play a vital role in soil nutrient cycling. However, since most of the current research has focused on a singular group of nematodes, the herbivore/plant-parasitic nematodes, very little is known about their overall contribution in agricultural as well as natural systems. In this study, we analyzed the shift in nematode community composition as influenced by native and invasive weed species in the Lower Rio Grande Valley (LRGV). We explored the influence of soil of edaphic soil properties on nematode community.

Our results indicate a significant difference in the composition of the soil nematode community amongst native and invasive weed species in the LRGV. The major differences were observed as individual nematode species such as *Helicotylenchus* spp. and *Pratylenchus* spp. Along with the different plant species, soil edaphic properties also had significant influence on the soil nematode community. These results have significant implications on both invasive species and plant parasitic nematode management.

DEDICATION

The completion of my master's studies is dedicated to my family, friends, and future first-generation Mexican Americans. Thank you for your support in furthering my education to my father, mother, brother, sister-in-law, nieces, and friends I made along the way.

ACKNOWLEDGMENTS

I'm grateful to Dr. Pushpa Soti for her guidance and mentorship for the past four years in my undergraduate and graduate career. She has been a role model of perseverance, professionalism, strength, and excellence in the world of academia. I have witnessed Dr. Soti's hard work firsthand, guiding future scientists and providing opportunities no matter their academic dreams.

Secondly, I would like to acknowledge Dr. Rupesh Kariyat & Dr. Alexis Racelis for their approaches and guidance on my research experiment, constantly providing feedback/resources for my success. Furthermore, I will expand my gratitude to all my academic professors along the way, such as Dr. Mirayda Torres-Avila. They have been present since the first day of my undergraduate studies.

Thirdly, I would like to express my gratitude to all the farmers and owners of my study sites for conducting to my research. In particular, I would like to acknowledge Juan Raygoza and Hilltop Gardens, who openly offered me assistance with my soil/plant collection. Thank you to my lab partner, Andrea Mota, for your assistance throughout my research for the last three years in processing, collecting, and analyzing samples. Lastly, thank you, to my parents, Onofre Garcia & Diana L. Garcia, for their constant support in my endeavors.

TABLE OF CONTENTS

	Page
ABSTRACT	iii
DEDICATION	iv
ACKNOWLEDGMENTS.....	v
TABLE OF CONTENTS	vi
LIST OF TABLES	viii
LIST OF FIGURES.....	ix
CHAPTER I. SOIL NEMATODES AND COMMON WEEDS IN THE LOWER RIO	
GRANDE VALLEY	1
Abstract	1
Introduction.....	2
CHAPTER II. DIFFERENTIAL INFLUENCE OF NATIVE AND INVASIVE WEEDS ON	
SOIL NEMATODE COMMUNITY DYNAMICS.....	9
Abstract	9
Introduction.....	10
Materials and Methods.....	12
Results.....	16
Discussion.....	28
Conclusions.....	31
CHAPTER III. CONCLUSION AND RECOMMENDATIONS	33

REFERENCES.....	35
BIOGRAPHICAL SKETCH	42

LIST OF TABLES

	Page
Table 2. 1 Monthly averages of recorded temperatures and precipitation in the LRGV.....	14
Table 2. 2 Nematode community assessment and the indices with references.	15
Table 2. 3 Mean rhizosphere soil characteristics under different weeds during different sampling periods.....	17
Table 2. 4 Relative abundance of different nematodes under the 4 weed species all three seasons pooled. Dominant species (>10% relative abundance) in bold.	19
Table 2. 5 Results of GLM analyzing the effects of plant and sampling period (season) on the relative abundance of nematode trophic groups, total nematodes, and nematode community.	25
Table 2. 6 Multivariate correlation between different soil properties and soil nematode community, r followed by P- values in parentheses	27

LIST OF FIGURES

	Page
Figure 1. 1 Nematode trophic groups based on morphology: plant- parasitic (a), fungivore (b), bacteria feeder (c).	2
Figure 1. 2 Invasive grasses species in the Lower Rio Grande Valley (LRGV): <i>Megathyrsus</i> <i>maximus</i> (a), <i>Pennisetum ciliare</i> (b).	6
Figure 1. 3 Weedy species native to the Lower Rio Grande Valley (LRGV): <i>Solanum</i> <i>elaegnifolium</i> (a), <i>Helianthus annuus</i> (b).	7
Figure 2. 1 Different sampling sites in Hidalgo County, Texas.	14
Figure 2. 2 The total mean number of soil nematodes per 100 grams of dry soil amongst four weed species: BG (buffelgrass), GG (Guinea grass), SF (sunflower), SLN (silverleaf nightshade). Similar letters on each trophic group indicate no significant difference ($P \leq 0.05$).	20
Figure 2. 3 Seasonal varitaion (N=3) by plant speceis (N=4) with total mean of soil nematode trophic groups, a: BG (buffelgrass), b: GG (Guinea grass), c: SF (sunflower), d: SLN (silverleaf nightshade).....	24

CHAPTER I

SOIL NEMATODES AND COMMON WEEDS IN THE LOWER RIO GRANDE VALLEY

Abstract

Soil nematodes can be categorized into various trophic groups: fungivores, herbivores, bacterivores, omnivores, and predatory. These nematode trophic groups are vital in the soil ecosystem as their composition indicates and the soil conditions. While they are great soil health indicators, little is still known about their dynamics with weedy plant species (native/ invasive), particularly in the Lower Rio Grande Valley, a semi-arid region in south Texas. In this study, the nematode community composition in the rhizosphere of two native species, *Solanum elaeagnifolium* and *Helianthus annuus*, were compared to the rhizosphere nematode community of two invasive grass species, *Megathyrsus maximus* and *Pennisetum ciliare* which coexist along roadsides and farm edges. Although the invasive success can be due to a multitude of factors including, but not limited to such as adaptation to abiotic stress, enemy release, and other ecological traits, to name a few. Estimating the role of nematodes in weedy plant success and possible range expansion is not only interesting but will also add another layer of information on our understanding of weed and the ecological interactions they mediate.

Introduction

Nematodes, also known to most individuals as roundworms, are classified under the phylum *Nematoda*. Nematodes are found in both aquatic and terrestrial environments. In terrestrial ecosystems, nematodes are the most abundant organisms and feature in the major trophic levels in the soil food web (van den Hoogen et al., 2019). Nematodes occupy the water filled pore space in soil around soil organic matter and plant roots. The soil nematodes can be classified as plant-parasitic or herbivores that feed on plants (Figure 1.1.a), fungivore (Figure 1.1.b) that feed on fungi, bacteria feeders (Figure 1.1.c) feeding on bacteria, and predators that feed on other nematodes. Nematodes are also reported to switch between trophic groups depending on available food sources (Neher., 2002). This feeding behavior of nematodes influences their functional role in the terrestrial ecosystem.

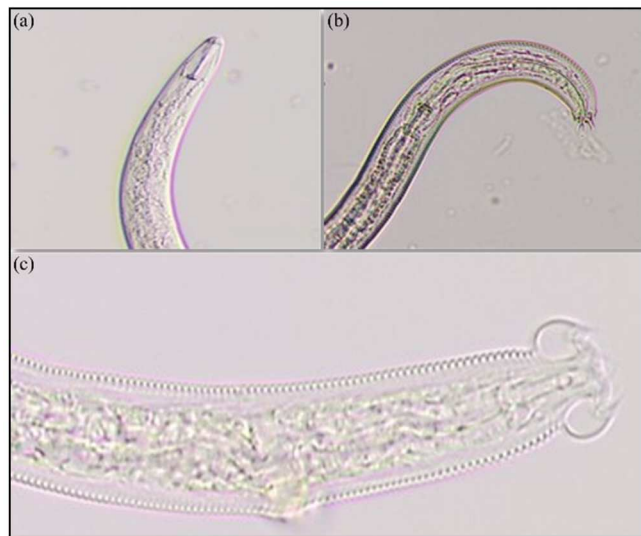


Figure 1. 1 Nematode trophic groups based on morphology: plant- parasitic (a), fungivore (b), bacteria feeder (c).

The trophic groups of each of the soil nematode community play a vital part in the soil ecosystem, as some have specialized roles and serve as health indicators. Bacterial and fungivore nematodes play a crucial role in turnover of soil microbial biomass that influences plant uptake (Yeates., 2003). This process is done directly or indirectly as bacteria feeding nematodes excrete nutrients and control bacteria population size (Yeates., 2003). It is estimated that 40 percent of mineralization in some ecosystems are attributed to soil nematodes (Yeates., 2003). The trophic groups of omnivorous and predators are key to the suppression of over populations of plant parasitic nematodes. Additionally, due to the suppression of plant parasitic nematodes, predatory nematodes relieve stress on plant species and as well secrete nutrients (Khan and Kim., 2007). In agro-ecosystems, soil suppressiveness of plant parasitic nematodes is correlated with the ratio of both predatory and omnivorous nematodes (Sánchez-Moreno and Ferris., 2007). Thus, the management of this complex nematode food web can be essential to the success or downfall of crops and agricultural systems.

Nematodes are a critical component of the soil ecosystem which regulate the composition of vegetation and influence species composition. Soil nematode communities are in turn influenced by the vegetation. This is done through chemical cues for examples those of volatile organic compounds (VOCs) and N-acyl-L-homoserine lactones (AHLs) that influence an array of soil microbes (Ortiz-Castro et al., 2009). Chemicals like VOCs that are secondary plant metabolites can spread through water filled pores within soil allowing for plant- soil biota communication this can be witness in stressed plants for example those suffering a fungal infection can attract antifungal organisms (Schultz-Bohm et al., 2018). This plant nematode feedback has an important implication in agriculture and natural systems where soil nematodes

can influence the competitive advantage of weeds over crops and invasive plants over the natives.

Invasive plants and soil nematodes

Release from the both the aboveground and belowground herbivores (enemy release) is a prominent mechanism which allows for the extensive growth of invasive species in the introduced range (Mitchell and Power., 2003). Enemy Release Hypothesis states that the success of invasive species can be due to the lack of predators in this cases herbivores against the invading species in the invaded region while natives are still being regulated. For example, van der Putten et al. (2005) reported that invasiveness of a dune grass, *Ammophila arenaria*, correlates with escape from feeding specialist nematodes (sedentary endoparasitic cyst and root knot nematodes). However, there is limited research focused on the overall invasive plant-nematode feedback and how invasive plants shift the soil nematode community. In this study we focus on the impact of invasive grasses on the soil nematode community in subtropical semi-arid environment.

Study Species

Pennisetum ciliare (Family: *Poaceae*) (Figure 1.2 a), buffelgrass, is a perennial grass species which has become invasive in the subtropical arid regions worldwide including Australia, Mexico, and the United States (Abella et al., 2012; Soti et al., 2020). This grass species was introduced in Texas by the Soil Conservation Service nursery in San Antonio in 1946, then was officially released for production in 1949 (Wied et al., 2020). In recent years, buffelgrass has invaded roadsides, agricultural fields, and natural areas in the southwestern United States which has caused a significant decline in the native grass species in the region

(Abella et al., 2012). In a recent study, 25% of *P. ciliare* had a 73% reduction in native forb canopy and 64% decline in species richness in Texas (Sands et al., 2009). This species also has impact on the ecosystem by increasing the probability of fires (Fusco et al., 2019).

Megathyrsus maximus (Family: *Poaceae*) (Figure 1.2 b), guinea grass, is a perennial C4 grass species originally from tropical and subtropical Africa which was introduced worldwide as a forage grass species because of its tolerance to grazing and adverse environmental conditions. *M. maximus* is considered one of the most cultivated for livestock farming in tropical climates with optimal growth temperature ranging from 30 to 40 degree Celsius (Olivera Vicedo et al., 2019). *M. maximus* is currently reported to be an invasive species in most of the introduced range (Soti and Thomas., 2021). *M. maximums* is best adapted to frost free areas (Aganga and Tshwenyane., 2004). This species is reported to be introduced to south Texas during the 1970s, but previous introductions have occurred without rapid expansion or prolong duration (Wied et al., 2020). The extensive spread of *M. maximus* in south Texas can be attributed to unauthorized planting of the species from an agricultural experiment in Weslaco, TX (Wied et al., 2020). Currently, *M. maxiums* invades roadsides, farm margins, rangelands, and natural areas in the region (Soti et al., 2020).



Figure 1. 2 Invasive grasses species in the Lower Rio Grande Valley (LRGV): *Megathyrsus maximus* (a), *Pennisetum ciliare* (b).

Solanum elaeagnifolium (Family: *Solanaceae*) (Figure 1.3.a), silver leaf nightshade, is a native weed species to Texas. Silver leaf nightshade is characterized by having hairlike projections called trichomes with glandular/non-glandular variations (Kariyat et al., 2019) and they're toxic to animal species (Soti et al., 2020). The weed can also be seen having a bright colored flower varying from purple, violet, and white (Mekki., 2007). It is reported that silver leaf nightshade near areas of Texas and Oklahoma are part of a group of 10 weeds that cause 70% of cotton loss (Mekki., 2007) causing significant agricultural loss in its own home range of southwestern Texas and northern Mexico (Kasper et al., 2021). Additionally, in some introduced regions like Australia silverleaf nightshade has caused a significant decline in crop yield as well (Mekki., 2007; Lefoe et al., 2020).

Helianthus annuus (Family: *Asteraceae*) (Figure 1.3.b), common sunflower, is a native annual weed in the LRGV with bright yellow terminal flowers with prickly hairs surrounding the

stems has built herbicidal resistance (Soti et al., 2020). The leaves can be egg-shaped/ triangular with the center of the flowers being reddish-brown bearing seeds (USDA, 2006) These seeds play a food source to multiple animal species. The common sunflower can be seen in areas such as North America, Southern Canada, and Mexico appearing at elevation levels below 1900 meters (USDA., 2006). This weed species can be a pest to agricultural crops such as corn and soybeans (Soti et al., 2020).

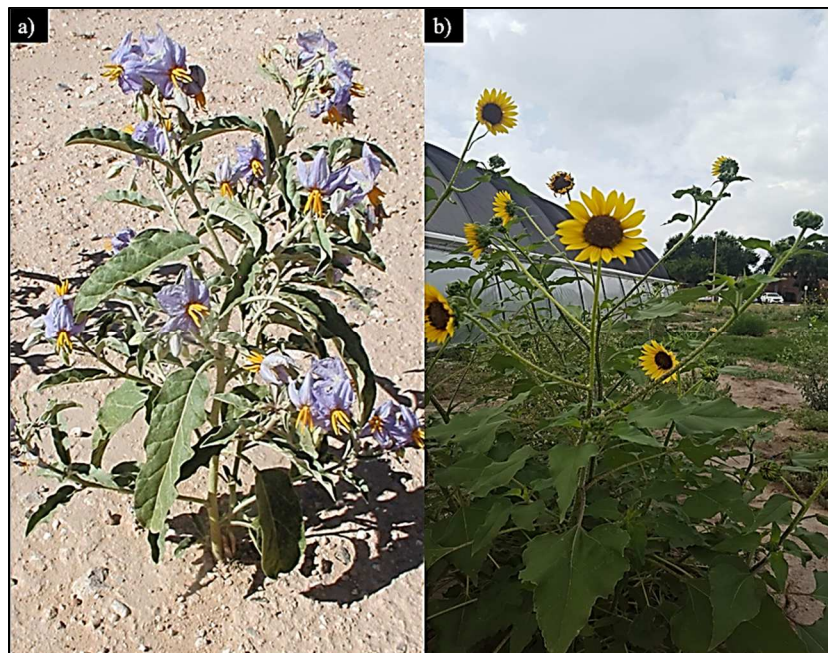


Figure 1. 3 Weedy species native to the Lower Rio Grande Valley (LRGV): *Solanum elaeagnifolium* (a), *Helianthus annuus* (b).

Site: The Lower Rio Grande Valley (LRGV)

The Lower Rio Grande Valley is in the southern region of Texas bordering Mexico towards its south and the Gulf of Mexico to the east. The region is a semi-arid

subtropical region composed of four counties: Starr, Cameron, Hidalgo, and Willacy. LRGV experiences little precipitation with long summers and relatively short winter season. The growing season in this region is from September through May. While the fallow period is during summers months from June to August.

CHAPTER II

DIFFERENTIAL INFLUENCE OF NATIVE AND INVASIVE WEEDS ON SOIL NEMATODE COMMUNITY DYNAMICS

Abstract

Soil nematodes, as they occupy key positions in soil food web, play a significant role in nutrient cycling and ecosystem functions. The soil environment, vegetation type, and their interactions have a considerable impact on the soil nematode community dynamics. In this study, we analyzed the differences in the nematode community under four different weed species, two native forbs: silverleaf nightshade (*Solanum elaeagnifolium* Cav.), common sunflower (*Helianthus annuus* L.), and two invasive grasses: Guinea grass (*Megathyrsus maximus* (Jacq.) B.K.Simon & S.W.L.Jacobs), and buffelgrass (*Pennisetum ciliare* L.) at different stages of growth/seasons. Our results show that there was significant difference in the soil nematode community composition under different weed species. All weed species had higher abundance of herbivore nematodes, however the invasive grasses had higher abundance of *Helicotylenchus* spp. while the native forbs had higher abundance of *Pratylenchus* spp. In addition, the native forbs had higher relative abundance of bacterivore nematodes compared to the two invasive grasses. The difference in the soil nematode community composition varied across the three sampling periods with changes in the environmental conditions and different stages of plant growth. However, we did not find any significant difference in the diversity indices. These

results show that while the invasive weeds have not yet influenced the soil nematode diversity, they strongly influence in the population of certain group of nematodes.

Introduction

Due to their abundance in all environments and high sensitivity to disturbance and nutrient enrichment (Bongers and Bongers., 1998), soil nematodes are considered indicators of soil health (Šalamún et al., 2012; Moura and Franzener., 2017; Bosch et al., 2018). As the soil nematodes feed on a wide range of organisms including plants, bacteria, fungi, and other nematodes they play a crucial role in the soil food web influencing nutrient cycling and ecosystem functions. For example, predatory nematodes are known to check the populations of herbivore nematodes thereby benefiting the plants (Ferris., 2010). Similarly, fungivore, bacterivore, along with the omnivore nematodes are known to feed on the soil microbes and release nutrients for plant uptake (Bonkowski et al., 2000; Ferris., 2010). In addition, fungivore and bacterivore nematodes are reported to increase soil mineral N by more than 20%, alleviating N deficiency in plants (Ferris et al., 2004). Though herbivore nematodes are generally reported to feed on plants and cause damage, in lower numbers, they can benefit plants. Herbivore nematodes are known to trigger the release of nutrient rich root exudates promoting soil microbial activity in the rhizosphere of plants (Yeates et al., 1999; Ferris, 2010). Herbivore nematodes have also been documented to improve the competitive advantage and fitness of plant species in agroecosystems promoting weeds over crops (Schroeder et al., 2005) and range-expanding species over the natives (Wilschut., 2017). Thus, influencing the ecosystem functions and succession (Van der Putten., 2003). Clearly, soil nematodes have both ecosystem service and disservice functions, based on their relative abundance and interaction with other organisms

(Ferris., 2010). Consequently, changes in the soil nematode assemblages will result in the substantial changes in the soil ecosystem functions.

In natural systems, soil nematodes contribute to the plants and other associated other organisms' community composition and diversity. Plants in turn influence the soil nematode community directly through litter input and rhizodeposition (Wardle et al., 2006; Wuyts et al., 2006) and indirectly through the changes in soil environment such as moisture and temperature (Thakur et al., 2014). Plant metabolites exuded from roots are one of these examples as they are known to repel or attract nematodes influencing the nematode community (Sikder and Vestergård., 2020; Manohar et al., 2020). For example, nitrogen fixing plants are reported to increase fungivores, and bacterivores by their increasing food source (Ye et al., 2020). Similarly, plant species which serve as the preferred host of herbivore nematodes contribute to the shift in the nematode community assemblages (Yeates., 1999). While forbs are generally associated with higher number of bacterivore and fungivore nematodes, grasses are generally reported to have higher number of herbivore nematodes (Talavera and Navas., 2002).

Given the significant damage posed by herbivore nematodes in agriculture production, most studies on nematodes have primarily focused on a few selected species of plant feeding nematodes, which compose only a small portion of the overall soil nematode community (Ferris et al., 2012; Wilschut and Geisen., 2021). There is limited research on the overall soil nematode community and the influence of soil abiotic factors, the plant species, and seasonal variation which leads to the changes in both the plant growth and soil conditions.

The purpose of this study was to analyze the impact of different weed species, native (forbs): silverleaf nightshade (*Solanum elaeagnifolium* Cav., Solanaceae), common sunflower (*Helianthus annuus* L, Asteraceae), and invasive grasses: Guinea grass (*Megathyrsus maximus*

(Jacq.) B.K.Simon & S.W.L.Jacobs, Poaceae), and buffelgrass (*Pennisetum ciliare* L, Poaceae) on the soil nematode communities at different stages of growth. Silverleaf nightshade and common sunflower are flowering forbs native to the region. Both these plants are considered serious weeds and thrive in disturbed habitats (Soti et al., 2020). The two grass species, Guinea grass and buffelgrass are introduced forage grass species which have escaped confinement in ranches and currently spreading at an alarming rate in the region and are considered invasive threatening both natural and agricultural systems (Soti et al., 2020).

Since lower abundance of herbivore nematodes is generally associated with the successful range expansion of invasive plants (Engelkes et al., 2008), we hypothesized that the two invasive grasses Guinea grass and buffelgrass would have lower abundance of herbivore nematodes than the two native forbs, common sunflower, and silverleaf nightshade. We also hypothesized that the relative abundance of bacterivore and fungivore nematodes would increase at senescence when there is higher organic matter in the soil.

Materials and Methods

Study sites and soil sampling

Since the soil nematode community are highly influenced by agrochemicals and soil tillage, we selected 5 different organic vegetable farms in south Texas, the Lower Rio Grande Valley (LRGV), (Figure 2.1). The LRGV is characterized by a semi-arid subtropical climate with long hot summers and mild winters. The vegetable growing season in these farms is September through May. The summer months June through August are generally fallow. Soil samples were collected 3 different times during the study period, summer (May-June): early

growth stage, fall (August-September): flowering and seeding stage, and winter (January-February): senescence of the selected weed species.

Since the selected weeds are common in the farm margins, and the farm margins in organic farms are generally undisturbed, we randomly selected 5 sites with a monoculture of each weed species at the farm margins of each farm. Once one of the major weed species was identified, rhizosphere soil samples were collected at 0-10cm depth with a soil probe from each weed species. The soil was obtained by removing the top organic layer to avoid any plant residues. 2-3 soil cores were taken at the rhizosphere of each weed species until a proximately over 100 grams of soil were withdrawn from the rhizosphere.

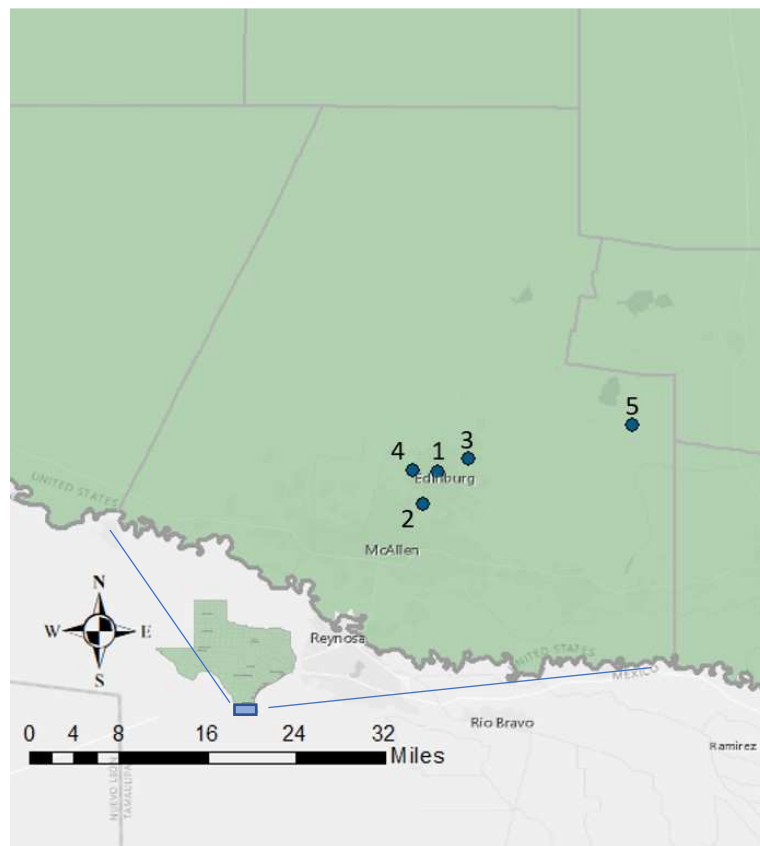


Figure 2. 1 Different sampling sites in Hidalgo County, Texas.

Table 2. 1 Monthly averages of recorded temperatures and precipitation in the LRGV.

Sampling time	Maximum Temp (□)	Minimum Temp (□)	Precipitation (mm)
<i>Summer 2020</i>			
May	33.49	23.19	5.08
June	33.82	24.43	5.33
<i>Fall 2020</i>			
August	35.86	25.31	0.76
September	33.18	22.93	4.064
<i>Winter 2021</i>			
January	22.91	5.82	0.5
February	21.67	10.16	0.2

Soil edaphic properties analysis

We analyzed, soil organic matter, pH, moisture, salinity, and total C and N in each soil sample. Soil moisture was measured gravimetrically. Organic matter was determined by the dry combustion method (500°C 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 be 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).

Soil nematode extraction and quantification

Soil nematodes were extracted from 100 g of soil following the sucrose centrifugal-flotation method (Jenkins., 1964). After extraction, nematodes were stored in a 4°C refrigerator for 24 hours. After 24 hours, the nematodes in each sample were identified morphologically under an inverted compound microscope (Leica Dmi1, Wetzlar, Hesse, Germany). The nematodes were grouped under different trophic groups: fungal feeders, bacteria feeders,

predators, and plant parasites. When possible, nematodes were further identified at the genus level.

Soil nematode community analysis

For nematode community analysis, the nematodes were assigned into different trophic groups and relative abundance of each trophic group was determined. The nematode community structure was further characterized by Shannon-Weiner Diversity Index (H'), evenness index ($E_{H'}$), Simpson Index (D), and nematode channel ratio (NCR) as shown in Table 2.2.

Table 2. 2 Nematode community assessment and the indices with references.

Index	Formulas	Reference
Shannon-Weiner Diversity Index	$H' = -\sum p_i(\ln p_i)$	Yan et al., 2018
Evenness Index	$E_{H'} = H' / \ln(S)$	Yan et al., 2018
Simpsons Index	$D = 1 - \frac{\sum n(n-1)}{N(N-1)}$	Yan et al., 2018
Nematode Channel Ratio	$NCR = \frac{Ba}{(Ba + Fu)}$	(Yeates, 2003; Yan et al., 2018)

Data analysis

Data for soil parameters, total number of nematodes, and nematode populations under different plant species during different sampling periods were analyzed using 2 way-ANOVA, followed by a post hoc comparison using Tukey's HSD test. Significance was determined at the $P < 0.05$ level. We used Generalized Linear Model (GLM) with Poisson error distribution to assess the difference in nematode communities in different weed species across the different sampling periods. Correlation analysis was done to determine the association between the

environmental variables and soil nematode communities. All data were analyzed using the JMP Pro15.

Results

Rhizosphere soil characteristics

Our results show that the soil characteristics (pH, salinity, organic matter, and total carbon, and total nitrogen) significantly differed under different weed species (Table 2.3) across different sampling periods. Soil pH was higher under silverleaf nightshade while lowest in Guinea grass. However, for soil salinity, Guinea grass had the highest average at 410.36 $\mu\text{s}/\text{cm}$ while silverleaf nightshade lowest at 312.12 $\mu\text{s}/\text{cm}$, however this difference was not statistically significant. Organic matter was highest under Sunflower (3.49%) followed by silverleaf nightshade (3.24%), and Guinea grass (3.22%), while buffelgrass had the lowest (2.98%). Similar results were also seen in soil moisture; sunflower had the highest (9.04%) followed by silverleaf nightshade (8.40%) while the two invasive grasses had the lowest, Guinea grass (7.29%) and buffelgrass (6.67%). Total carbon was highest under Guinea grass, followed by buffelgrass and sunflower 1.61%, and lowest in silverleaf nightshade. Finally, total nitrogen was highest in Sunflower (0.087%), followed by silverleaf nightshade (0.082%), and Guinea grass (0.069%), and lowest in buffelgrass (0.063%), this difference was also not statistically significant.

Table 2. 3 Mean rhizosphere soil characteristics under different weeds during different sampling periods.

Source	DF	F	P
<i>Salinity</i>			
Season	2	22.33	<0.0001
Plant	3	0.218	0.883
Season*Plant	6	0.632	0.704
<i>pH</i>			
Season	2	35.519	<0.0001
Plant	3	8.464	<0.0001
Season*Plant	6	2.572	0.0200
<i>OM%</i>			
Season	2	5.129	0.0067
Plant	3	2.015	0.112
Season*Plant	6	1.507	0.177
<i>Moisture %</i>			
Season	2	11.251	<0.0001
Plant	3	3.571	0.0160
Season*Plant	6	1.607	0.146
<i>Total C%</i>			
Season	2	27.792	<0.0001
Plant	3	1.429	0.235
Season*Plant	6	0.201	0.976
<i>Total N%</i>			
Season	2	4.300	0.0148
Plant	3	1.725	0.162
Season*Plant	6	1.552	0.162

Soil nematode community composition

During the three sampling periods in the different organic farms at the Lower Rio Grande Valley (LRGV) a total of 222 soil samples collected. The 222 soil samples yielded a total of 331,070 individual nematodes with almost 1500 nematodes per 100 grams of dry soil. We identified 23 different species of nematodes, of which 10 herbivores, 5 fungivores, 3 bacterivores, 1 predator, and 4 species were not identified and are listed as unknowns. Overall, herbivores had the highest relative abundance, 64.02%, followed by bacterivores 18.16%, and fungivores 7.13%, with predators and the unknowns lowest in number, 1.91% and 1.44% respectively (Table 2.4).

When pooled for all sampling periods, *Helicotylenchus* sp. 1 was the most dominant across all weed species (Table 2.4). The relative abundance of *Helicotylenchus* sp. 1 was highest under the two invasive grasses, Guinea grass and buffelgrass 44.6% and 39.7 % respectively. Similarly, *Helicotylenchus* sp. 2 was also more dominant in the invasive grasses compared to the native weeds. Interestingly, *Pratylenchus* sp. 1 was more dominant in the native weeds, 25.12% sunflower and 11.94% in silverleaf nightshade compared to the invasive grasses with 3.64% in buffelgrass and 2.44% in Guinea grass. Bacterivore sp. 1, “B1”, (Table 4.1) was the second most dominant nematode species amongst all weeds, with the highest number in silverleaf nightshade (20.80%) followed by sunflower (19.65%), while buffelgrass had 17.37% and Guinea grass had 14.62%. *Aphelenchoides* spp. was the most dominant fungivore species with relative abundance ranging from 4.52% in buffelgrass to 9.06% in Guinea grass (Table 2.4). Predators followed by unknowns had the lowest relative abundance and were the least dominant.

Table 2. 4 Relative abundance of different nematodes under the 4 weed species all three seasons pooled. Dominant species (>10% relative abundance) in bold.

Species	Weed Species			
	BG	SF	SLN	GG
Herbivores				
<i>Tylenchus</i> spp. 1	5.34	3.94	5.66	4.08
<i>Helicotylenchus</i> 1	39.72	26.26	25.38	44.60
<i>Tylenchus</i> spp. 2	0.51	0.45	0.66	0.38
<i>Pratylenchus</i> spp. 1	3.64	25.12	11.94	2.44
PPV	1.60	0.43	1.35	0.71
<i>Tylenchus</i> spp. 3	0.01	-	0.08	-
<i>Paratylenchus</i> spp. 1	0.10	0.18	0.13	0.18
<i>Pratylenchus</i> spp. 2	3.73	1.45	2.67	4.07
<i>Helicotylenchus</i> spp. 2	7.45	3.05	5.20	8.14
<i>Mesocriconema</i> spp. 1	3.63	1.23	6.21	1.14
Fungivores				
F1	3.59	3.93	5.11	5.57
F2	1.05	0.87	0.89	0.57
F3	0.84	0.60	0.97	0.34
F4	0.82	1.55	1.21	0.76
<i>Aphelenchoides</i> spp.	4.52	7.30	6.17	9.06
Bacterivores				
B1	17.37	19.65	20.80	14.62
B2	-	0.07	0.17	0.01
B3	2.17	0.63	1.34	0.45
Predators				
PD1	2.18	1.90	2.59	1.56
Unknowns				
UC1	0.38	0.37	0.31	0.43
UC2	0.61	0.10	0.04	0.03
UC3	0.09	0.17	0.04	0.07
UC4	0.65	0.75	1.06	0.80

Soil nematodes under different weed species

Overall, there was a significant difference in the nematode community composition among the different weed species (Figure 2.2). Among the four weed species analyzed, Guinea grass had highest herbivore nematodes ($\mu=1479.40$; $SE= 262.24$) which was also statistically significant compared to sunflower ($P=0.0442$) and silverleaf nightshade($P=0.0067$). The second largest herbivore numbers were buffelgrass ($\mu=869.03$; $SE= 156.95$) followed by sunflower ($\mu=765.79$; $SE=125.86$), and the lowest numbers coming from silverleaf nightshade ($\mu=577.45$; $SE=95.56$).

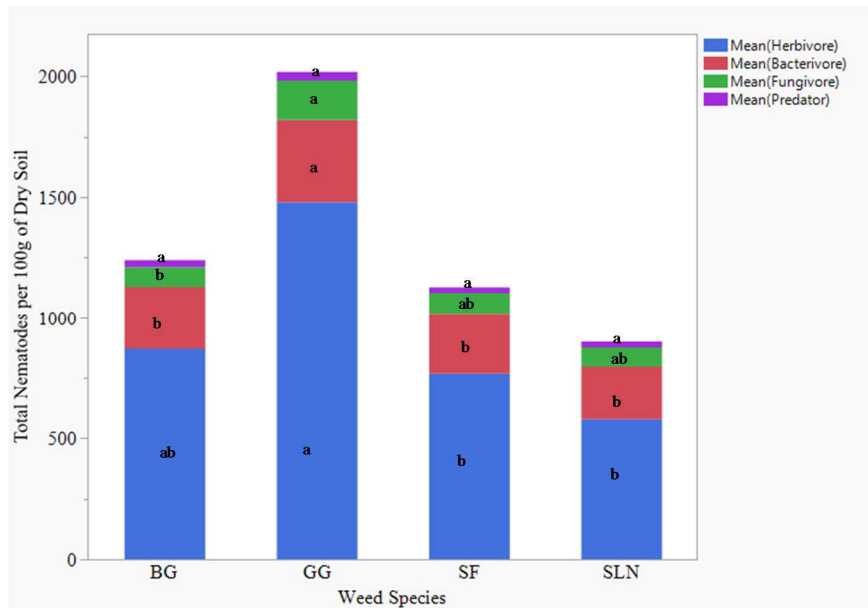


Figure 2. 2 The total mean number of soil nematodes per 100 grams of dry soil amongst four weed species: BG (buffelgrass), GG (Guinea grass), SF (sunflower), SLN (silverleaf nightshade). Similar letters on each trophic group indicate no significant difference ($P\leq 0.05$).

Similar to herbivores, Guinea grass also had significantly higher number of bacterivore nematodes compared to the other weed species, buffelgrass ($P=0.0405$), sunflower ($P=0.0139$), silverleaf nightshade ($P=0.0020$). Guinea grass ($\mu=339.62$; $SE= 32.11$) had the highest followed

by buffelgrass ($\mu=258.39$; $SE= 34.94$) and sunflower ($\mu=250.99$; $SE=37.43$) with silverleaf nightshade the lowest ($\mu=217.36$; $SE= 31.04$). There was no significant difference in the total number of bacterivore nematodes among the other weed species. While Guinea grass had significantly higher number of fungivore nematodes compared to buffelgrass ($P=0.0123$), there was no significant difference among other weed species. Similarly, there was no significant difference in the total number of predator nematodes among the different weed species.

Seasonal variation in nematode populations

There were some notable shifts in the nematode community composition over the three-sampling periods among the different weed species (Figure 2.3, Table 2.5). Buffelgrass had significantly higher number of herbivore nematodes during winter ($\mu= 1449.20$; $SE=319.00$) compared to the fall ($P=0.0092$; $\mu=596.88$; $SE=211.07$) and summer ($P= 0.0035$; $\mu=403.91$; $SE=125.40$). Guinea grass also had highest number of herbivore nematodes in winter ($\mu=2091.77$; $SE= 478.87$) compared to fall ($P= 0.0470$; $\mu=1008.17$; $SE=298.04$) and summer ($P=0.0439$; $\mu=820.39$; $SE=367.21$). Sunflower, a native weed, had higher number of herbivores during the fall compared to summer ($P < 0.0001$; $\mu=290.35$; $SE=86.53$) and winter ($P= 0.0014$; $\mu=824.69$; $SE=222.29$). Silverleaf nightshade, another native weed, had no significant difference in the herbivore nematodes during different sampling periods.

All the weed species had the lowest number of bacterivore nematodes during the summer sampling period ($P<0.001$). Sunflower had highest number in winter ($\mu=475.45$; $SE=96.82$) followed by fall ($\mu=348.25$; $SE=54.10$) and lowest in summer ($\mu=75.92$; $SE=19.23$) and this difference was statistically significant, $P<0.0001$. Silverleaf nightshade had highest number of

bacterivore nematodes in fall ($\mu=423.78$; $SE=68.48$) followed by winter ($\mu=267.58$; $SE=44.35$) and lowest in the summer ($\mu=69.39$; $SE=12.48$) which was also statistically significant, $P<0.0001$. Buffelgrass, an invasive, had higher numbers in the winter ($\mu=435.01$; $SE= 61.47$) then fall ($\mu=222.49$; $SE= 40.997$) with summer ($\mu=63.57$; $SE= 24.91$) coming last in bacterivores. There were significant differences in seasons shifts winter to summer ($P<.0001$), winter to fall ($P=0.0058$), and summer to fall ($P=0.0012$). Guinea grass followed the same trend as the other invasive grass with winter ($\mu= 452.53$; $SE=54.26$) being the highest, summer ($\mu=113.20$; $SE=31.17$) being the lowest and fall ($\mu=294.72$; $SE=34.02$) somewhere in between the two. There were significant seasonal shifts from winter to summer ($P=0.0003$) and summer to fall ($P=0.0014$) but there was no difference in population from winter to fall ($P=0.0572$).

Similar pattern of lower numbers in summer was also seen in the fungivore nematodes. Sunflower had the highest number of fungivores in winter ($\mu=189.21$; $SE=55.10$) followed by fall ($\mu=98.21$; $SE=25.00$) and lowest in summer ($\mu=24.56$; $SE=6.17$). This difference was statistically significant, $P=0.0017$ and $P=0.0062$ respectively. Silverleaf nightshade had the highest number of fungivores in fall ($\mu=147.42$; $SE=35.43$) followed by winter ($\mu=64.94$; $SE=13.42$) and the lowest in summer ($\mu=46.17$; $SE=11.94$). While the difference between fall and summer was statistically significant ($P=0.0160$), there was no significant difference in the fungivore nematodes in silverleaf nightshade between winter and fall and summer and winter. Similarly, in buffelgrass there was significant difference in the fungivore nematodes from winter to summer ($P=0.0071$) and fall ($P=0.0138$). Winter had the largest number of fungivores ($\mu=169.15$; $SE=48.82$) followed by fall ($\mu= 35.87$; $SE=11.23$) and summer ($\mu=22.41$; $SE=6.62$). In Guinea grass, there was significant difference in the number of fungivore nematode between summer and winter ($P=0.0040$) and fall ($P=0.0259$), but there was no difference between winter

and fall ($P=0.6541$). The total number of fungivore nematodes was highest in winter ($\mu=204.28$; $SE=58.35$) followed by fall ($\mu=168.65$; $SE=51.32$), and lowest in summer ($\mu=25.51$; $SE=10.44$).

Finally, for predators, sunflower had the most in fall ($\mu=34.34$; $SE=8.71$) which was significantly different than winter ($\mu=27.72$; $SE=9.60$) and summer ($\mu=14.74$; $SE=7.16$) ($P=0.0049$). Seasonal difference in the predator nematodes was also observed in Guinea grass, where there was a significant difference between summer and fall numbers ($P=0.0284$) with fall having the highest ($\mu=46.33$; $SE=12.29$) followed by winter ($\mu=34.58$; $SE=10.52$) and lowest in the summer ($\mu=8.39$; $SE=4.62$). For silverleaf nightshade there were highest in number in fall ($\mu=34.14$; $SE=10.68$), followed by winter ($\mu=24.38$; $SE=12.85$), and lowest in summer ($\mu=20.30$; $SE=5.55$), but this difference was not statistically significant. Similarly, buffelgrass had the highest number in fall ($\mu=39.37$; $SE=10.68$), followed by winter ($\mu=28.25$; $SE=10.32$) and lowest in summer ($\mu=17.42$; $SE=8.02$).

Our results show a seasonal shift in the relative abundance of soil nematode trophic groups (Table 2.5; Figure 2.3). The relative abundance of herbivore nematodes increased in the winter months there was decline in the relative abundance of bacterivores ($R^2=0.51$; $P<0.0001$) and fungivores ($R^2=0.09$; $P<0.0001$).

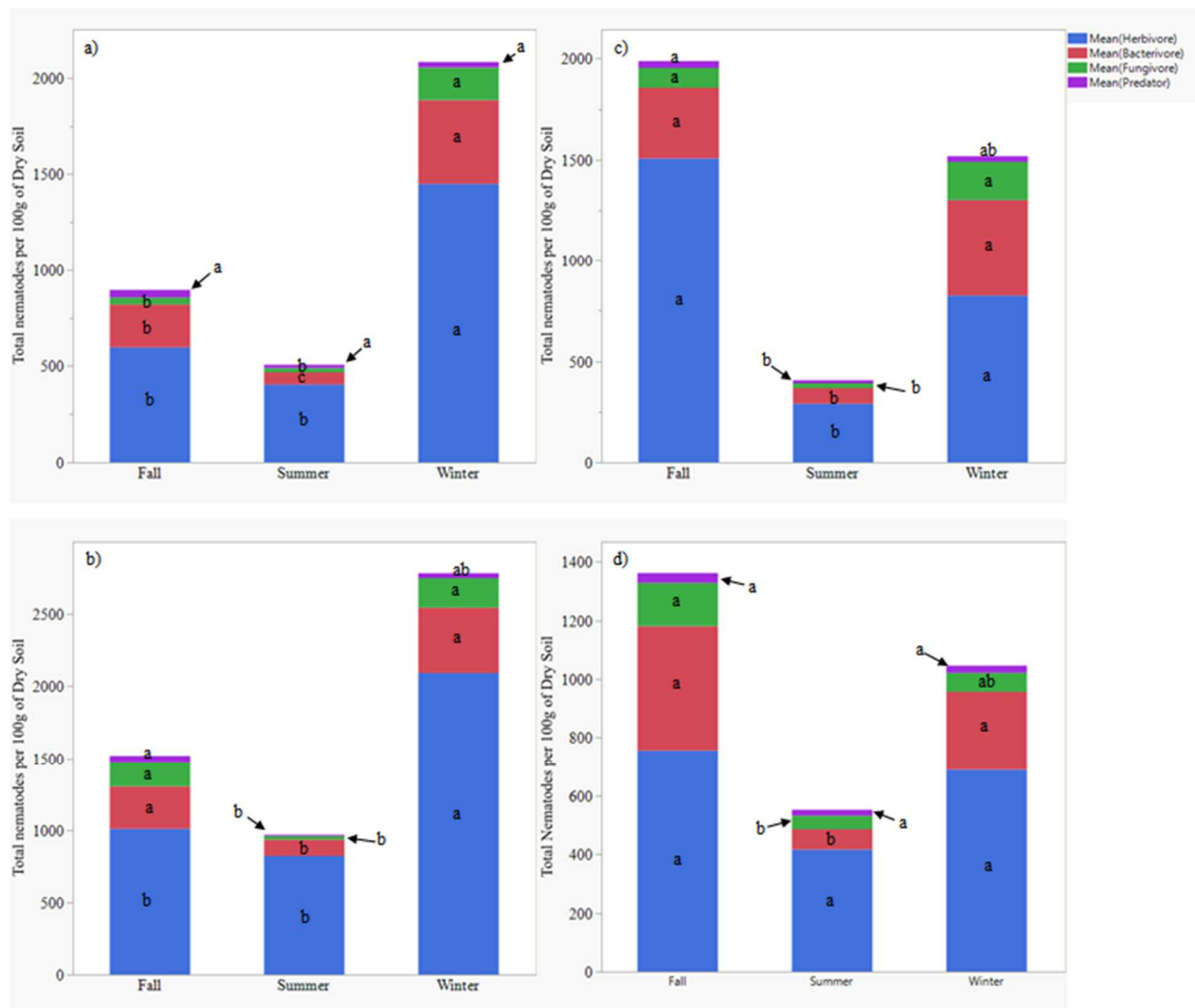


Figure 2.3 Seasonal variation (N=3) by plant species (N=4) with total mean of soil nematode trophic groups, a: BG (buffelgrass), b: GG (Guinea grass), c: SF (sunflower), d: SLN (silverleaf nightshade).

Table 2. 5 Results of GLM analyzing the effects of plant and sampling period (season) on the relative abundance of nematode trophic groups, total nematodes, and nematode community.

Effect	df	χ^2	P
<i>a. Herbivore nematodes</i>			
Season	3	20.256	<0.0001
Plant	2	12.541	0.0057
Plant \times Season	6	160.722	<0.0001
<i>b. Bacterivore nematodes</i>			
Season	3	242.836	<0.0001
Plant	2	16.222	0.0010
Plant \times Season	6	145.79	<0.0001
<i>c. Fungivore nematodes</i>			
Season	3	94.11	<0.0001
Plant	2	52.712	<0.0001
Plant \times Season	6	110.5118	<0.0001
<i>d. Predator nematodes</i>			
Season	3	50.504	<0.0001
Plant	2	14.327	0.0025
Plant \times Season	6	57.305	<0.0001
<i>e. Total nematodes</i>			
Season	3	36366.049	<0.0001
Plant	2	13960.347	<0.0001
Plant \times Season	6	13791.806	<0.0001
<i>f. Shannon Diversity Index</i>			
Season	3	0.080	0.9610
Plant	2	0.439	0.9322
Plant \times Season	6	0.770	0.9929
<i>g. Evenness</i>			
Season	3	0.400	0.8189
Plant	2	0.186	0.9798
Plant \times Season	6	0.231	0.9998
<i>h. Simpson Diversity Index</i>			
Season	3	0.092	0.9549
Plant	2	0.112	0.9904
Plant \times Season	6	0.183	0.9999
<i>i. NCR</i>			
Season	3	0.624	0.7320
Plant	2	0.065	0.9956
Plant \times Season	6	0.227	0.9998

Seasonal variation in nematode community

We calculated the Shannon Diversity Index and Simpsons Diveristy Index to determine the diversity of nematodes, evenness index to evaluate the abundance of different nematodes. We also calculated the NCR to analyze the decomposition pathway under different weeds species

during different sampling period. That there was no significant difference in the Shannon Diversity Index and Simpsons Diveristy Index, evenness index, and (NCR) among the different weed species, the different sampling periods, and the interaction of the two (Table 2.5).

Correlation between soil properties and nematode communities

We found significant correlation between the nematode communities and soil parameters (Table 2.6). Though not very strong, there was significant correlation between soil nitrogen and Shannon Diversity Index ($r=0.1772$, $P=0.0081$), Simpsons Index ($r=0.1970$, $P=0.0032$), and Evenness Index ($r= 0.1390$, $P=0.0385$). Soil nitrogen was negatively correlated with nematode channel ratio ($r= -0.2047$, $P=0.0024$) and bacterivore relative abundance ($r=-0.1565$, $P=0.0197$). Soil carbon was positively correlated with herbivore relative abundance ($r=0.1807$, $P=0.0070$), fungivore relative abundance ($r=0.1122$, $P=0.0953$), Simpsons Index ($r=0.0500$, $P=0.4582$), and Shannon Diversity Index ($r=0.1220$, $P=0.0697$). While soil moisture was positively correlated with the herbivore relative abundance ($r=0.3626$, $P<0.0001$), soil moisture was negatively correlated with nematode channel ratio ($r=-0.2620$, $P<0.0001$) and the relative abundance of bacterivore nematodes ($r=-0.3863$, $P<0.0001$). Similarly soil organic matter was negatively correlated with nematode channel ratio ($r=-0.2952$, $P<0.0001$), bacterivore relative abundance ($r-0.3013$, $P<0.0001$), and predator relative abundance ($r=-0.1768$, $P=0.0083$) while it was positively correlated with herbivore relative abundance ($r=0.2470$, $P=0.0002$). Soil pH was negatively correlated with bacterivore relative abundance ($r=-0.1795$, $P=0.0073$). There was a negative correlation between soil salinity and evenness index ($r=-0.2402$, $P=0.0003$) while there was a positive correlation with herbivore relative abundance ($r=0.1345$, $P=0.0454$).

Table 2. 6 Multivariate correlation between different soil properties and soil nematode community, r followed by P- values in parentheses.

Index	OM%	pH	Salinity	Moisture	Carbon%	Nitrogen%	C: N
Shannon Weiner Diversity Index	0.1276 (0.0576)	0.0827 (0.2199)	0.1244 (0.0643)	0.0530 (0.4321)	0.1220 (0.0697)	0.1772 (0.0081)	-0.076 (0.253)
Evenness Index	-0.0152 (0.8215)	0.1076 (0.1098)	-0.2402 (0.0003)	0.0514 (0.4462)	-0.1467 (0.0288)	0.1390 (0.0385)	-0.028 (<0.0001)
Simpsons Index	0.1163 (0.0839)	0.1048 (0.1195)	0.0349 (0.6055)	0.0640 (0.3426)	0.0500 (0.4582)	0.1970 (0.0032)	-0.0164 (0.014)
Nematode Channel Ratio	-0.2952 (<.0001)	-0.0740 (0.2765)	-0.0019 (0.9783)	-0.2620 (<.0001)	-0.1239 (0.0678)	-0.2047 (0.0024)	0.070 (0.300)
Herbivore Relative Abundance	0.2470 (0.0002)	0.0777 (0.2487)	0.1345 (0.0454)	0.3626 (<.0001)	0.1807 (0.0070)	0.0820 (0.2238)	0.117 (0.081)
Bacterivore Relative Abundance	-0.3013 (<.0001)	-0.1795 (0.0073)	0.0690 (0.3063)	-0.3863 (<.0001)	-0.0215 (0.7497)	-0.1565 (0.0197)	0.089 (0.185)
Fungivore Relative Abundance	0.1280 (0.0568)	-0.0982 (0.1446)	0.0976 (0.1470)	0.0058 (0.9321)	0.1122 (0.0953)	0.1033 (0.1250)	-0.002 (0.969)
Predator Relative Abundance	-0.1768 (0.0083)	-0.0860 (0.2018)	-0.0763 (0.2574)	-0.2326 (0.0005)	-0.0042 (0.9510)	0.0069 (0.9182)	-0.053 (0.425)

Discussion

Nematodes association with the different weed species

In this study, using samples collected from multiple sites in organics farm in LRGV, we examined the impact of different weedy plants on the soil nematode communities during different growth stages. We found that nematode density and species distribution varied across weed species and seasons. Overall, the nematode community was dominated by herbivore nematodes, particularly the *Helicotylenchus* spp. with the invasive grasses having the highest numbers. *Helicotylenchus* are known to inhabit many soil types (William Crow., 2017) and are generally associated with crops, ornamentals, weeds, and turfgrass species (William Crow., 2017). They are known to be adapted to drought conditions and generally found in higher numbers (Yan et al., 2018). This higher abundance of *Helicotylenchus* in the two invasive grass soil could potentially be explained by the ability of this two grass species to grow in a wide range of environmental conditions including drought, salinity, pH, texture, and nutrient levels and adapted to arid and semi-arid conditions, prevalent in the Lower Rio Grande Valley. The second largest group of herbivore nematodes were the *Pratylenchus* spp. These nematodes and are known to infect both monocots and dicots (Smiley et al., 2014), however, in our study, *Pratylenchus* seemed to prefer forbs compared to grasses. The high overall abundance of generalist herbivore nematodes indicates their close relationship with these weeds which were collected from the field margins of organic vegetable farms. With higher number of herbivore nematodes under the invasive grasses, our results show that invasive plants are susceptible to generalist herbivore nematodes in their introduced range as reported by van der Putten et al., (2005).

The total number of bacterivore nematodes was highest in the invasive Guinea grass. However, the relative abundance of bacterivore nematodes was highest in the two native weeds, silverleaf nightshade and sunflower. Soils with nematode communities dominated by bacterivores are known to have higher decomposition rates influencing the nutrient availability to plants (Ferris et al., 2004). Higher number of these nematodes in the rhizosphere of the two native weeds indicates an availability of easily decomposable organic matter under forbs (Garibaldi., 2007), along with the increase in microbial activity as reported by Wasilewska (1998) compared to the invasive grasses. The dominance of fungivore nematodes was relatively lower compared to the bacterivore nematodes as expected. Among the fungivore nematodes, *Aphelenchoides* spp., which is one of the most common fungivore nematodes, (Ferris and Bongers., 2006) was the most dominant in all weed species with slightly higher relative abundance in Guinea grass. Taken together, our nematode community data clearly shows higher abundance of herbivore nematodes in grasses compared to forbs as reported in previous studies (Talavera and Navas., 2002).

Soil characteristics and nematodes

Nematode populations are known to vary depending on soil conditions (Gregor Yeates., 2003). Relative abundance of herbivore nematodes was positively correlated with the soil moisture in our study, which is a key factor limiting primary productivity, particularly in arid and semi-arid regions. This is consistent with other studies which report a strong influence of soil moisture or precipitation on herbivore nematodes (Gbadegesin et al., 1993; Griffin et al., 1996; Todd et al., 1999). Herbivores were also positively correlated with soil organic matter and total C, bacterivores were negatively correlated with the soil organic matter, while the fungivores did

not show any difference. This was a rather surprising result as soil organic matter is a food source for bacteria and fungi, which are the food source for the bacterivorous and fungivore nematodes. These results are also in contrast with Cheng et al., (2021) who reported that areas with low plant litter having higher number of herbivore nematodes and lower bacterivore and fungivores. Bacterivore nematodes, the group with second largest relative abundance, along with predators were negatively correlated with the soil moisture. This could be the result of the water filled soil aggregates providing the habitable environment for bacterivores and predators along with their prey (Griffiths et al., 2003; Landesman et al., 2011). The fungivores and bacterivores are known to shift in composition with the change in soil C: N and the decomposition pathway (Wang and McSorley., 2005). However, we did not find such shift in our study, indicating limited nematode community succession in agricultural fields due to constant soil disturbance. Shannon and Simpsons diversity index and evenness index were positively correlated with the total nitrogen in soil indicating a richer diversity of nematodes under high soil nitrogen. This result is in contrast with previous studies which report inhibition of nematode diversity and abundance with soil nitrogen enrichment (Saratchandra et al., 2001; Song et al., 2015). Nematode channel ratio, a key indicator of organic matter decomposition (Gregor Yeates., 2003), had a negative correlation with all soil variables. Overall, our results show that difference in soil properties resulting from the changes in environmental conditions have significant impact on the soil nematode community. The diversity of soil nematodes was more influenced by the soil nitrogen than the plant species identity or the sampling periods. Our results show that soil nematode communities are influenced by both the soil environmental conditions and the vegetation, however, did not have an influence in the nematode diversity in the short term.

Seasonal Shifts in soil nematode community

Nematode communities are known to be able to respond rapidly to the changes in the environment (Neher., 2002). In our study both the diversity indices and evenness remained unchanged in the different weed species across different sampling periods. While each plant species has a complex interaction with microbial community which varies at different growth stages and soil environment conditions, similar results of no significant difference in the rhizosphere nematode diversity has been reported in agricultural fields (Ortiz et al., 2016). There was a significant shift in the total number of nematodes and the populations of the different trophic groups. The total number of nematodes was lowest in the summer months when the temperature was relatively high and soil moisture was low. Herbivores were generally higher during the winter and fall months, where the primary productivity is highest in the vegetable farms in the region. Similar shift in numbers was also seen in the bacterivore and fungivore population from the hotter months in summer to the cooler months. Higher temperatures are reported to cause a decline in the herbivore nematodes in semi-arid regions (Yan et al., 2018) leading to an increase in bacterivores and fungivores (Thakur et al., 2014) which was also observed in our study. Difference in the nematode populations in different seasons was also plant species specific. For example, we did not find any significant differences in the herbivore nematodes in silverleaf nightshade, a native forb, during different sampling periods.

Conclusions

Overall, both the sampling period/season and plant species had a significant impact on the soil nematode trophic groups. The sampling season had larger impact than the identity of the plant species, this can be caused by a multitude of ecological factors such as seasonal temperature, moisture, plant development, and species preferability. Finally, our results show

that the most problematic weeds have a significant influence in the soil nematode community. A rather surprising result was, the nematode community remained relatively stable in silverleaf nightshade, a native perennial weed in the region. The two invasive grasses had a high abundance of herbivore nematodes which are known to cause a significant damage to global agriculture production. However, these weeds in our sampling sites did not show any signs of nematode damage during soil sample collection. Our results indicate these weeds serving as hosts of herbivores nematodes may have a significant influence in the agroecosystems and rangelands. Given the invasion success of the two invasive grasses (buffelgrass and Guinea grass) in the region, the herbivore nematodes can potentially stimulate the growth of these two plants by stimulating microbial activity. Thus, further research is necessary to determine the threshold for the herbivores in these plants. These results show that while the invasive weeds have not yet influenced the soil nematode diversity, they strongly influence in the population of certain group of nematodes. For the detailed understanding of the impact of invasive grasses on soil nematode communities further controlled environment experiments testing the plant nematode feedback across different growth stages of the plants and environmental factors are needed.

CHAPTER III

CONCLUSION AND RECOMMENDATIONS

In conclusion, this study indicates that weedy plants have a differential influence on the soil nematode community dynamics. The invasive grasses, *Megathyrsus maximus* and *Pennisetum ciliare*, had higher numbers of herbivorous nematodes compared to their native counterparts (Figure 5.1). This gives further insight into weedy plants being capable to shift the composition of the trophic groups amongst the nematode community. These shifts were further analyzed revealing weedy plants can also influence nematodes at the genus level. Invasive grasses in the study had higher relative abundance of *Helicotylenchus spp* (Table 4.1) while native weed species had higher *Pratylenchus spp* (Table 4.1). These species both are herbivore nematodes which can cause significant damage to their hosts, but none of the plant species in our study showed any symptoms or impairment.

Our results also show that soil properties had considerable influence on the soil community. Moisture out of all the edaphic properties had one of the largest impacts on herbivores, bacterivores, and predator nematodes (Table 6.1). Organic matter as well had similar correlations as moisture with the different trophic groups. Additionally, organic matter had a negative correlation with the nematode channel ratio which gives insight into on how organic matter had a negative correlation with the decomposition pathway (6.1). While soil temperature was not measured in this study, soil temperature has both direct and indirect impacts on soil nematode community dynamics (Bakonyi et al., 2007; Castillo et al., 1996). Temperature

as a variable is critical not only on the nematode community, but on plant species as it influences growth and root development (Kaspar and Bland., 1992; Went., 1953).

Our study was limited to the morphological characterization of the soil nematodes. Incorporating molecular techniques, that could provide detailed species analyses, could be vital to community analysis including the community maturity index (Yan et al., 2018; Yeates et al., 1993) and plant parasitic index (Yan et al., 2018; Yeates et al., 1993). Having information on the colonizer vs persister indicate nematode life strategies in ecosystems and reflect the soil disturbance status. Colonizer (r-strategist) use resources rapidly while persister are the opposite, prolonging resources (Bongers and Bongers., 1998). In addition, this information can provide insight into nematode community shifts triggered by the changes in environmental variables (Ferris et al., 2001). Though our study was limited to the genus level, our results demonstrate that these weedy plants showed no differences in diversity, distribution, and decomposition pathway (Table 5.1) indicating invasive grasses could cause a shift in dominance of different nematode trophic groups but not in the nematode community diversity.

Despite our hypothesis, that invasive grasses would have a lower abundance of herbivore nematodes we found the opposite results. The two invasive grasses in our study had a high abundance of herbivore nematodes in their rhizosphere, though the plants did not show any signs of nematode damage. Our results show that these two invasive grasses not only compete with the native plants and crops in agricultural fields for resources but can also harbor herbivore nematodes. This change in the soil nematode community could have an impact on the restoration of natural habitats and agricultural fields. Thus, any management plan to control these invasive grasses should consider not only the removal and restoration with native species but also the legacy effect, the changes in the soil nematode community.

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BIOGRAPHICAL SKETCH

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