ELUCIDATING THE EFFECT OF ANTHROPOGENIC LAND MANAGEMENT ON SOIL NEMATODE COMMUNITY STRUCTURE

by

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DEDICATION

To my family for your love and patience.

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ABSTRACT

Nematodes as a taxonomic phylum are incredibly diverse and play an important role in soil biology, nutrient cycling, and soil food web function. Nematodes can be categorized into five major trophic groups including bacterivores, fungivores, herbivores, predators, and omnivores. Plant-parasitic nematodes (PPNs) affect soil food web resources through direct herbivory, while free-living (non-pathogenic) bacterivores and fungivores graze on microbes and contribute significantly to soil nutrient pools. Predatory nematodes regulate the soil food web by preying on other nematodes and invertebrates in the soil. An unbalanced soil food web community can lead to unintended impacts to other species and create a cascading effect. In agriculture, this impact can lead to low crop production and reduced revenue by means of soil ecological degradation.

The goal of this project was to elucidate the nematode community structure changes under different management strategies in both agricultural and range settings. The hypotheses we tested were 1) that crop rotations eliminating fallow would positively and significantly impact the soil nematode community that would in turn self-regulate the PPN population and 2) native sagebrush steppe would have a more diverse nematode community than converted sagebrush steppe managed for livestock grazing or other uses. We did so with the following studies:

1. Quantitatively assessed nematode community structure under barley monoculture and barley-fallow vs. barley-pea rotations using multiple ecological measures and indices and correlated those measures and indices with soil chemical and physical properties as well as agronomic parameters of each system.
2. Quantitatively assessed nematode community structure under wheat-tilled fallow, wheat-no-till fallow, and no-till wheat monoculture vs. several no-till wheat-pulse rotations using multiple ecological measures and indices to evaluate long term impacts of cropping system to the nematode community.
3. Quantified taxonomic diversity and ecological indices of disturbed and undisturbed sagebrush steppe in the Bangtail Mountains west of Wilsall, Montana to evaluate disturbance regimes in a reclaimed environment.

CHAPTER ONE

REVIEW OF RELEVANT LITERATURE

Abstract

Nematodes occupy a central position in the soil food web, occurring at multiple trophic levels and having the potential to provide useful insights into the structure and function of the soil food web. Nematodes can be categorized into five major trophic groups including bacterivores, fungivores, herbivores, predators, and omnivores. Plant-parasitic nematodes affect soil food web resources through direct herbivory, while free-living (non-pathogenic) bacterivores and fungivores graze on decomposer microorganisms and contribute significantly to soil nutrient pools. Predatory nematodes regulate the soil food web by preying on other nematodes and invertebrates in the soil. As has been observed with other ecological communities, an unbalanced community can lead to unintended impacts on other species and create a cascading effect. In agriculture, this impact can lead to low production and reduced revenue by means of soil ecological degradation.

The goal of this project was to elucidate the nematode community structure changes under different management strategies in both agricultural and range settings. The hypotheses we tested were 1) crop rotations eliminating fallow positively and significantly impact the soil nematode community that will in turn self-regulate the PPN population and 2) native sagebrush steppe has a more diverse nematode community than former sagebrush steppe managed for livestock grazing. We examined these impacts through the following studies:

1. Quantitatively assessed nematode community structure under barley monoculture and barley-fallow vs. barley-pea rotations using multiple ecological measures and indices, and correlated those measures and indices with soil chemical and physical properties as well agronomic parameters of each system.
2. Quantitatively assessed nematode community structure under tilled wheat-fallow, no-till wheat-fallow, and no-till wheat monoculture vs. several no-till wheat-pea rotations using multiple ecological measures and indices, and correlated those measures and indices with soil chemical and physical properties as well agronomic parameters of each system.
3. Quantified nematode taxonomic diversity and ecological indices of disturbed and undisturbed sagebrush steppe in the Bangtail Mountains west of Wilsall, Montana.

Literature Review

When beneficial organisms are mentioned, the first animals that come to mind probably are not nematodes. The very mention of nematodes in agriculture likely conjures images of sickly plants and lost yield potential. Agricultural researchers have long focused on a subgroup of the larger nematode community, the herbivorous species or plant parasites. However, nematodes as a taxonomic phylum are incredibly diverse and play an important role in soil biology, nutrient cycling, and the soil food web function. Nematodes have been studied as a means of early detection of soil ecological changes, often referred to as bio-indicators (Briar et al., 2007; Ferris and Bongers, 2006; Nesbitt and Adl, 2014; Thoden et al., 2011). Studying nematode community structure in agricultural settings where management has changed will indicate whether those management practices are having a positive or negative impact on soil biology.

Nematode Ecology

Nematodes are the most abundant multicellular animal (Kiontke and Fitch, 2013) and can be found in nearly every environment on the planet (Borgonie et al., 2011; Freckman and Virginia, 1997). They are a diverse and highly speciated group in the soil environment. Occupying multiple trophic levels, this group of organisms can provide useful insights into the structure and function of the soil food web (Neher, 2001; Ritz and Trudgill, 1999). Broadly, nematodes can be grouped into five major trophic groups: bacterivores, fungivores, herbivores (including plant parasitic nematodes or PPNs), predators, and omnivores (Yeates et al., 1993). PPNs are considered primary consumers, affecting soil food web resources through direct herbivory. Although many agriculturalists focus on the negative impact of PPNs due to crop damage, nematodes have many important roles in soil ecology. Bacterivore and fungivore nematodes graze on decomposer microorganisms, thus contributing to soil nutrient pools, while predatory nematodes regulate the soil food web by preying on other nematodes and invertebrates in the soil (Ferris and Bongers, 2006; Ferris and Matute, 2003). Thus, a holistic approach must recognize the ecological value of a diverse and balanced nematode community. The community can be considered a ‘canary-in-the-mine’, so to speak, and indicate fundamental shifts in soil microbiology that could aid producers in making informed management decisions.

Nematode ecology is continually advancing as a field. Ecological indices continue to be developed, quantifying multiple facets of the nematode community. These indices often focus on the number and prevalence of various trophic groups and genera: a colonizer-persister (cp) scale based on life history, food sources, and nematode responses to soil disturbance (Bongers, 1990; Bongers et al., 1995), trophic groups (defined by feeding habits), and grouping into guilds of combined feeding habit and cp value (Bongers and Bongers, 1998; Ferris et al., 2001).

The Basal Index indicates the prevalence of stress tolerant, *r*-strategist (characterized by high fecundity and short life cycles) nematodes; the Enrichment Index measures the abundance of bacterivore and fungivore nematodes responding to relative abundance of nutrients and resources in the soil; the Structure Index quantifies the abundance of high cp value, *K*-strategist (characterized by low fecundity and relatively longer lifecycles) nematodes that are sensitive to disturbance; the Maturity Index gives a weighted average of the cp value for the free-living (non-herbivorous) nematode community; the Plant Parasitic Index gives a weighted average of the cp value of the plant parasitic nematode (PPN) community; and the ∑ Maturity Index is a weighted average of the cp value of the whole nematode community (Bongers, 1990; Bongers, 1999; Bongers and Bongers, 1998; Ferris et al., 2001; Freckman and Ettema, 1993; Yeates et al., 1993). The Maturity Index, ∑ Maturity Index, and Plant Parasitic Index are all indicators of the progression and diversity of the nematode community in terms of environmental stress and soil quality (Bongers, 1990; Bongers, 1999; Bongers et al., 1995). The metabolic footprint family of indices provides a quantified measure of ecosystem services provided by each functional nematode guild by way of quantifying carbon (C) respiration (Ferris, 2010).

Nematode Community Structure

Soil nematode community studies from native and perennial ecosystems are wide and varied, including even the impact of climate change on soil nematode communities in Antarctica (Freckman and Virginia, 1997; Velasco-Castrillon and Stevens, 2014). Studies on native and perennial ecosystems show that subtle disturbances can impact nematode communities. Variations in soil texture, moisture, and temperature are strong drivers of the nematode community. Where soil moisture is low and temperature high, nematode communities often exhibit reduced species richness and diversity (Freckman et al., 1979; Griffin, 1996; Griffin et al., 1996). In a study from Utah, Griffin (1996) and Griffin et al. (1996) determined the impact of soil texture on pathogenicity and reproduction of several PPN species, finding that sandy loam soils increased pathogenicity and reproduction rate of *Merlinius brevidens*, *Pratylenchus neglectus*, and *Tylenchorhynchus acutus*. Gray et al. (2011), utilizing phospholipid-derived fatty acids (PLFA), measured soil microbial biomass finding that low precipitation environments had higher microbial biomass and that under higher soil temperatures a shift favoring bacteria over fungi.

Nematode communities have been studied in semiarid cropping systems, but no such research exists for the Northern Great Plains. While cereal production and fallow still prevail, efforts continue that aim to diversify and intensify rotations, and reduce the fallow period. Research in other climates and regions has shown that conversion to no-till and diversifying crop rotations can have positive impacts on the nematode community by increasing total numbers and diversity of genera present (Bakonyi et al., 2007; Eisenhauer et al., 2011; Ito et al., 2015a; Ito et al., 2015b; Pan et al., 2012). A 2015 study noted that tillage has the largest impact on the nematode community, greater than either cover crop or fertility (Ito et al., 2015a). By simply limiting soil disturbance, farmers can foster a more diverse and resilient nematode community, thereby fostering more soil ecosystem services (e.g. higher rates of soil nutrient cycling) suggesting no-till as a viable option to increase soil ecosystem services of nematodes.

Research has documented a mutualistic relationship between a fungivorous nematode (*Paraphelenchus acontioides*) and the endophytic fungi *Fusarium* cf. *torulosum* in invasive downy brome (*Bromus tectorum* L.) communities (Baynes et al., 2012), suggesting that the nematode cultivates the fungus on the roots of the invasive downy brome to maintain a steady supply of food. The fungi also had no negative impact on the growth and development of the downy brome. The impact of the interaction of nematode, fungus, and grass on the landscape is not known. Reports of *P. acontioides* are almost entirely from Asia and Europe with only one report in North America in Illinois, suggesting the nematode may also be an invader. The commonality between these studies are the impacts of anthropogenic and natural disturbances on soil physical properties, the soil nematode community and the soil microbial community.

Plant Parasitic Nematodes in Crop Production

Plant parasitic nematodes are responsible for an estimated $80 billion in crop losses annually across the globe (Handoo, 1998). Losses associated with PPNs are likely underestimated because of misdiagnosis as abiotic stress or attributed to some other pest. Traditional management options have typically included crop resistance, rotation to non-host plant species, and nematicides (Galal et al., 2014; Kretschmer et al., 1997; Smiley and Yan, 2010; Smiley et al., 2014). Developing crop and soil management strategies to diversify biological communities could suppress PPNs and improve soil biological nutrient cycling in a safer, economical way. instead of applying highly toxic and expensive nematicides (Held et al., 2003; Stark Jr. et al., 2000), as well as the long wait for the release of new resistant varieties. While research on methods to control PPNs is extensive, the impact of these methods on the broader soil nematode community is less understood. Knowledge gaps in nematode ecology, specifically in dryland farming systems, still exist (Neher, 2010). To encourage soil biological diversity, an aboveground approach to diversity might be the answer.

Crop rotation is a long-recognized tool for integrated pest management (Francis and Clegg, 1990; Francis et al., 1986). Rotation inhibits the buildup of detrimental PPN populations by utilizing non-host plant species (Rahman et al., 2007). More recently, rotating crops has been shown to have significant benefits to soil quality (Yao et al., 2013). The incorporation of legumes in cereal-based rotations not only increases soil labile nitrogen, but also soil quality (O'Dea, 2011). Increasing markets for pulses (particularly dry peas (*Pisum sativum* L.), lentils (*Lens culinaris* M.), and chickpeas (*Cicer arietinum* L.)) have increased their adoption throughout the Northern Great Plains (NGP). The Montana Department of Agriculture reported nearly 500,000 hectares of pulses in 2016, more than double the hectares reported in 2013.

Pulses also are targeted as a potential pest management option in dryland cereal farming. Along with being outside the host range of many PPNs, the legumes break other disease and pest cycles as well as build soil quality through N fixation. However, even given their growing market, many producers in Montana still rely heavily or solely on cereals for much of their revenue and production. Research at Montana State University (Miller et al., 2015) highlighted the economic value of incorporating pulses into cereal production. An untested benefit of adding pulses to a cereal rotation might be a positive effect on the soil nematode community. Eisenhauer et al. (2011) showed that plant diversity in grasslands can induce positive changes in nematode communities by increased species diversity and richness, along with greater stimulation and stability of nutrient cycling, suggesting that diversifying crop rotations could have a similar effect in dryland farming systems.

While plant resistance and crop rotation continue to be of value for PPN control, reports are beginning to surface of PPNs, specifically *Pratylenchus* spp., infesting rotational crops like peas, lentils, and other pulses as well as brassica species (Fatemy et al., 2006; Riga et al., 2008). An Oregon study assessed multiplication rates of the opportunistic plant-feeding nematodes *Pratylenchus neglectus* and *P. thornei* on several crop species, providing a guide to crop rotations for control of *Pratylenchus* spp. (Smiley et al., 2014). Another study performed similar assays in Montana, finding possible control options among varieties of pea, barley, canola, and lentil (Zuck, 2010). Other research indicates reduced susceptibility among brassicas high in glucosinolates (Potter et al., 1999).

Effect of Cropping System on Nematode Community Structure

Crop management has a significant impact on nematode community structure. Cover crop, fertilizer source and rate, and tillage all impact nematode communities in various ways.

The effects of cover crops are species dependent, with rye (*Secale cereal* L.) and rapeseed (*Brassica napus* L.) having a higher abundance of plant-associated nematodes than that of a radish (*Raphanus raphanistrum* subsp. *sativus* L.) or a bare fallow (Gruver et al., 2010). Conversely, other studies indicate that cover crops, regardless of species, had a more enriched and structured nematode food web than fallow (Dupont et al., 2009; Leslie et al., 2017). Ito et al. (2015a) observed that under cover crop mixes of rye and hairy vetch (*Vicia villosa* Roth) total population, bacterivores, omnivores, facultative root feeders, and obligatory root feeders all increased compared to fallow.

Fertilizer source and rate also affect nematode community structure. Opportunistic nematodes increase under high fertilizer input (Akhtar, 1998; Cheng et al., 2008; Forge et al., 2005; Pan et al., 2010) as do PPNs in at least one case (Briar et al., 2007). Additionally, C-rich sources of fertilizer increased species richness, nematode population, Structure Index, and Enrichment Index in one study (Liu et al., 2016) and increased the abundance of the families Tylenchidae and Cephalobidae in another study (Treonis et al., 2018).

Tillage also has a stronger impact on nematode community than many other disturbances or management practices, such as pesticides, crop rotation, or fertilizer. Several studies have shown either reduced total populations or higher incidence of PPNs under various tillage treatments (Govaerts et al., 2007; Ito et al., 2015a; Ito et al., 2015b). However, Govaerts et al. (2007) observed that while tillage affected the nematode community under maize (*Zea mays* L.), it did not have an effect under wheat (*Triticum aestivum* L.). Berkelmans et al. (2003) observed that tillage following oats (*Avena sativa* L.) led to higher root knot nematode infestation in the subsequent year. Overall, studies often have concluded that reducing or eliminating tillage was beneficial to the nematode community.

Preliminary Work

A survey of eleven central Montana fields was conducted in October 2015 to assess the nematode genera present. The enrichment and structure indices were calculated and plotted to indicate relative soil food web condition based on Ferris et al. (2001; Figure 1.1). A faunal diagram was created for each soil sample using the enrichment and structure indices. Faunal diagrams consist of four quadrats that define the conditions of the soil food web, based on the system’s level of ecological disturbance. Figure 1.2 illustrates the faunal diagram for the samples collected in central Montana, illustrating soils that are largely either degraded or disturbed. Table 1.1 enumerates the free-living nematodes and PPNs identified within these Central Montana soils. Inherent in agricultural settings is a certain level of soil disturbance (whether using a moldboard plow or no-till disc opener drill), and concurrently in some of the more degraded fields are issues related to fertilizer management. Two fields (HW-1 and HW-2) in the survey exhibited exceptionally low pH and high available aluminum in the soil leading to stunted, low yielding cereal crops. This low pH and high aluminum negatively impacted the nematode community by decreasing species richness and diversity and simplifying the nematode community with a higher proportion of opportunistic microbivores.

Rationale and Significance

The aim of this research was to examine the impact of anthropogenic land management strategies on the soil nematode community. The objectives of the project were to encourage more sustainable production methods by showing impact of cropping sequence and system, and the effects of ecosystem disturbance on soil health. This approach will generate novel and valuable data that will lead to more sustainable and resilient agricultural systems within the NGP.

Table 1.1: List of genera found during field survey with associated Colonizer - Persister values (cp values) in Central Montana per 100 g dry soil weight. (Briar, S. 2015. Unpublished data)

Cp group	Genus	CARC		Denton		Geraldine		Hobson	Highwood			Winifred	
		F1	F2	F1	F2	F1	F2	F1	F1	F2	F3	F1	F2
Cp 1 Bacterivore	Rhabditis	137	0	9	1	22	11	17	7	12	5	12	4
Cp 1 Bacterivore	Panagrolaimus	26	2	0	2	0	5	45	0	6	11	0	1
Cp 1 Bacterivore	Monhystera	5	10	2	0	2	0	4	0	0	80	0	4
Cp 1 Bacterivore	Diplogaster	0	0	0	0	0	0	0	0	0	0	3	0
Cp 3 Bacterivore	Achromadora	3	0	0	0	0	0	2	0	0	0	3	0
Cp 2 Bacterivore	Acrobeloides	8	2	24	7	0	3	22	15	31	4	12	5
Cp 2 Bacterivore	Acrobeles	0	5	5	0	0	0	0	0	0	0	3	0
Cp 2 Bacterivore	Cephalobus	98	112	107	57	76	41	48	31	366	83	123	43
Cp 2 Bacterivore	Eucephalobus	21	0	5	0	18	0	15	20	0	7	6	1
Cp 2 Bacterivore	Chiloplacus	13	0	0	3	0	3	11	18	18	0	3	3
Cp 2 Bacterivore	Plectus	0	14	0	3	4	1	17	0	0	0	0	4
Cp 2 Fungivore	Aphelenchoides	13	31	44	21	31	15	48	34	428	48	3	13
Cp 2 Fungivore	Aphelenchus	62	10	29	26	9	12	11	6	12	0	3	5
Cp 2 Fungivore	Aprutides	0	0	0	0	0	0	0	0	0	0	0	0
Cp 2 Fungivore	Neopsilenchus	0	0	0	0	0	0	0	0	0	0	3	0
Cp 4 Fungivore	Tylencholaimus	0	0	0	0	28	2	0	0	0	0	0	0
Cp 4 Predator	Mononchus	0	0	2	0	0	0	0	0	0	0	0	0
Cp 4 Omnivore	Dorylaimus	10	0	5	4	9	4	19	0	6	2	23	3
Cp 4 Omnivore	Prodorylaimus	0	0	0	0	0	0	2	0	0	0	9	0
Cp 4 Omnivore	other dorylaimids	0	3	5	0	4	0	2	0	0	0	6	1
Cp 2 Herbivore	Tylenchus	28	36	38	30	44	14	24	17	6	0	47	19
Cp 3 Herbivore	Pratylenchus	8	17	51	6	15	29	15	17	6	35	38	12

Cp 3 Herbivore	Helicotylenchus	0	0	0	0	0	0	32	0	0	0	0	0
Cp 3 Herbivore	Tylenchorhynchus	104	55	34	19	7	3	9	0	0	0	0	4
Total	Total nematodes	536	297	360	177	269	143	343	164	892	275	297	120

† F = Field, CARC = Central Agricultural Research Center

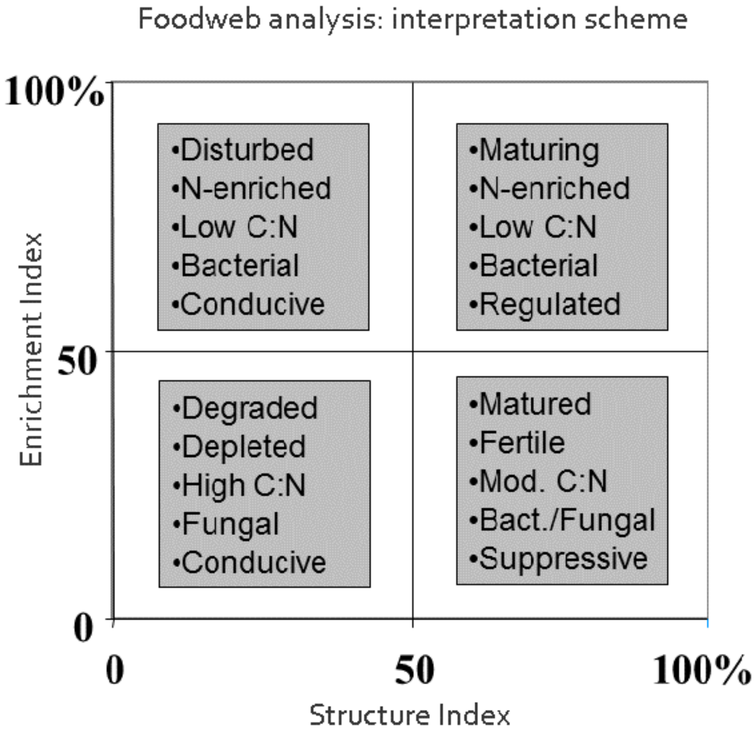

Figure 1.1: Determining soil conditions using enrichment and structure indices. (Ferris et al., 2001).

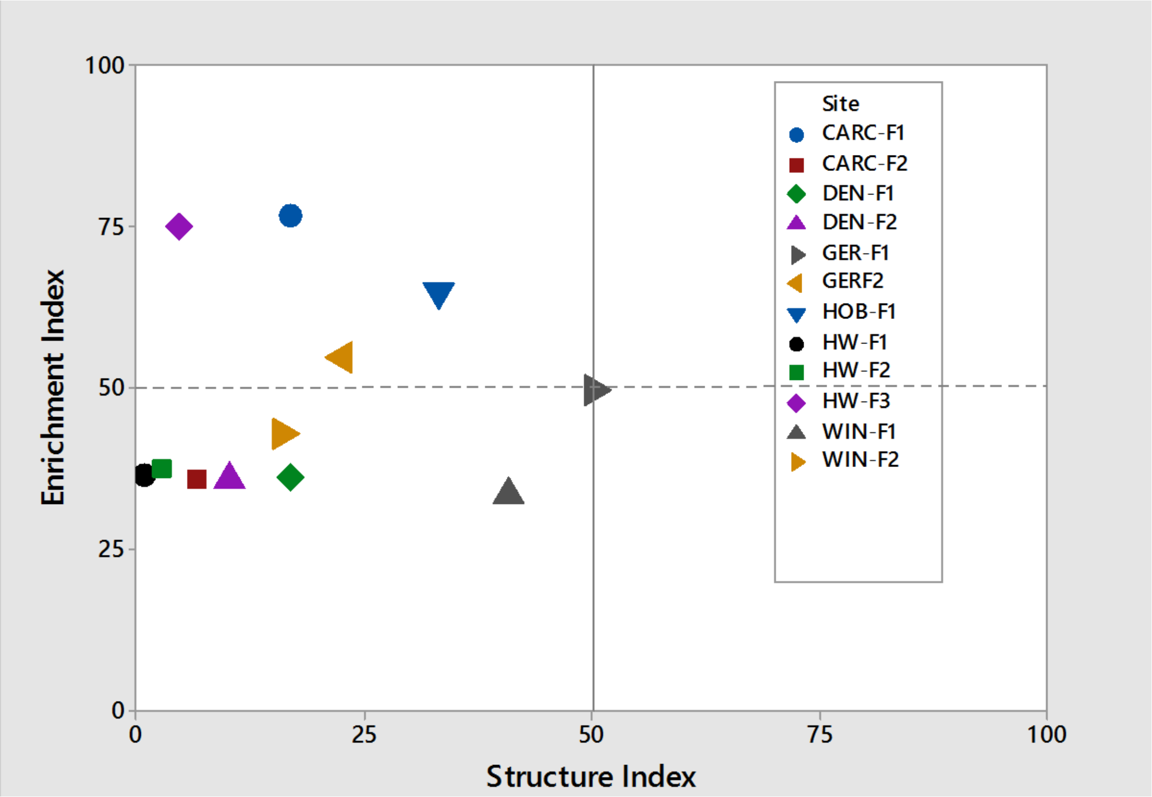

Figure 1.2: Probable condition of the soil food web: Enrichment index is based on the nematodes which respond to soil nutrient enrichment while the structure index is based on the prevalence of higher c-p value nematodes which are sensitive to disturbance. (Briar, S.S. 2015. Unpublished data).

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CHAPTER TWO

PERENNIAL CROP LEGACY EFFECTS ON NEMATODE COMMUNITY STRUCTURE IN SEMI-ARID WHEAT SYSTEMS

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Manuscript Information

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Abstract

The effects of diversifying wheat-based cropping systems in the Northern Great Plains (NGP) on soil chemical and physical properties is well documented: better soil tilth, improved water infiltration, and higher soil organic matter with crop rotations. However, the impact of crop rotations on soil biology is not as well understood. Nematode communities reflect soil quality and are directly observable, readily quantifiable, and occupy most of the consumer trophic levels in the soil food web. Within more humid climates, the community structure is better characterized to make associations with soil health and crop management strategies, but little is known about their community structure in semiarid regions such as the NGP. For this study, soils under contrasting cropping systems were sampled in the 15th year of a long-term study to quantify and assess the nematode community. Prior to planting, wheat-chemical fallow had a higher total nematode population than that of wheat-tilled fallow ($P<0.05$). A wheat-pulse system with a history of crop perennation had a greater abundance of uncommon, omnivorous nematodes than a wheat-pulse system without a prior history of crop perennation. However, plant parasitic nematodes also were higher in abundance under the converted perennial system. Our results suggest that reducing soil disturbance and including a perennial component to cropping systems will foster a more diverse and balanced nematode community under semiarid dryland conditions, but potentially at the expense of increased plant parasitic nematode pressure.

Introduction

Research over several decades has focused on intensifying and diversifying rotations and reducing fallow acres in the Northern Great Plains (NGP), a region comprised of all or part of Montana, Nebraska, Wyoming, North Dakota, and South Dakota in the U.S., along with the Prairie Provinces of Canada (Padbury et al., 2002). The NGP is characterized by a harsh climate with strong fluctuations in weather (Peterson, 1996). Within Montana, crop production is dominated by cereals and, increasingly, pulse crops (National Agricultural Statistics Service, 2018).

The Conservation Reserve Program (CRP), a cost-share and rental program where farmers are paid by the USDA Farm Service Agency to set aside cropland in perennial cover to reduce soil erosion, comprised 14 million hectares at its peak across the USA. In Montana, peak CRP area totaled roughly 1.4 million hectares in 2006 (Barbarika, 2007). By 2017, fewer than 530,000 ha of CRP remained in the state (Barbarika, 2017). This decline in CRP enrollment in Montana can be attributed to two events: high commodity crop prices in the late 2000s (McBride, 2017), and steadily decreasing land rental payments from CRP contracts, causing many producers to rethink the economic viability of their CRP acres. However, the inclusion of a perennial phase to cropping systems can increase soil carbon (C) in integrated crop-livestock systems (Acosta-Martínez et al., 2010), soil biopore density in fodder crops (Han et al., 2015), and soil N while improving weed control during transition to organic wheat production (Borrelli et al., 2015).

Adoption of no-till and reduction of fallow became prevalent across much of the NGP prior to the reduction of CRP (Tanaka et al., 2010). The benefits of no-till and elimination of fallow are well documented in this region (Cutforth and McConkey, 1997; Cutforth et al., 2002; Engel et al., 2017; Nielsen et al., 2005), and multiple studies show the positive impact of no-till and annual cropping to soil fungal and microbial communities (Ellouze et al., 2013; Helgason et al., 2010; Sharma-Poudyal et al., 2017; Stromberger et al., 2007; Stromberger et al., 2011). Therefore, adoption of these practices could potentially benefit farmers in yield-limited dryland environments with positive impacts to soil physical, chemical, and biological properties.

Describing soil food webs, such as those of nematodes, has become a way to assess soil function and potential for ecosystem services (Chertov et al., 2017; Morriën, 2016; Olena et al. 2017; Rousk, 2016; Zhang et al., 2017). Nematode communities are sensitive to disturbances within their environment and are used as indicators of soil quality (Briar et al., 2007a,b; Briar et al., 2011; Briar et al., 2012; Neher and Olson, 1999; Yeates and Bongers, 1999). Nematode taxa differ in their life-history strategies. *r*-strategists typically have high fecundity, small body size, short life cycles, and are tolerant to disturbances; while K-strategists typically have low fecundity, long life cycles, larger body size, and are intolerant of disturbance (MacArthur and Wilson, 1967). The colonizer-persister (cp) value of a nematode life history strategies: low rank nematodes (cp 1 and 2) behave more as *r*-strategists; while those with a high cp value (3-5) follow more of a K trajectory (Bongers, 1990). High cp value nematodes indicate that the soil food web is in a mature and stable state, while a soil dominated by low cp value nematodes indicate a disturbed and degraded food web.

Soil nematode communities are also classified based on the prevalence of stress tolerant, *r*-strategist nematodes, using the Basal Index; on the abundance of bacterivore and fungivore nematodes responding nutrients and resources in the soil, applying the Enrichment Index; on the abundance of high cp value, *K*-strategist nematodes that are sensitive to disturbance, with the Structure Index; and on the weighted average of the cp value of the whole nematode community, using the ∑ Maturity Index (Bongers, 1990, 1999; Bongers and Bongers, 1998; Ferris et al., 2001; Freckman and Ettema, 1993; Yeates et al., 1993). Subsets of the nematode community are also described, for example, the Maturity Index gives a weighted average of the cp value for the free-living (non-herbivorous) nematode community, and the Plant Parasitic Index gives a weighted average of the cp value of the plant parasitic nematode (PPN) community. The Maturity Index, ∑ Maturity Index, and Plant Parasitic Index are all indicators of the progression and diversity of the nematode community in terms of environmental stress and soil quality (Bongers, 1990, 1999; Bongers et al., 1995). The metabolic footprint family of indices provides a quantified measure of ecosystem services provided by each functional nematode guild by way of quantifying C respiration (Ferris, 2010).

Multiple studies have focused on how these quantitative measures of the nematode community change in the face of crop management. Carbon-rich organic fertilizers buffered soil resiliency by increasing species richness and total abundance (Liu et al., 2016). Conversely, application of N-rich fertilizers (both organic and inorganic sources) decreased species richness, species diversity, Maturity Index, and Structure Index, but increased the abundance of PPNs and enrichment opportunist microbivores. Just a single year of tillage decreased diversity of nematode communities (Berkelmans et al., 2003). Our objective was to determine long-term effects of tillage and cropping system on the nematode community structure in wheat-based cropping systems under dryland management in Montana.

Materials and Methods

Study site and experimental design

The trial area is located at the Montana State University Arthur H. Post Research Farm 7 km west of Bozeman, MT. The soils of the Post Farm (1474m asl) are Amsterdam-Quagle silt loam soils (fine-silty, mixed, superactive, frigid Typic Haplustolls) (Soil Survey Staff, 2017). The field was transitioned to no-till in 2000 and the rotation study was established in 2002. On 1 May 2017, the soil water profile was at field capacity to a depth greater than 1.2 m (data not shown) and further Fig. 2.1 shows precipitation and average daily temperature for the Arthur H. Post Farm for 2017.

Eight cropping systems were compared to determine the impact of dryland cropping systems on soil nematodes. The systems included wheat-tilled fallow, wheat-chemical fallow, continuous wheat, wheat-pulse grain, wheat-pulse forage (pulses harvested for forage), wheat-pulse manure (pulses terminated with herbicide at first bloom), organic wheat-pulse, and wheat-pulse grain (previously alfalfa-grass mix to mimic Conservation Reserve Program (CRP) from 2003-2012). The cropping systems were established in 7.6 m by 22.9 m plots in a randomized complete block design with cropping system treatments replicated four times. All systems except wheat-tilled fallow and organic wheat-pulse were managed under no-till practices. Table 2.1 includes a description of the crop sequence and cumulative applied nitrogen (N) fertility for each cropping system from 2003-2017.

Nitrogen fertility was managed so 50 kg N ha^{-1} Mg $grain^{-1}$ was available at wheat planting in all cropping systems. Fertilizer rates were calculated based on a target yield (6.0 Mg ha^{-1} for winter wheat, 4.0 Mg ha^{-1} for spring wheat), available soil nitrate-N, N mineralization from the previous year’s leguminous residues where present (20 kg ha^{-1} prior to 2013 and 30 kg ha^{-1} since 2013 if harvested for grain; 30 kg ha^{-1} prior to 2013, 60 kg ha^{-1} from 2013 to 2015, and 45 kg ha^{-1} since 2016 if used for hay or manure), and N mineralization from soil organic matter over winter (25 kg ha^{-1}) based on previous soil lab test results. Urea fertilizer was applied by subsurface banding at sowing.

Soil sampling

Two soil cores per plot per sampling date were extracted 21 April 2017, prior to sowing spring crops or implementing fallow practices, and 6 July 2017, while crops were actively growing in the field. Sampling immediately prior to planting provided a snapshot of the nematode community present for plant colonization, while sampling during the growing season indicated succession within the community after plant colonization. One core was used to determine gravimetric and volumetric soil moisture to standardize nematode counts on a dry soil weight basis and the second core was used for nematode extraction and faunal analysis. Each sample was put in a polypropylene-lined tin-tie soil bag (i.e., ‘coffee’ bag) and placed inside a cooler immediately after sampling for transport. Samples were refrigerated at 4°C until processing, typically within two weeks of extraction.

Soil nematode analysis

Soil extractions of no less than 25 g of fresh soil were performed using the Baermann funnel technique (Flegg and Hooper, 1970). Extractions ran for 72 hr, after which water suspension samples of at least 15 mL were collected. Nematodes were counted and identified on a nematode counting slide (Chalex Corp.) using a Motic® AE2000 inverted microscope with phase contrast. Nematode density was adjusted to total individuals per 100g on a dry soil basis. Nematodes were assigned to a trophic group, a cp value, and a functional guild (Bongers, 1990; Bongers et al., 1995; Freckman and Ettema, 1985; Freckman and Ettema, 1993). Community structure was assessed using trophic group and cp value information and the following ecological indices: Maturity Index, Σ Maturity Index, Plant Parasitic Index, Basal Index, Structure Index, and Enrichment Index (Bongers, 1990; Bongers and Bongers, 1998; Ferris et al., 2001; Freckman and Ettema, 1993; Yeates et al., 1993). Composite, enrichment, structure, herbivore, fungivore, bacterivore, omnivore, and carnivore metabolic footprints were calculated for components of the nematode community as described by Ferris (2010). Calculations of C respiration footprints were facilitated using the Nematode INdicator Joint Analysis (NINJA) 2.0 (http://ninjanemaplex.ucdavis.edu/main/) R Shiny application developed by Sieriebriennikov et al. (2014).

Statistical analysis

Data were subject to analysis of variance (ANOVA) for a randomized complete block design using the lmer function in the lme4 mixed-effects model package in R version 3.3.2 (Bates et al., 2015; R Core Team, 2013), where cropping system was a fixed effect and block was a random effect. Linear contrasts among cropping systems means were conducted using the emmeans package (Lenth, 2017) between the CRP conversion and the wheat-pulse grain rotations to better assess the perennial effect from CRP, between the tilled fallow (wheat-tilled fallow) and no-till fallow (wheat-chemical fallow) systems to assess the impact of tillage, and between the wheat-chemical fallow and continuous wheat to assess the impact of fallow versus annual cropping. Where the assumptions of normality and homoscedasticity were not met, data were transformed using ln(x+1) prior to analysis. Back-transformed data means are reported. Differences among treatment means were assessed using a protected LSD post-hoc at $\alpha<0.05$.

Non-metric multidimensional scaling (NMDS) was used to assess the data and provide a framework for analysis of the significance and effect sizes of candidate explanatory variables using the labdsv package in R (Roberts, 2016). Briefly, a Bray-Curtis dissimilarity matrix was calculated from ln(x+1) transformed taxon abundance data. To generate the NMDS results, the minimum stress result was calculated from 100 random starts for both two- and three-dimensional solutions. The lowest dimensionality results with a stress of less than 20 were selected for further analysis.

Explanatory variables of interest were fitted to the ordination with a generalized additive model (GAM) using the ordination coordinates as explanatory variables, and appropriate error structures for individual variables (Gaussian for environmental variables, negative binomial for species abundances). Goodness-of-fit was assessed with deviance explained (D^2=1-(residual deviance/null deviance)) and considered significant for D^2 values ≥ 0.70.

Results

Forty genera of nematodes were identified across the cropping systems in 2017 (Supplementary Tables 2.1 and 2.2). Nematode taxa counts were standardized by relative abundance of individuals per 100 g dry soil.

Evaluation of Nematode Community Dimensionality

During exploratory analysis with NMDS, three dimensions were found to reduce stress below 20 (stress = 18.6). Distances among points in the ordination were highly correlated (r=0.89) with the original data. Within the first two dimensions, total population and fungivore footprint explained significant proportions of the dissimilarity, with D^2 = 0.71 and 0.70, respectively (Fig. 2.2, left panel). From this we can assert that where total population is greater there is a high likelihood of a higher fungivore footprint. Within the first and third dimensions, species richness and bacterivore footprint had significant D^2, both at 0.75 (Fig. 2.2, right panel). Within these two dimensions, we can assert that where species richness is greater so is the bacterivore footprint. The second versus third dimensions had no D^2 greater than 0.70. NMDS failed to show any significant separation or clustering of cropping system, but it did show clustering of sampling date when viewed from this perspective (Fig. 2.3). This clustering of sampling dates likely represents the difference in soil environment from pre-plant to in-season sampling. Gravimetric soil moisture declined by an average of 5% across all cropping systems and soil temperature increased roughly 10° C at 5cm under bare ground between sampling dates (Fig. 2.1). NMDS confirmed associations among nematode communities.

Cropping systems effects

Prior to planting, Basal Index, a measure of the abundance of stress tolerant nematodes, was higher under wheat-chemical fallow and wheat-pulse hay (72 and 69, respectively) than under continuous wheat, wheat-pulse manure, organic wheat-pulse grain, and CRP conversion (47, 48, 46, and 47, respectively, Table 2.2), indicating increased stress to the nematode community under wheat-chemical fallow and wheat-pulse hay. Conversely, Enrichment Index was higher under continuous wheat, wheat-pulse manure, organic wheat-pulse grain, and CRP conversion (38, 42, 43, and 37, respectively) than the wheat-chemical fallow treatment (19, Table 2.2), indicating low resource availability for nematodes under wheat-chemical fallow. Both ∑ Maturity Index, the whole nematode community maturity, and Plant Parasitic Index, were higher under CRP conversion (2.6 and 3.0, respectively, Table 2.2) than no-till and organic wheat-pulse grain (2.3 and 2.6 under no-till and 2.2 and 2.5 under organic) and wheat-pulse manure (2.3 and 2.6). These higher indices indicate both an increase in higher cp, stress susceptible nematodes, and a higher abundance of high cp value herbivores, particularly *Helicotylenchus*, *Pratylenchus,* and *Tylenchorhynchus*.

Tillage effects

Tillage negatively impacted total abundance of nematode. Total nematodes, total free-living nematodes, and total cp 2-5 nematodes were all higher under chemical fallow compared to tilled fallow prior to planting (Tables 2.3 and 2.4), meaning reduced populations in the spring were directly linked to tillage. During the growing season, a higher proportion of fungivores and the fungivore footprint occurred under tilled fallow

(Tables 2.2 and 2.4), indicating higher fungal hyphae density or higher abundance of fungi susceptible to nematode predation under tillage. Cp 3 herbivores were higher under chemical fallow (Table 2.3).

Fallow effects

Fallow had little effect on the nematode community structure but did impact population totals. Total free-living and total cp 2-5 nematodes were higher prior to planting under wheat-chemical fallow than continuous wheat (Tables 2.3 and 2.4). During the growing season, no significant effects were observed.

Effects of perennation

Perennation had both positive and negative effects on community structure. When the wheat-pulse grain rotation was compared to the CRP conversion, we observed higher ∑ Maturity Index, Plant Parasitic Index, and cp 3 herbivores under CRP conversion prior to planting, indicating more stress susceptible genera and more PPNs of economic importance were present under CRP conversion. Cp 2 herbivores were higher under wheat-pulse grain prior to planting. During the growing season, cp 4 nematodes and proportion of omnivores were higher under CRP conversion (Tables 2.3 and 2.4). The ∑ Maturity Index accounts for the cp value of the whole community, while the Plant Parasitic Index only accounts for the cp value of the herbivorous portion. The increase in these two indices was largely due to higher abundance of cp 3 and 5 PPNs and cp 4 omnivores under CRP conversion.

Discussion

Tillage, cropping system, sampling date, and previous perennation are the key factors influencing nematode communities in this study. Tillage deleteriously affects the nematode community structure by creating physical disturbance that reduces the abundance of stress susceptible nematodes. We observed our largest total population variations in the spring and by summer, those variations were gone, and the differences observed were within the structure of the population. The population declines were likely associated with a decrease in soil moisture and increases in soil temperature, as noted by both Bakonyi et al. (2007) and Thompson et al. (2018). Fewer free-living nematodes and cp 2-5 nematodes were observed under a continuous wheat system versus wheat-chemical fallow. This is counter to a study by Govaerts et al. (2007) in corn-wheat systems in Mexico, where nematode populations were higher under continuous wheat.

The nematode communities were different under tillage versus no-till. The tillage effects we measured—a decreased population prior to tillage, coupled with an increase in fungivores after tillage—corroborate those of Ito et al. (2015a, b), where total nematode population under rice-soybean systems in Japan were detrimentally affected by tillage even though total fungivores increased. However, our results contradict those from Griffiths et al. (2012) in the United Kingdom for a continuous barley system and those from Sharma-Poudyal et al. (2017) for dryland wheat cropping systems in the Pacific Northwest, where abundance of fungivores increased under zero and minimum tillage systems compared to moldboard or chisel plow. Griffiths et al. (2012) correlated their findings in the nematode community with their detection of an increased proportion of fungi in the microbial community under no-till and minimum till practices.

In our study, tillage negatively affected cp 3 herbivores as a percentage of total herbivores during the growing season, but total herbivore abundance remained three-fold higher under tilled fallow. Thus, tillage served to simplify the nematode community but did not reduce the total population. In fact, our research suggests that tillage encouraged a large flush of opportunistic nematodes, as evidenced by the higher Basal Index during the spring and the higher proportion of opportunistic fungivores during the summer under tilled fallow.

The effects of annual cropping were less pronounced. Continuous wheat, wheat-pulse manure, organic wheat-pulse, and CRP conversion had a higher pre-plant Enrichment Index and lower Basal Index than wheat-chemical fallow, but not wheat-tilled fallow. The low Basal Index under CRP conversion, organic wheat-pulse, wheat-pulse manure, and continuous wheat is likely due to more crop residue being returned to the soil, in contrast to both wheat-chemical fallow and wheat-pulse forage. The high Enrichment Index may be for similar reasons. Few studies have associated the effects of fallow on nematode populations, and those that have made associations have focused largely on the PPN population (Stirling et al., 2001; Thompson et al., 2012). Our study is the first to make associations about nematode community structure under fallow versus annually cropped systems.

A legacy of perennation within one cropping system was associated with a more stable and mature nematode community in the current study. CRP has been shown to have beneficial impacts to soil microbial communities in the Southern Great Plains (Li et al., 2018), providing crucial pollinator and wildlife habitat (Grovenburg et al., 2011; Otto et al., 2018), and playing an important role in soil C storage (Engel et al. 2017; O'Connell et al., 2016). In our study, the CRP conversion system had higher pre-plant Σ Maturity Index, Plant Parasitic Index, and percentage cp 3 herbivores, as well as greater proportions of omnivores and cp 4 nematodes in the growing season, indicating a nematode community comprised of infrequent, predominantly omnivorous, and higher cp value nematodes. Higher abundance of these cp 3-5 nematodes under CRP conversion suggests a more balanced soil food web than the other cropping systems. The proportion of cp 4 nematodes under CRP conversion was nearly triple that of the wheat-pulse grain rotation, and the proportion of omnivores was similarly high. Under CRP conversion, the higher Σ Maturity Index was driven by the higher proportion of omnivores and the Plant Parasitic Index was driven by the higher percentage of cp 3 herbivores. Unpublished data from the study comparing the wheat-pulse grain system to the CRP system under conversion indicate that following conversion, soil moisture, yield, and net returns were less, while soil N supply was higher (P. Miller, personal communication). Reduced wheat yield in the system has been attributed to the high soil N due to 'haying off', however the higher cp 3 herbivores under CRP conversion were dominated by genera important to crop production including *Pratylenchus*, *Helicotylenchus*, and *Tylenchorhynchus*.

Both high soil N and high abundance of herbivores in the system may have contributed to a negative impact to crop production. The differences in Σ Maturity Index and Plant Parasitic Index were not observed during the growing season, and we hypothesize that decreasing water availability in the soil begins to have a dominant effect on the nematode community as the growing season progresses. The higher abundance of omnivores during the growing season may also be influencing herbivore abundance through predation.

Berkelmans et al. (2003) suggested the use of Basal Index and Structure Index as soil health indicators, where high Basal Index would indicate poor soil ecosystem health and high Structure Index would indicate a healthy, steady soil ecosystem. While no differences in Structure Index were observed among cropping systems, CRP conversion had the lowest Basal Index, suggesting that more stress susceptible nematode taxa were present in the community as supported by the Σ Maturity Index and proportion of omnivores in the nematode community. This low Basal Index indicate there could be an advantage for the inclusion of a perennial phase to overall soil health.

Our results suggest a benefit from decreasing soil disturbance and including a perennial crop phase in semi-arid wheat production systems on fostering a more balanced and interconnected soil nematode community. Similarly, soil organic C and soil total N also were favored by reductions in tillage and perennation in the same field experiment (Engel et al., 2017), with both being elevated in the top 10 cm under CRP compared to all cropping systems. We speculate that where soil organic C has been significantly increased, there is a benefit to soil nematodes.

Cumulative fertilizer application and associated changes in soil pH likely impacted nematodes in our study. Cumulative N fertilizer application was markedly reduced in the CRP conversion compared to all conventionally managed systems (e.g., 214 kg ha^{-1} for the

CRP conversion compared to 2300 kg ha^{-1} for continuous wheat). Unpublished data from this study indicated greater soil pH for the CRP conversion system compared with the continuous wheat system. However, without additional soil pH and N data, our associations to soil chemistry are only speculative. Any future work will require detailed soil chemical analysis in tandem with a soil nematode community analysis to understand how soil chemistry impacts the nematode community.

Conclusions

Our study highlights the interaction between cropping system and the soil nematode community. A legacy effect from perennation to multiple components of the nematode community was observed four years after conversion from a perennial to annual cropping system. Further work is necessary to add to our knowledge of the nematode community in such a perennial system and how converting it to annual cropping systems affects the nematode community. The effect of tillage was observed in decreased total population prior to planting in the spring.

Fostering a more diverse nematode community is a means to achieving sustainable production, but the possibility of further incorporating management practices into PPN management by better understanding how PPNs are affected by crop rotation and management warrants further research. This is the first published work comparing CRP versus annual cropping systems to nematode community structure. Our sampling of the study was done four years after the conversion from CRP, and effects from perennation were still evident. What these effects were in the first year and how long the effects will linger is not known.

Acknowledgements

The authors would like to acknowledge the Montana Wheat and Barley Committee for their financial support of the project.

Table 1. Cropping sequences and cumulative applied nitrogen fertilizer for all systems.

Cropping system			Wh-Tilled Fallow	Wh-Chemical Fallow	Continuous Wh	Wh-Pulse Gr	Wh-Pulse For	Wh-Pulse Man	Org. Wh-Pulse	CRP conversion
Tillage			tilled	-----------------------------------no-till-------------------------------------						
2-year sequence	2003-2008		fallow-w wh	fallow-w wh	spr wh-w wh	w pea (gr)-w wh	w pea (for)-w wh	w pea (for)-spr wh	w pea (gr)-w wh	---alfalfa-grass mixture----
4-year sequence	2009		fallow	fallow	spr wh	spr pea (gr)	spr pea (for)	spr pea (man)†	spr pea (gr)	
	2010		spr wh	spr wh	spr wh	spr wh	spr wh	spr wh	spr wh	
	2011		fallow	fallow	w wheat	spr pea (gr)	spr pea (for)	spr pea (man)	spr pea (gr)	
	2012		w wh	w wh	w wh	w wh	w wh	w wh	w wh	
	2013		fallow	fallow	spr wh	spr pea (gr)	spr pea (for)	spr pea (man)	spr pea (man)	spr pea (gr)
	2014		spr wh	spr wh	spr wh	spr wh	spr wh	spr wh	spr wh	spr wh
	2015		fallow	fallow	w wh	w pea (gr)	w pea (for)	w pea (man)	w pea (man)	w pea (gr)
	2016		w wh	w wh	w wh	w wh	w wh	w wh	w wh	w wh
	2017		fallow	fallow	spr wh	spr lentil (gr)	3 sp CCM (forage)‡	3 sp CCM (manure)	spr lentil (gr)	spr lentil (gr)
Cumulative applied N fertilizer		kg ha^{-1}	1146	1185	2300	1075	983	811	0	214

†Where a pulse manure was grown, termination was achieved through herbicide application at first bloom, except in the case

of the organic system, where termination was achieved at first bloom with tillage.

‡Cover crop mix comprised the following: fababean, proso millet, and tillage radish.

§w = Winter, spr = Spring, wh = wheat, for = forage, gr = grain, man = manure, sp = species, CCM = cover crop mix.

Table 2.2. Ecological indices and metabolic footprints of the nematode community from different crop rotations at two sampling dates (standard error).

Treatment	Sampling Date		Ecological Indices								Metabolic Footprints	
			Basal Index		Enrichment Index		∑ Maturity Index		Plant Parasitic Index		Herbivore	Fungivore
											--------µg C kg^{-1}--------	
Cropping system												
Wheat-Tilled Fallow	21-Apr-17		62(5)	ab	28(3)	abc	2.3(0.0)	bc	2.8(0.0)	abcd	41(9)	29(7)
Wheat-Chemical Fallow	21-Apr-17		72(6)	a	19(4)	c	2.3(0.1)	bc	2.7(0.1)	abcd	94(15)	36(5)
Continuous Wheat	21-Apr-17		47(4)	b	38(3)	ab	2.5(0.0)	ab	2.9(0.1)	abc	69(22)	30(4)
Wheat-Pulse Grain	21-Apr-17		63(5)	ab	23(3)	bc	2.3(0.1)	bc	2.6(0.1)	bcd	65(15)	21(7)
Wheat-Pulse Forage	21-Apr-17		69(3)	a	22(2)	bc	2.4(0.1)	abc	2.9(0.1)	ab	61(17)	30(9)
Wheat-Pulse Manure	21-Apr-17		48(4)	b	42(4)	a	2.3(0.1)	bc	2.6(0.1)	cd	76(20)	28(7)
Org. Wheat-Pulse	21-Apr-17		46(9)	b	43(12)	a	2.2(0.1)	c	2.5(0.2)	d	120(56)	41(11)
CRP conversion	21-Apr-17		47(4)	b	37(3)	ab	2.6(0.1)	a	3.0(0.0)	a	112(18)	31(5)
Wheat-Tilled Fallow	06-Jul-17		42(5)		38(3)		2.3(0.1)		2.5(0.1)		208(73)	56(67) ‡
Wheat-Chemical Fallow	06-Jul-17		42(8)		37(7)		2.6(0.1)		2.8(0.1)		51(10)	10(3)
Continuous Wheat	06-Jul-17		39(5)		34(2)		2.4(0.1)		2.4(0.1)		34(54)	21(6)
Wheat-Pulse Grain	06-Jul-17		47(4)		31(4)		2.3(0.0)		2.6(0.1)		31(11)	12(4)
Wheat-Pulse Forage	06-Jul-17		44(7)		48(7)		2.2(0.1)		2.6(0.1)		134(30)	44(9)
Wheat-Pulse Manure	06-Jul-17		45(4)		49(6)		2.2(0.1)		2.7(0.1)		56(15)	28(11)
Org. Wheat-Pulse	06-Jul-17		43(4)		35(4)		2.3(0.0)		2.3(0.0)		66(11)	37(4)
CRP conversion	06-Jul-17		37(5)		31(5)		2.5(0.1)		2.5(0.1)		80(28)	18(5)
ANOVA		*df*	*p* values									
Cropping system	21-Apr-17	7	0.03	*	0.04	*	0.04	*	0.03	*	0.62	0.91

	06-Jul-17	7	0.97	0.22	0.28	0.11	0.41	0.21
1 df contrast								
Tilled vs chemical fallow	21-Apr-17	1	0.32	0.26	0.90	0.84	0.24	0.61
	06-Jul-17	1	0.99	0.92	0.14	0.06	0.07	0.02 *
Fallow vs annual	21-Apr-17	1	0.09	0.14	0.36	0.99	0.99	0.52
	06-Jul-17	1	0.84	0.48	0.13	0.42	0.20	0.94
CRP vs. Wheat-Pulse grain	21-Apr-17	1	0.09	0.11	0.01 *	0.02 *	0.29	0.48
	06-Jul-17	1	0.35	0.98	0.19	0.78	0.56	0.56

* Significant at *p*<0.05

†Based on three replicates.

‡Back-transformed from ln(x+1)

§Numbers followed by the same letter are not significantly different at *P*<0.05 based on one-way ANOVA followed by an LSD test.

Table 2.3. Cp value compositions for cropping systems at two sampling dates (standard error).

Treatment	Sampling Date		Total cp 2-5		Free-living cp 4	Herbivores				
						cp 2		cp 3		cp 5
					------------------------------%-------------------------------					
Cropping system										
Wheat-Tilled Fallow	21-Apr-17		1275 (330)		3 (2)	22 (4.3)	ab	76 (4.6)	abcd	0 (0)
Wheat-Chemical Fallow	21-Apr-17		3196 (632)		5 (1)	18 (6.2)	abc	74 (6.2)	abcd	0 (0)
Continuous Wheat	21-Apr-17		882 (86)		11 (3)	12 (8.2)	bc	86 (8.2)	abc	0 (0)
Wheat-Pulse Grain	21-Apr-17		1461 (619)		7 (2)	29 (7)	ab	64 (6.9)	bcd	0 (0)
Wheat-Pulse Forage	21-Apr-17		1430 (360)		4 (1)	6 (8.2)	cd	91 (8.2)	ab	0 (0)
Wheat-Pulse Manure	21-Apr-17		1021 (242)		5 (1)	32 (9.6)	ab	59 (9.5)	cd	0 (1)
Org. Wheat-Pulse	21-Apr-17		1164 (253)		7 (2)	45 (17.6)	a	46 (17.6)	d	0 (0)
CRP conversion	21-Apr-17		1055 (187)		8 (2)	2 (0.6)	d	96 (1.1)	a	1 (1)
Wheat-Tilled Fallow	06-Jul-17		1816 (861)	‡	7 (2)	54 (7.9)		43 (8.2)		3 (1)
Wheat-Chemical Fallow	06-Jul-17		509 (205)		12 (3)	19 (9.2)		80 (9.4)		1 (1)
Continuous Wheat	06-Jul-17		758 (213)		13 (3)	59 (12.5)		41 (12.5)		0 (0)
Wheat-Pulse Grain	06-Jul-17		635 (166)		7 (3)	43 (10.6)		57 (10.6)		0 (0)
Wheat-Pulse Forage	06-Jul-17		1383 (678)		4 (1)	40 (8.7)		59 (8.4)		1 (1)
Wheat-Pulse Manure	06-Jul-17		825 (327)		2 (2)	29 (9.5)		71 (9.6)		0 (1)
Org. Wheat-Pulse	06-Jul-17		1033 (157)		14 (3)	71 (3.3)		29 (3.3)		0 (0)
CRP conversion	06-Jul-17		1053 (230)		23 (7)	49 (7.1)		51 (7.1)		0 (0)
ANOVA		*df*	*p* values							
Cropping system	21-Apr-17	7	0.06		0.43	<0.01	**	0.04	*	0.45
	06-Jul-17	7	0.62		0.22	0.14		0.17		0.65
1 df contrast										

Tilled vs chemical fallow	21-Apr-17	1	0.01	*	0.67		0.77		0.84		*N/A*
	06-Jul-17	1	0.07		0.50		0.05		0.05	*	0.33
Fallow vs annual	21-Apr-17	1	0.02	*	0.21		0.58		1.00		0.88
	06-Jul-17	1	0.79		0.56		0.63		0.75		0.10
CRP vs. Wheat-Pulse grain	21-Apr-17	1	0.56		0.87		<0.001	***	0.04	*	0.06
	06-Jul-17	1	0.46		0.05	*	0.76		0.75		0.83

* Significant at $p<0.05$

** Significant at $p<0.01$

*** Significant at $p<0.001$

†Based on three replicates.

‡Back-transformed from ln(x+1)

§Numbers followed by the same letter are not significantly different at $P<0.05$ based on one-way ANOVA followed by an LSD test.

Table 2.4. Population totals and guild compositions for different crop rotations at two sampling dates (standard error).

Treatment	Sampling Date	Total	Total free-living	Total community	
				Fungivores	Omnivores
				-------------%---------------	
Cropping system					
Wheat-Tilled Fallow	21-Apr-17	1712 (393)	1314 (346)	19 (4)	2 (1.0)
Wheat-Chemical Fallow	21-Apr-17	4201 (606)	3215 (634)	11 (2)	2 (0.5)
Continuous Wheat	21-Apr-17	1665 (216)	904 (92)	25 (4)	8 (2.6)
Wheat-Pulse Grain	21-Apr-17	2058 (684)	1496 (621)	13 (3)	4 (0.8)
Wheat-Pulse Forage	21-Apr-17	2185 (528)	1442 (364)	14 (4)	2 (0.5)
Wheat-Pulse Manure	21-Apr-17	1854 (363)	1112 (265)	24 (4)	3 (0.8)
Org. Wheat-Pulse	21-Apr-17	2139 (421)	1248 (194)	23 (4)	4 (0.4)
CRP conversion	21-Apr-17	2404 (353)	1077 (188)	16 (2)	4 (1.2)
Wheat-Tilled Fallow	06-Jul-17	2600 (1250) ‡	1879 (859) ‡	27 (4)	4 (1.5)
Wheat-Chemical Fallow	06-Jul-17	984 (263)	535 (211)	14 (2)	7 (1.5)
Continuous Wheat	06-Jul-17	1028 (463)	799 (216)	21 (3)	9 (1.9)
Wheat-Pulse Grain	06-Jul-17	925 (218)	660 (172)	17 (4)	5 (1.5)
Wheat-Pulse Forage	06-Jul-17	2607 (854)	1618 (763)	22 (2)	2 (0.7)
Wheat-Pulse Manure	06-Jul-17	1413 (510)	953 (379)	28 (3)	1 (1.0)
Org. Wheat-Pulse	06-Jul-17	1479 (186)	1038 (160)	31 (5)	10 (2.7)
CRP conversion	06-Jul-17	1504 (402)	1083 (237)	14 (2)	18 (5.6)

ANOVA		*df*	*p* values							
Cropping system	21-Apr-17	7	0.09		0.07		0.26		0.51	
	06-Jul-17	7	0.62		0.65		0.07		0.25	
1 df contrast										
Tilled vs chemical fallow	21-Apr-17	1	<0.01	**	0.01	*	0.23		0.92	
	06-Jul-17	1	0.15		0.09		0.05	*	0.70	
Fallow vs annual	21-Apr-17	1	0.05		0.02	*	0.36		0.24	
	06-Jul-17	1	0.70		0.90		0.70		0.75	
CRP vs. Wheat-Pulse grain	21-Apr-17	1	0.67		0.55		0.58		0.96	
	06-Jul-17	1	0.46		0.49		0.66		0.05	*

* Significant at $p<0.05$

** Significant at $p<0.01$

†Based on three replicates.

‡Back-transformed from ln(x+1)

§Numbers followed by the same letter are not significantly different at $P<0.05$ based on one-way ANOVA followed by an LSD test.

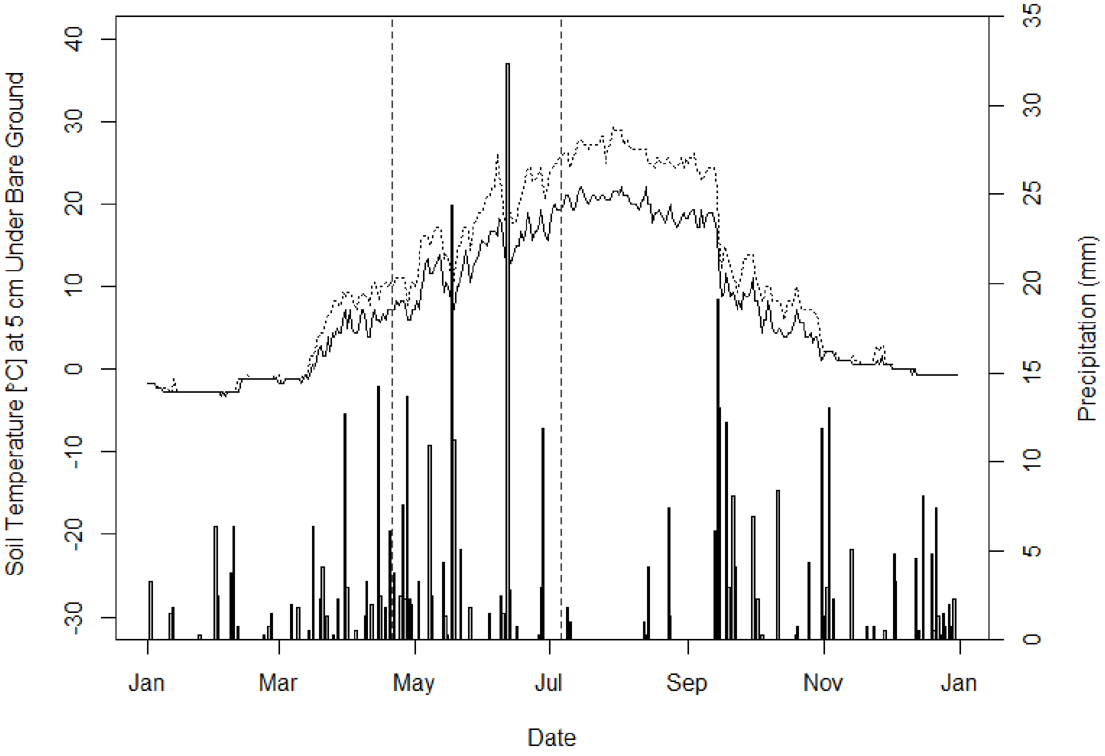

Figure 2.1: Precipitation (bars) and maximum (dotted line) and minimum (solid line) daily soil temperature at 5 cm below bare ground at the Arthur H. Post Research Farm for 2017. Dashed lines indicate sampling dates, 21 April and 6 July. Total precipitation between sampling dates was 156 mm.

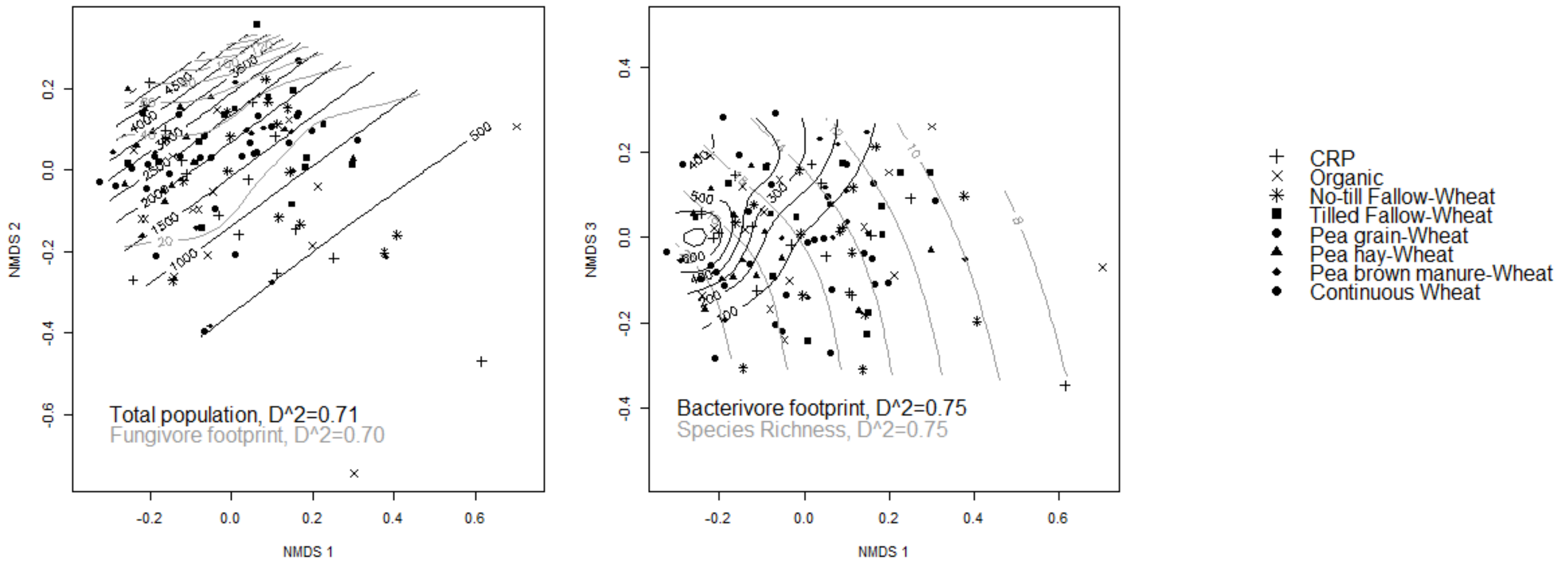

Figure 2.2: Non-metric dimensional scaling surface plots. The panel on the left shows the total population (black) and fungivore footprint (grey) on the x and y axes; while the panel on the right shows the bacterivore footprint (black) and species richness (grey) on the x and z axes. These four response variables explained the largest proportion of the dissimilarity in the data. However, both metabolic footprints skewed largely to the right, whereas total population and species richness had greater capture of the data’s dissimilarity.

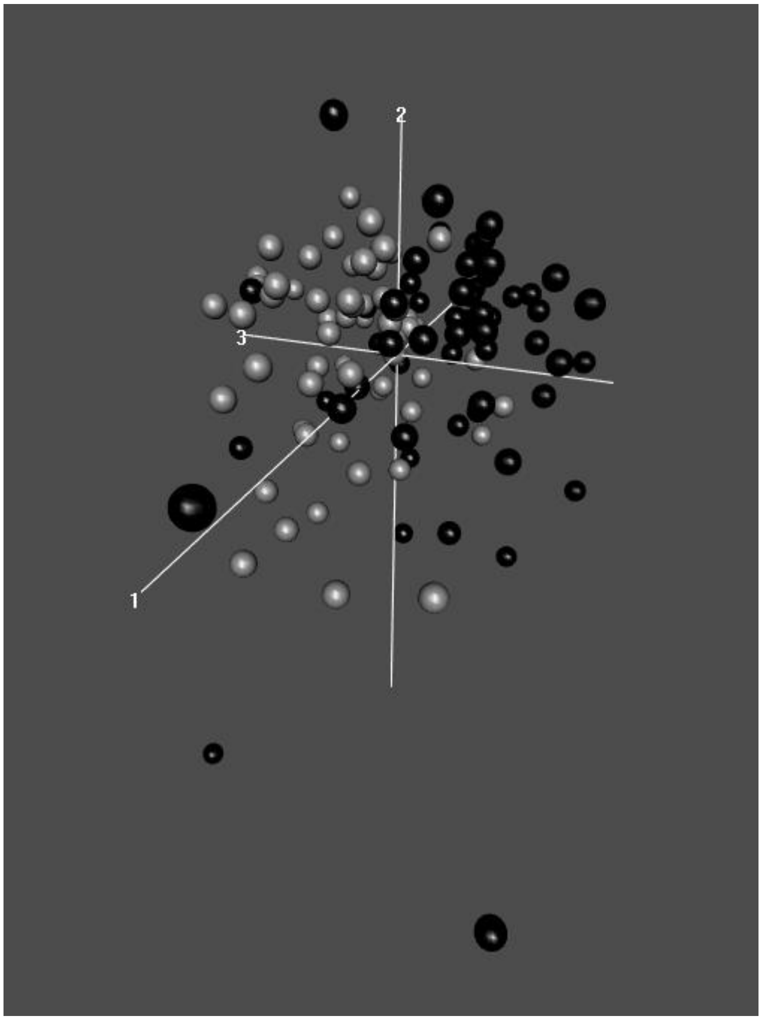

Figure 2.3: Three-dimensional model of the NMDS, showing grouping of the data by sampling date (grey = pre-plant, black = in-season). Axes indicate the optimized dissimilarity of the data. Overlap was observed, but in general sampling date did cluster together. We hypothesize that sampling date clustered together due to environmental changes from April to July. Gravimetric soil moisture decreased an average of 5% between sampling dates while air temperature increased roughly 15° C in that same time.

Supplemental Material

Supplementary Table 1. Average genus abundance counts by cropping system for 21 April 2017. Counts are standardized per 100 g dry soil.

Genus (guild and cp value)	21-Apr-17							
	Wheat-Tilled Fallow	Wheat-Chemical Fallow	Continuous Wheat	Wheat-Pea Grain	Wheat-Pea Forage	Wheat-Pea Manure	Organic Wheat-Pea	CRP conversion
	---per 100 g dry soil----------------------------- ---------							
Panagrolaimus (Ba1‡)	0	0	0	0	10	0	0	0
Rhabditis (Ba1)	39	19	21	35	2	90	84	22
Acrobeles (Ba2)	16	41	27	17	13	45	51	32
Acrobeloides (Ba2)	318	1210	65	580	334	173	198	178
Cephalobus (Ba2)	280	1265	89	406	567	252	199	163
Cervidellus (Ba2)	49	71	69	44	55	58	100	9
Chiloplacus (Ba2)	0	0	0	0	0	0	0	0
Eucephalobus (Ba2)	2	0	33	11	2	6	0	0
Monhystera (Ba2)	81	59	21	29	0	0	0	89
Plectus (Ba2)	0	43	4	20	10	5	0	4
Tylocephalus (Ba2)	0	0	0	0	0	0	0	0
Wilsonema (Ba2)	0	0	55	44	31	34	42	61
Prismatolaimus (Ba3)	99	39	20	0	0	103	25	108
Teratocephalus (Ba3)	0	0	0	0	0	0	0	0

Discolaimus (Ca5)	0	0	0	0	0	0	0	0
Mononchus (Ca5)	0	0	0	0	0	0	0	0
Aphelenchoides (Fu2)	334	296	316	158	261	176	336	229
Aphelenchus (Fu2)	0	29	4	20	49	107	74	84
Ditylenchus (Fu2)	4	33	4	20	10	11	19	12
Filenchus (Fu2)	25	41	74	50	54	25	36	18
Nothotylenchus (Fu2)	3	0	0	0	0	0	5	11
Diphtherophora (Fu3)	0	0	0	0	0	0	0	0
Doryllium (Fu4)	4	6	0	0	0	0	6	0
Tylencholaimellus (Fu4)	0	0	0	0	0	0	0	0
Tylencholaimus (Fu4)	0	0	0	0	0	0	0	0
Ecumenicus (Om4)	14	32	12	43	15	9	47	41
Enchodelus (Om4)	0	0	0	0	0	0	0	0
Epidorylaimus (Om4)	11	0	0	0	0	6	5	0
Eudorylaimus (Om4)	0	22	4	0	0	0	0	0
Labronema (Om4)	20	8	10	17	14	11	17	19
Mesodorylaimus (Om4)	0	0	77	0	13	0	5	0
Other Dorylaimids (Om4)	11	0	0	0	0	0	0	0
Prodorylaimus (Om4)	0	0	0	0	0	0	0	0
Paratylenchus (Pp2)	8	30	8	13	0	0	30	0
Psilenchus (Pp2)	0	18	20	13	12	0	22	4
Tylenchus (Pp2)	79	173	67	189	59	181	447	18

Helicotylenchus (Pp3)	55	18	51	10	0	23	0	97
Pratylenchus (Pp3)	205	600	579	251	583	451	298	1043
Tylenchorhynchus (Pp3)	52	147	32	86	90	88	94	152
Xiphinema (Pp5)	0	0	4	0	0	0	0	11
Total	1712	4201	1665	2058	2185	1854	2139	2404

†Based on three replicates.

‡Ba = Bacterivore, Ca = Carnivore, Fu = Fungivore, Om = Omnivore, Pp = Herbivore.

Supplementary Table 2. Average genus abundance counts by cropping system for 6 July 2017. Counts are standardized per 100 g dry soil.

Genus (guild and cp value)	06-Jul-17							
	Wheat-Tilled Fallow	Wheat-Chemical Fallow	Continuous Wheat	Wheat-Pea Grain	Wheat-Pea Forage	Wheat-Pea Manure	Organic Wheat-Pea	CRP conversion
	---per 100 g dry soil-------------------------------------							
Panagrolaimus (Ba1†)	5	5	0	0	39	0	4	1
Rhabditis (Ba1)	26	18	24	27	492	276	3	31
Acrobeles (Ba2)	39	24	0	32	46	18	34	72
Acrobeloides (Ba2)	395	81	207	147	236	167	88	188
Cephalobus (Ba2)	109	59	54	116	335	231	76	77
Cervidellus (Ba2)	146	49	54	52	94	57	136	32
Chiloplacus (Ba2)	0	0	0	0	0	0	0	0
Eucephalobus (Ba2)	29	6	0	4	88	29	4	26
Monhystera (Ba2)	102	137	172	92	105	80	35	100
Plectus (Ba2)	5	5	0	47	4	4	31	24
Tylocephalus (Ba2)	0	0	0	12	5	0	4	0
Wilsonema (Ba2)	85	9	14	33	20	65	36	87
Prismatolaimus (Ba3)	144	131	32	101	115	107	9	149
Teratocephalus (Ba3)	5	0	0	0	0	9	0	0
Discolaimus (Ca5)	9	2	27	7	5	0	7	2
Mononchus (Ca5)	0	0	0	0	0	0	0	0

Aphelenchoides (Fu2)	1206	95	170	77	460	157	172	124
Aphelenchus (Fu2)	16	7	52	35	77	93	82	47
Ditylenchus (Fu2)	248	5	8	0	14	5	21	6
Filenchus (Fu2)	178	45	76	55	133	350	156	40
Nothotylenchus (Fu2)	0	11	0	0	0	0	0	0
Diphtherophora (Fu3)	7	0	0	7	5	0	16	6
Doryllium (Fu4)	0	0	0	0	0	0	0	0
Tylencholaimellus (Fu4)	0	0	0	0	0	9	0	5
Tylencholaimus (Fu4)	18	0	5	0	0	4	0	0
Ecumenicus (Om4)	16	2	5	12	13	5	18	19
Enchodelus (Om4)	0	6	0	0	0	0	20	24
Epidorylaimus (Om4)	0	0	0	0	0	0	0	0
Eudorylaimus (Om4)	54	31	38	20	13	4	26	11
Labronema (Om4)	16	28	38	11	43	27	70	36
Mesodorylaimus (Om4)	36	5	30	2	46	0	19	144
Other Dorylaimids (Om4)	0	0	0	0	0	0	0	0
Prodorylaimus (Om4)	0	2	0	0	0	0	0	0
Paratylenchus (Pp2)	16	17	11	25	51	78	27	74
Psilenchus (Pp2)	0	2	0	26	0	0	30	11
Tylenchus (Pp2)	905	68	106	82	388	113	250	179
Helicotylenchus (Pp3)	5	57	11	4	0	33	23	185
Pratylenchus (Pp3)	328	273	60	102	642	330	75	68
Tylenchorhynchus (Pp3)	86	67	89	28	50	56	37	72
Xiphinema (Pp5)	3	5	0	0	11	0	0	5

Total	4239	1253	1282	1156	3532	2307	1508	1847

†Ba = Bacterivore, Ca = Carnivore, Fu = Fungivore, Om = Omnivore, Pp = Herbivore.

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CHAPTER THREE

PLANT PARASITIC NEMATODES FAVORED UNDER DISTURBED CONDITIONS COMPARED TO A NATIVE SAGEBRUSH STEPPE OF MONTANA

Abstract

Biological diversity is necessary component of any healthy ecosystem. The Red Dog Ranch in the Bangtail Mountains near Wilsall, MT, offers a unique location to study the impact of disturbance on native ecosystems and biological diversity. Livestock grazing was eliminated from much of the ranch in the late 1990’s allowing native sagebrush plant communities to re-establish themselves. In this study, soil samples were collected in June 2017 from six transects representing three sagebrush steppe plant communities and three adjacent disturbed plant communities on an elevation gradient to assess nematode community diversity and structure. Results from this study indicate a significantly increased species richness within all three native plant community transects and higher species diversity within transect 1, a native plant community transect. Numbers of migratory endoparasitic nematodes (comprising entirely *Pratylenchus* sp.) were several orders of magnitude higher per unit soil mass under a grass pasture than the native plant community transects, or the other two non-native plant community transects, suggesting low diversity plant communities are more prone to accumulate plant parasitic nematodes within the soil community.

Introduction

Soil nematodes (phylum Nematoda) perform important ecological functions within the greater soil biological community. They occupy all lower heterotrophic levels in the soil food chain: herbivores are primary consumers, fungivores and bacterivores are secondary consumers, and omnivores and carnivores are tertiary and sometimes quaternary consumers. They also inhabit most environments on the planet, even Antarctic soils (Freckman and Virginia, 1997). Importantly, nematodes are valuable bio-indicators of soil function and quality (Ferris, 2010a; Ferris and Bongers, 2006). The wide range of diversity among nematode species allows inferences to be made about the soil food web and ecological links between soil fauna, their environment, and the health of the ecosystem.

Describing soil nematode community structure can provide information about soil function and assess ecosystem services within the soil food web (Chertov et al., 2017; Morriën, 2016; Olena et al.; Rousk, 2016; Zhang et al., 2017). Taxa within the nematode community respond differently to environmental disturbances and can be used as indicators of soil quality (Briar et al., 2007; Neher and Olson, 1999; Yeates and Bongers, 1999). Nematode taxa are classified by feeding habit and a colonizer-persister (cp) value based upon *r*-k selection strategies. K-strategists typically have low fecundity, long life cycles, larger body size, and are intolerant of disturbance while *r*-strategists typically have high fecundity, small body size, short life cycles, and are tolerant to disturbances. The cp value of a nematode is a rank from 1-5 where low cp value nematodes (cp 1 and 2) behave more as *r*-strategists while high cp value 3-5 follow more of a k trajectory. High net cp values for nematode communities indicate that the system is in a mature and stable state; while low net cp values for nematode communities indicate a disturbed and degraded state of the soil food web. Once assigned a feeding habit and cp value, they are further grouped into functional guilds, a combination of the feeding habit and cp value.

Multiple studies have described how disturbance, plant community diversity, and environmental factors impact the nematode community. Kergunteuil et al. (2016) found that elevation within alpine meadows impacted nematode communities, finding that as elevation increased, so too did nematode diversity and their metabolic carbon footprint. A study by Freckman et al. (1979) on California grasslands observed that soil moisture and temperature were the determining factors of nematode diversity and community structure and not grazing intensity. Other studies determined that aboveground plant community restoration efforts often have positive impacts on nematode diversity (Eisenhauer et al., 2011; Hu et al., 2016)

These studies all demonstrate the impact of environmental shifts and biodiversity on soil nematode communities. In this study, we observed the differences on nematode diversity between three native and undisturbed sagebrush steppe communities and three disturbed plant communities. We hypothesized that decreased plant community diversity would significantly reduce nematode community diversity.

Materials and Methods

Study Site Description

The study site was the Red Dog Ranch located west of Wilsall, MT. In part, this site was selected because livestock had been excluded from grazing much of the land starting in the 1990's, allowing the return of a mountain big sagebrush steppe community with a high level of native plant diversity in terms of both species and functional groups. The study site consisted of a plant community comprised of 100% native plant species, with a diversity of native shrubs, including perennial bunchgrasses and forbs, the latter including caespitose forbs (e.g., *Arenaria* spp., and perennial *Eriogonum* spp.), parasites (e.g., Orobanchaceae spp.), nitrogen-fixers belonging to the legume genus *Astragalus*, and early- and late-season flowering native perennials (e.g., *Erigeron* spp. and *Senecio* spp. versus *Solidago* spp. and *Symphyotrichum* spp.). Six transects previously sampled for plant and microbial communities, representing varying degrees of disturbance and elevation, and measuring 10 m by 1000 m (1 ha) had soil sampled on 28 June 2017 at five randomly generated distances for nematode faunal analysis (Figure 3.1). One core per transect distance was sampled to a depth of 15 cm using a slide hammer probe. Each sample was put in a polypropylene-lined tin-tie soil bag and placed inside a cooler immediately after sampling. Samples were stored at 4º C until processing.

The six transects were each located on gentle terrain and along an elevation gradient, the uppermost averaging 1701 m in elevation and the lowest 1576 m. The upper two transects, differing on average by 34 m elevation, were established in undisturbed mountain big sagebrush steppe dominated by *Artemisia tridentata* subsp. *vaseyana* (taxonomic nomenclature follows Lesica 2012). The third transect, adjacent to the second, comprised mountain big sagebrush steppe along a somewhat well-traveled private gravel road. The fourth transect was located on former sagebrush steppe converted to perennial forage grasses dominated by thickspike, western and slender wheatgrass (*Agropyron* *dasystachyum*, *A. smithii*, and *A. trachycaulum*). The fifth site was located in tall-statured mountain big sagebrush steppe. The sixth and lowest elevation transect closest to the stream was established on former sagebrush steppe converted to a grass hay field dominated by Kentucky bluegrass (*Poa pratensis*), quackgrass (*Agropyron repens*), and smooth brome (*Bromus inermis*), but included a diversity of introduced and native plant species.

Soil Nematode Analysis

Soil nematode extractions were performed using the Baermann funnel technique (Barker, 1985). Baermann funnel extractions were run for approximately 72 hr and water suspensions were collected. Nematodes were identified to genus level using a Motic® AE2000 inverted microscope with phase contrast on a nematode counting slide (Chalex Corp.). Counts were standardized to individuals per 100 g dry soil. Nematodes were assigned to a trophic group, a cp value, and a functional guild (Table 3.1) (Bongers, 1990; Bongers and Bongers, 1998; Ferris et al., 2001; Yeates et al., 1993). Species richness and Simpson's Reciprocal Diversity Index (1/D) were then calculated (Simpson, 1949).

Statistical Analysis

Exploratory analysis of the taxonomic counts was first performed using non-metric multidimensional scaling (NMDS) to assess the dimensionality of the data set. This provided a framework for analysis of the significance and effect sizes of candidate explanatory variables have using the labdsv package in R (Roberts, 2016). A Bray-Curtis dissimilarity matrix was calculated from ln(x+1) transformed taxon abundance data. To generate the NMDS results, the minimum stress result was calculated from 100 random starts for both two- and three-dimensional solutions. The lowest dimensionality result with a stress of less than 20 was selected for further analysis (Borg and Groenen, 2005).

Explanatory variables of interest were fitted to the ordination with a generalized additive model (GAM) using the ordination coordinates as explanatory variables, and appropriate error structures for individual variables (Gaussian for environmental variables, negative binomial for species abundances). Goodness-of-fit was assessed with deviance explained (D^2 = 1-(residual deviance/null deviance)) and considered significant for D^2 values ≥ 0.70.

Analysis of variance was performed on explanatory variables identified by NMDS in the R statistical software environment (R Core Team, 2017), with transect as the fixed model term. Significant differences among transects were assessed using the LSD post-hoc test in the emmeans package (Lenth, 2017) at a $p<0.05$ following a significant *F* test. Where significant differences did occur, multiple comparisons were performed using the multcomp package (Hothorn et al., 2008). As in NMDS, where normality and homoscedasticity assumptions were violated, data were transformed on a ln(x+1) scale and back-transformed data are reported.

Results

NMDS Results

NMDS ordination was performed to dissimilarity and dimensionality of the community taxa data. NMDS results suggested differences between the transects were best explained on three dimensions. D^2 values (similar in interpretation to R^2 values in regression) are given in Table 3.1 for each of the three dimensions combinations. Dissimilarity of dimensions 1 and 2 was best explained by gravimetric soil moisture ($D^2 = 0.91$), but the only differences were between transect 6 and other transects due to its high soil moisture content (Table 3.1). Total population explained the next highest dissimilarity within each sample for dimensions 1 and 2 ($D^2 = 0.79$). Transects 4 and 6 clustered nearly independently and separately from the rest of the data (Figure 3.2**,** left panel). Total population also best explained the dissimilarity within dimensions 1 and 3 ($D^2 = 0.78$). Transect 4 had significant overlap with transect 6, but no other transects (Figure 3.2, center panel). Dissimilarity of dimensions 2 and 3 was best explained by the percentage of cp 2 herbivores where Transect 4 had significantly fewer cp 2 herbivores than Transects 2, 3, and 5 and statistically similar percentage to Transects 1 and 6 (as seen by the overlapped in polygons in Figure 3.2, right panel, and ANOVA results and D^2 values in Table 3.1).

Analysis of Variance Results

Univariate analysis showed differences largely within the herbivorous portion of the nematode community. Genera richness and genera diversity (by means of Simpson's reciprocal diversity index, *H'*) indicated that transect 1 had the most genera present (25 on average) whereas transects 3, 4, and 6 (all three of the non-native plant community transects) all had the lowest genera richness (20, 18, and 20 respectively). The highest genera diversity was observed in transect 1 (*H'* = 14, Table 3.1). The high diversity and richness in Transect 1 indicate a more diverse and balanced community present in this transect than other transects in the study area. Transects 2 and 5, both undisturbed sagebrush steppe, had similar genera richness, but lower diversity, indicating differences in genera dominance patterns within these two transects compared to Transect 1.

Within the herbivorous community, several response variables showed differences among the transects. Differences were observed for most cp levels, as well as among *Pratylenchus* sp. (Table 3.1). The high concentration of cp 3 herbivores (comprised of *Pratylenchus* sp., *Heterodera* sp., *Tylenchorhynchus* sp., *Hoplolaimus* sp., and *Helicotylenchus* sp.) in transect 4 led to lower than average abundance of cp 2 herbivores, comprised by *Gracilicus* sp., *Paratylenchus* sp., *Psilenchus* sp., and *Tylenchus* sp. (Table 3.1). These cp 2 herbivores were highest in transects 2, 3, and 5, while transects 1 and 6 were intermediate. Differences among transects for cp 4 herbivores were based solely on *Trichodorus* sp. presence or absence. Transect 5 was the only transect where the genus was observed.

Variation in total population across the transects had a nonsignificant trend (p = 0.06). However, the data suggest that under simplified plant communities, such as Transect 4, nematode populations will be lower and, as evidenced above, comprised of more herbivorous than free-living nematodes. Our observations are similar to Wasilewska (1995) and Franco-Navarro and Godinez-Vidal (2015) where simplified plant communities often had low nematode diversity and populations while also being dominated by PPNs. The forage grass pasture, transect 4, showed significantly depressed populations in comparison to all other transects. The hay grass transect 6, while a similarly simplified plant community, had access to more soil moisture due to its position only meters from a creek, leading to a higher than average total population than transect 4. Transects 1, 2, 3, and 5 had statistically similar soil moisture to Transect 4 (Table 3.1) and yet, these same four transects all had double or more the average population compared to transect 4.

Conclusions

This study provides the first observations to sagebrush steppe plant communities to soil nematode communities. Our findings corroborate, in part, previous research which indicated that increased plant diversity is directly associated to increased soil nematode diversity (Eisenhauer et al., 2011; Hu et al., 2015; Hu et al., 2016; Kergunteuil et al., 2016). Our observations show that the herbivorous portion of the nematode community is impacted by disturbance and plant diversity more so than the free-living community. NMDS showed that even with these differences, the nematode communities across all six transects overlapped substantially in composition.

Many studies have looked at the impact of native range plant cover on nematode communities, but few have made these observations in sagebrush steppe ecosystems (Hodson et al., 2014; Huang and Cares, 1995; Jones et al., 2006; Morriën et al., 2012; Porazinska et al., 2014). The most relevant related study was in an arid desert in Israel, and their results indicate plant species did impact abundance of PPNs (Pen-Mouratov et al., 2008) but their assessment looked only at the impact of single plant species on the nematode community. In the present study, each transect was originally defined by the plant community, not a single species. More simplified plant communities were associated with an increased percentage of detrimental PPNs in the herbivore component of the community. However, the perennial nature of the systems meant each transect had relatively balanced free-living nematode communities and statistically similar abundance of herbivorous nematodes. The imbalance we observed, particularly in the herbivore community in transect 4, was limited to the relative abundance of certain species in the herbivore community and transect 4 specifically was defined by an unusually high abundance *Pratylenchus* sp. (a cp 3 herbivore).

Evidence also suggests that, all other environmental factors being roughly equal, particularly soil moisture, continued disturbance that favors a simplified plant community (in this case, a pasture for grazing) negatively impacts total population. Our findings show an association between aboveground plant community composition and the belowground composition of the nematode community. Continued landscape disturbance is likely to cause negative impacts to the soil nematode community thereby negatively impacting plant communities not accustomed to high feeding pressure from PPNs.

Tables and Figures

Table 3.1: Univariate analysis results indicated differences observed between transects were due to differences within the herbivorous nematode community. Transect 4, a grass pasture, had significantly higher herbivory pressure from cp 3 herbivorous nematodes, especially *Pratylenchus* sp. Numbers followed by the same letter are not significantly different at *P*<0.05.

Transect		Gravimetric Soil Moisture	Total Population	Genera Richness	H' †	Herbivore community composition			
						Pratylenchus sp. ‡	cp 2	cp 3	cp 4 ‡
		% soil water	Individuals per 100 g dry soil			----------------------------%----------------------------			
1 (undisturbed sagebrush steppe)		10 b	13620	25 a	14 a	6 b	34 ab	61 ab	0 b
2 (undisturbed sagebrush steppe)		11 b	14263	23 ab	11 b	1 bc	54 a	31 b	0 b
3 (converted roadside)		13 b	11008	20 bc	10 b	1 bc	42 a	32 b	0 b
4 (converted grass pasture)		13 b	4313	18 c	9 b	46 a	7 b	68 a	0 b
5 (undisturbed sagebrush steppe)		10 b	8731	21 abc	10 b	0 c	43 a	29 b	6 a
6 (converted grass hay field)		34 a	18323	20 bc	9 b	2 bc	34 ab	66 a	0 b
NMDS axes									
x vs y		0.91	0.79	0.21	0.51	0.34	0.21	0.04	0.13
x vs z		0.67	0.78	0.11	0.53	0.20	0.78	0.09	0.63
y vs z		0.35	0.36	0.17	0.46	0.17	0.16	0.06	0.71
ANOVA	*df*	F ratio							
Transect	5	6.94 ***	2.42	4.37 **	2.68 *	6.61 ***	2.98 *	2.70 *	5.64 **

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*Significant at $p < 0.05$.

**Significant at $p < 0.01$.

***Significant at $p < 0.001$.

†H' = Simpson's Reciproval Diversity Index

‡Back-transformed from ln(x+1)

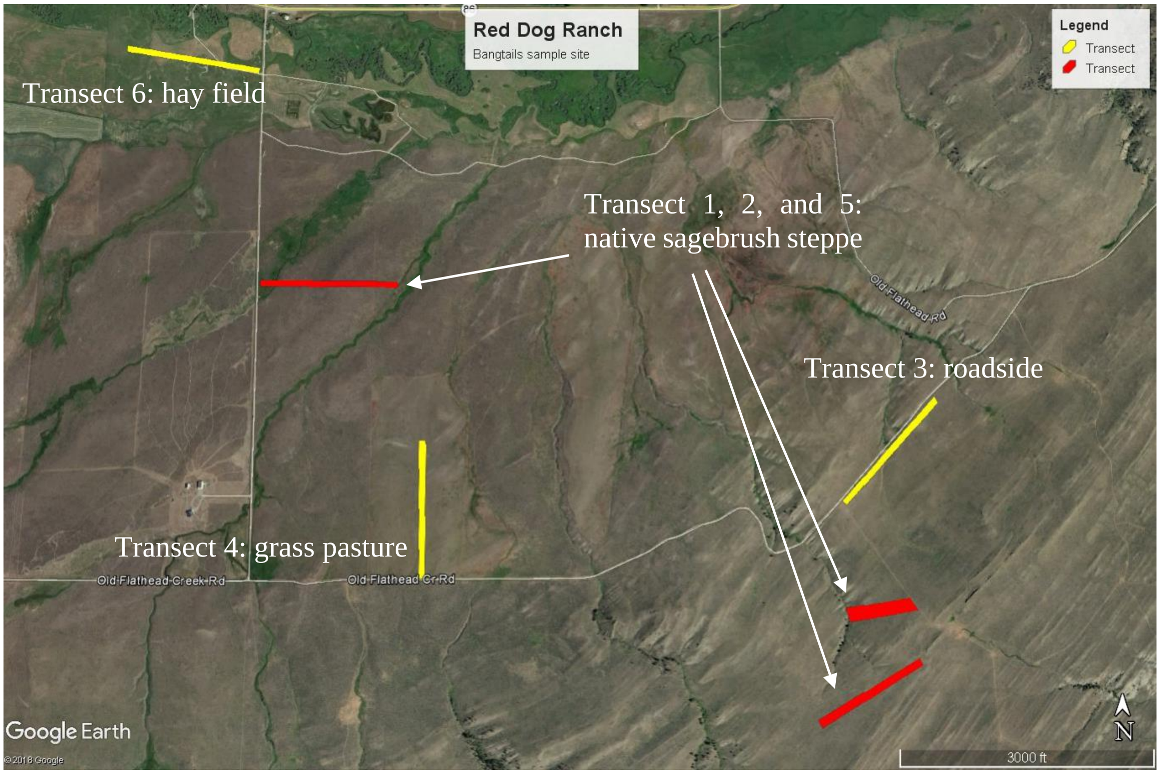
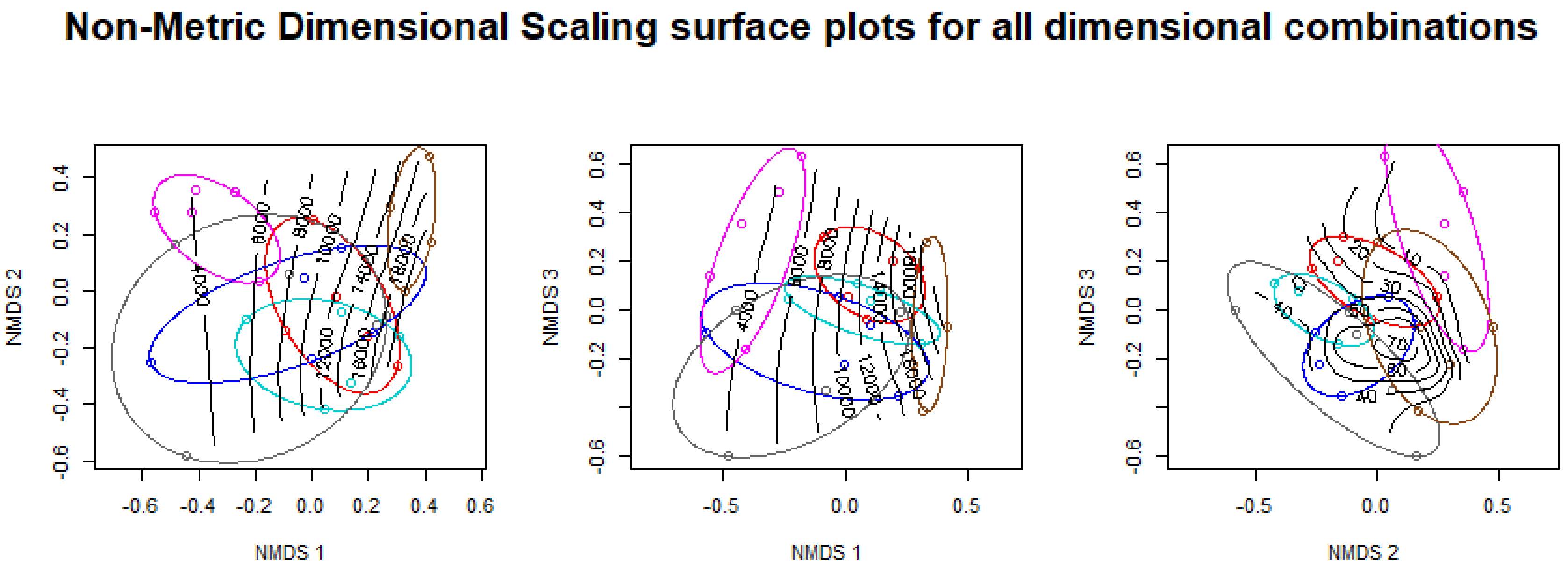


Figure 3.1: Google Earth image of Bangtails site. Red transects are undisturbed, native sagebrush steppe. Yellow transects are disturbed sites, with the specific disturbance indicated by the label.



Non-Metric Dimensional Scaling surface plots for all dimensional combinations

Figure 3.2: Surface plots from Non-Metric Multidimensional Scaling. Axes represent the ordination dimensions derived from the data matrices. Transects correspond to the following colors: red=1, turquoise=2, blue=3, magenta=4, grey=5, and brown=6. The left and center panels indicate total population dissimilarity for dimensions 1 and 2 (left) and 1 and 3 (center) where population generally increases from left to right, showing Transect 6 (brown) on the right in both panels. The right panel indicates transect dissimilarity for cp 2 herbivores for dimensions 2 and 3, showing Transect 4 in the top right having the fewest on average cp 2 herbivores to Transects 2, 3, and 5 and similar to Transects 1 and 6 where overlap in the polygons occurs. Across all dimensions, transect 4 (magenta, converted grass pasture) shows the most dissimilarity among transects followed by transect 6 (brown, hayfield).

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CHAPTER FOUR

CHARACTERIZATION OF SOIL NEMATODE COMMUNITY STRUCTURE IN SEMI-ARID DRYLAND BARLEY (*HORDEUM VULGARE* L.) SYSTEMS

Contribution of Authors and Co-Authors

Manuscript in Chapter 4

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Contributions: managed trial at Bozeman Post Farm, conducted sample collection, data collection and analysis, and prepared manuscript.

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Contributions: trained first author in nematological methods and techniques, participated in preparation of manuscript.

Co-Author: John M. Martin

Contributions: assisted with statistical analysis, participated in preparation of manuscript.

Co-Author: Patrick M. Carr

Contributions: managed trials at the Central Agricultural Research Center (CARC), collected field and harvest data at CARC, participated in preparation of manuscript.

Co-Author: Jamie Sherman

Contributions: provided financial support, supervised work, participated in preparation of manuscript.

Manuscript Information

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Abstract

Changes in soil nematode community structure and composition can inform crop managers about soil quality and function. However, few studies have assessed soil nematode community structure under agricultural systems in semi-arid regions such as the Northern Great Plains. Here we assess soil nematode community structure of continuous barley (*Hordeum vulgare* L.), barley-fallow, barley-pea (*Pisum sativum* L.) grain, and barley-pea manure cropping systems in Montana from 2016-2018 at two semi-arid dryland locations in three field experiments. Soils were sampled prior to planting in the spring and following grain harvest in late summer. Higher barley grain yield was correlated with higher populations of nematodes (r = 0.62) in a no-till environment, including herbivores (r = 0.63). However, the type of herbivore was important, as ectoparasitic nematodes were negatively correlated with yield (r = -0.46). Under tillage, herbivores were significantly reduced under barley-pea grain systems (67 individuals per 100 g dry soil) compared to continuous barley and barley-pea manure (113 and 130 individuals per 100 g dry soil, $P < 0.05$). Importantly, both barley-pea systems were better able to maintain more algal-moss-lichen feeding herbivores, whereas continuous barley was dominated by increases in economically important, yield-limiting herbivores, particularly cp 3 herbivores and *Xiphinema* spp. This study provides new information on nematode community structure in semiarid barley cropping systems that can serve as a basis for future research.

Introduction

Nematodes are a diverse and highly speciated group in the soil environment. Occupying multiple trophic levels, this group of organisms can provide useful insights into the structure and function of the soil food web (Neher, 2001; Ritz and Trudgill, 1999). Broadly, nematodes can be grouped into five major trophic groups: bacterivores, fungivores, herbivores, predators, and omnivores (Yeates et al., 1993). Plant-parasitic nematodes (PPNs) are primary consumers, affecting soil food web resources through direct herbivory. Bacterivore and fungivore nematodes graze on decomposer microbes, thus contributing to soil nutrient pools, while predatory and omnivorous nematodes regulate the soil food web by preying on other nematodes and invertebrates in the soil (Ferris and Bongers, 2006; Ferris and Matute, 2003).

Ecological indices are a way to quantify community connections, often focusing on the number and prevalence of various trophic groups and genera based on a colonizer-persister (cp) scale defined by life-history strategies, food sources, and nematode responses to soil disturbance (Bongers, 1990; Bongers et al., 1995). After being assigned a cp value, nematodes are assigned to trophic groups (defined by feeding habits), and grouped into functional guilds, which is the combination of cp value and feeding habit (Bongers and Bongers, 1998; Ferris et al., 2001). The Structure Index is a measure of soil food web stability as affected by disturbance, while the Enrichment Index is a measure of the abundance of opportunistic bacterivoes and fungivores. The Maturity Indices (Maturity Index, ∑ Maturity Index, p 2-5 Maturity Index, and Plant Parasitic Index) are means of the weighted cp value of the community or a component of the community. Abundance of low cp value nematodes indicate a stressed and degraded soil food web, while abundance of high cp value nematodes indicates a mature and stable soil food web.

PPNs were responsible for an estimated $80 billion in crop losses annually across the globe (Handoo, 1998). Losses associated with PPNs are likely underestimated due to misdiagnosis as abiotic stress or attributed to another pest. Traditional management options have typically included crop resistance, rotations that include non-host plant species, and nematicides (Galal et al., 2014; Kretschmer et al., 1997; Smiley and Yan, 2010; Smiley et al., 2014). Crop and soil management strategies which diversify biological communities could suppress PPNs and improve soil biological nutrient cycling in a safer, more economical way, potentially eliminating the need for highly toxic and expensive nematicides (Held et al., 2003; Stark Jr. et al., 2000) as well as the long wait for a new resistant variety to be released. Significant research efforts have focused on controlling PPNs using the methods described, while the free-living soil nematode community is less well understood. Knowledge gaps in nematode ecology, specifically in dryland farming systems, still exist (Neher, 2010). A better understanding of how aboveground diversity by means of crop rotation interacts with belowground nematode diversity would provide such a framework.

While continuous cereal production and the use of a fallow period are still prevalent, research efforts continue to advocate diverse and high-intensity rotations and reduced occurrence of fallow. Crop rotation has long been an important cultural practice in integrated pest management. Rotating crops can enhance soil quality (fertility, organic matter, and structure) and provide economic profitability by reducing fertilizer use and conserving energy (Badaruddin and Meyer, 1990; Biederbeck et al., 1996; Campbell et al., 1992; Coxworth et al., 1996; Green and Biederbeck, 1995; Wright, 1990; Yao et al., 2013; Zentner et al., 2001). Legumes are commonly used as a nitrogen source through nitrogen fixation, and research from Montana indicates an improvement in soil quality and available soil nitrogen and carbon under crop rotations that include a pulse (Engel et al., 2017; O'Dea, 2011). The increasing markets available to pulses (specifically field peas (*Pisum sativum* L.), lentils (*Lens culinaris* M.), and chickpeas (*Cicer arietinum* L.)) have increased their adoption throughout the Northern Great Plains (NGP). For example, pulse production in Montana grew from over 240,000_ha in 2013 to over 620,000 ha in 2017 (Montana Department of Agriculture, 2017). However, many crop producers, particularly in north central Montana, rely heavily or solely on cereal-fallow systems for income generation (Miller et al. 2015). Fallow hectares comprised roughly 30% of all cropland, contrasted to roughly 10% of all cropland in northeastern Montana and northwestern North Dakota (Soil Survey Staff et al., 2006). That same study demonstrated the economic value of incorporating pulses into cereal production, whereby incorporating peas into wheat systems increased net returns by \$287 ha^{-1} over 4 years for wheat-peas compared to wheat-fallow. Burgess et al. (2012) observed a 53% reduction in energy inputs in wheat-based cropping systems when pulses were incorporated into the system.

Even though this and other research since the 1990s have documented the benefits of incorporating annual legumes and pulses (Long et al., 2014a; Long et al., 2014b), little is known about the impact of cropping systems in the NGP on nematode community structure. Research in other climates and regions can provide clues of important impacts on nematodes in the NGP. For example, several studies indicate that conversion to no-till and diversifying crop rotations can have positive impacts on the nematode community by increasing total numbers and diversity of genera present (Bakonyi et al., 2007; Eisenhauer et al., 2011; Ito et al., 2015a; Ito et al., 2015b; Pan et al., 2012). Eisenhauer et al. (2011) found that plant diversity in grasslands induced positive changes in nematode communities by increasing species diversity and richness, as well as stimulating and stabilizing nutrient cycling, is suggestive of the impact diversifying crop rotations could have on soil nematodes in dryland farming systems. Importantly, a 2015 study noted that tillage had a larger impact on the nematode community than either cover crop or fertility (Ito et al., 2015a). Tillage treatments of no-till, rotary cultivator, and moldboard plow showed stark differences from one another, with no-till often having at least twice the abundance of nematodes than with moldboard plow. By limiting soil disturbance, farmers can foster a more diverse and resilient nematode community, thereby fostering more soil ecosystem services (e.g. higher rates of soil nutrient cycling). This suggests that no-till is a viable option to increase soil ecosystem services of nematodes.

The current study determined how four dryland barley cropping systems impacted nematode community structure. Specifically, our objective was to determine if integrating field peas into barley cropping systems positively impacted the soil nematode community by way of increased ecological function or genera diversity. We hypothesized that nematode community diversity would be greatest in a barley-pulse rotation and lowest in a barley-fallow system, with community diversity between those two extremes in a continuous barley monoculture.

Materials and Methods

Study Site and Experimental Design

The study included a 3-yr field experiment at the MSU Arthur H. Post Farm (Post Farm) near Bozeman in southwestern MT, and two, 3-yr field experiments at the MSU Central Agricultural Research Center (CARC) near Moccasin in central MT. The Post Farm site (45°40'45"N, 111°8'45"W) is at an approximate elevation of 1474 m on an Amsterdam-Quagle silt loam soil (fine-silty, mixed, superactive, frigid Typic Haplustolls) (Soil Survey Staff, 2017). Field history prior to the experiment was three years of chemical and tilled fallow. The seedbed was prepared using a cultivator equipped with S tines before sowing plots each spring. Each fall after harvest, soil was plowed once using a 1.8-m tandem disk. Precipitation for 2017 and 2018 growing seasons (April through September, 272 mm and 297 mm, respectively) was similar to, or exceeded, the 30-yr average (267 mm, Fig. 4.1). Growing-season precipitation totaled only 236 mm during 2016. The CARC site (47°3'30"N, 109°56'57"W) is at an approximate elevation of 1275 m on a shallow Danvers-Judith clay loam soil (fine, smectitic, frigid Vertic Argiustolls) (Soil Survey Staff, 2017). Prior to this study the plot area was planted to winter wheat (*Triticum aestivum* L. emend. Thell.) and the field had been managed under no-till for > 5 yr. Precipitation at CARC was above the 30-yr growing season average of 299 mm in 2016 and 2018 (330 mm and 329 mm respectively, Fig. 4.1). Growing season precipitation totaled only 261 mm during 2017. Plots at CARC were 4.6 x 6 m, while those at the MSU Post Farm were 3.7 x 6 m. Plots were seeded at the Post Farm with double disc openers mounted to a 1.2-m wide small-plot planter, while at the CARC two different 1.5-m wide small-plot planters were used to establish plots in separate field experiments each year: one with hoe openers and the other with Accu-Plant disc openers mounted to the frame. The two CARC field experiments were situated approximately 25 m apart in the same field.

The three field experiments were established in 2016 at both locations. The cropping systems included barley-pea for grain, barley-pea brown manure (i.e., pea crop terminated chemically at first flower (BBCH 60; Lancashire et al., 1991), continuous barley, and barley-fallow. Spring barley cv. ‘Hockett’, an MSU malting variety well adapted to dryland conditions, was seeded to achieve a density of 200 plants m^{-2} at both locations. A high-yielding spring yellow pea cultivar, 'Montech 4152', was seeded to achieve a density of 80 plants m^{-2}. The treatments were arranged so that all phases of each cropping system (e.g., barley and pea) were present each year of the study. The phases were established in a randomized complete block design with four blocks. in each field experiment. Grass and broadleaf weeds and insect pests were controlled using labeled pesticides when necessary. The pea brown manure treatment was terminated with glyphosate and 2,4-Dichlorophenoxyacetic acid. Barley was managed so 30 kg N ha^{-1} Mg grain^{-1} was available at planting. Fertilizer rates were calculated based on a target yield (2 Mg ha^{-1} for Post Farm and 1 Mg ha^{-1} for CARC), available soil nitrate-N from soil test results, nitrogen mineralization from the previous year’s leguminous residues where present (28 kg ha^{-1} if harvested for grain; 56 kg ha^{-1} if used as a manure; modified from McCauley et al., 2012), straw immobilization where previous crop was barley (45 kg ha^{-1}), and N mineralization from soil organic matter over winter (assuming 2% soil organic matter (SOM) is recalcitrant and each percent SOM above 2% provides 22 kg ha^{-1}) based on previous soil test results. Urea fertilizer was applied by subsurface banding just prior to sowing at CARC and by a surface broadcast application prior to sowing at Post Farm.

Sowing dates were as follows: the no-till disc opener trial was seeded on 20 April 2016, 11 May 2017, and 16 May 2018; the no-till hoe opener trial was seeded on 21 April 2016, 11 May 2017, and 15 May 2018; the tilled disc opener trial was seeded on 21 April 2016, 4 May 2017, and 4 May 2018. Additionally, two plots in the no-till disc opener trial were replanted on 13 June 2018 due to a sprayer error, 401 and 402, and one plot in the no-till hoe opener trial, 101.

Agronomic and Soil Data

Three soil cores per plot were extracted each spring prior to sowing crops or implementing fallow practices and in 2018 following harvest. In 2016 and 2017, two soil cores per plot were extracted after crops had been harvested. Sampling immediately prior to planting provided a snapshot of the nematode community present for plant colonization, while sampling after harvest indicated succession within the community after plant colonization. The first set of cores during a sampling period were used to determine gravimetric and volumetric soil moisture to standardize nematode counts on a dry soil basis, while the second set of cores were used for nematode extraction and faunal analysis. When taken, the third set of soil cores were used for soil chemical analysis. Each soil core was put in a polypropylene-lined tin-tie soil bag (i.e. ‘coffee’ bag) and placed inside a cooler immediately after sampling for transport. Samples were refrigerated at 4^{o} C until processing.

Soil chemical analysis was performed by Agvise Laboratories in Northwood, ND, according to prescribed laboratory methods for soil nitrate (0-15cm and 15-30cm) and soil organic matter (Combs and Nathan, 2011; Gelderman and Beegle, 20111).

Grain from barley and pea from the middle 1.2-m at the Post Farm and 1.5-m at the CARC in each plot was collected using a small-plot combine for yield. After harvest, grain was cleaned of detritus, weighed, and grain moisture determined using a Dickey-John® Grain Analysis Computer (GAC®) 2500 (Dickey-John Corporation, 5200 Dickey John Rd, Auburn, IL 62615). Yield was calculated using grain clean weights and reported on a 14% moisture basis.

Soil Nematode Analysis

Soil extractions of approximately 25 g of fresh soil were performed using the Baermann funnel technique (Figure 4.2, Flegg and Hooper, 1970). Extractions ran for 72 hr after which water suspension samples of at least 15 mL were collected. Nematodes were counted and identified on a nematode counting slide (Chalex Corp.) using a Motic® AE2000 inverted microscope with phase contrast (Motic® North America). Nematode density was adjusted to total individuals per 100 g on a dry soil basis. Nematodes were assigned to a trophic group, a cp value, and a functional guild. Community structure was assessed using trophic group and cp value information followed by calculation of ecological indices. Metabolic footprints were computed for components of the nematode community as described by Ferris (2010) and were facilitated using the Nematode INdicator Joint Analysis (NINJA) 2.0 (http://ninjanemaplex.ucdavis.edu/main/) R Shiny application developed by Sieriebriennikov et al. (2014).

Statistical Analysis

Data were subjected to analysis of variance (ANOVA) for a randomized block split-split plot design using the lmer function in the lme4 mixed-effects model package in the R software environment (Bates et al., 2015), where cropping system was the whole plot, year was treated as the subplot, and sample timing was the sub-sub plot. Year and sample timing were sub and sub-sub plots because measurements were taken on the same plot over years and sample timing. Thus, they are repeated measures. Block was a random effect, and all other factors were considered fixed. Each field experiment was analyzed separately. The analysis was then combined across the two CARC trials to assess if the CARC field experiments showed similar results for nematode community responses. The no-till disc drill and the no-till hoe drill trials at the CARC location gave similar results in terms of mean values. So, the two trials at CARC were considered as one environment and the Post Farm a second environment for further analysis. This was achieved by using the location instead of the trial as a model term.

The baseline data from the pre-plant sampling in 2016 were subjected to ANOVA to assess any inherent differences across the field trials. Sample timing was assessed by subtracting pre-plant from post-harvest data in a given year. These data were analyzed as described above except the timing factor was deleted from the model. Following these analyses, the difference between the pre-plant baseline sampling in 2016 and the endpoint sampling in 2018 was analyzed to assess how the cropping systems had changed the nematode community over the course of the three years. These data were analyzed as a randomized complete block design. Pearson's product-moment correlations were obtained for total soil nitrate in the 30 cm profile at each location utilizing all data where soil test results were present (n = 112 at Post Farm and n = 223 at CARC (missing datum from post-harvest 2016 sampling for barley-fallow)) and the correlation between barley grain yield and nematode community structure at each location utilizing all post-harvest data (n = 48 at Post Farm and n = 96 at CARC) with the cor.test function in base R.

Linear contrasts were conducted between the continuous barley and the barley-pea systems using the emmeans package (Lenth, 2017) to compare differences among cropping system means where a significant *F* ratio was obtained. Where the assumptions of normality and homoscedasticity were not met, data were transformed using ln(x+1) prior to analysis. Back-transformed data means are reported. Differences among treatment means were assessed using a protected LSD post-hoc at an $\alpha<0.05$. Where interaction of terms occurred, differences were assessed using the predictmeans package in R (Luo et al., 2018).

Results

Nematode Communities at Each Location

The two CARC field experiments were similar in their results for barley and pea grain yield, soil properties, and nematode community composition and structure (data not presented), and so are presented as one location. The CARC and Post Farm varied in a number of environmental parameters (e.g., precipitation) as well as management (i.e., no-till seedbed at the CARC and tilled seedbed at the Post Farm). Supplemental Tables S4.1 to S4.3 report nematode count averages by system per sample timing and year by trial.

There was a shift from a fungivore dominated community in 2016 to a bacterivore dominated community by 2018 at the Post Farm (Table 4.1). Fungivores comprised 75% of the non-herbivorous community prior to planting during 2016, but only 29% by the final sampling in fall 2018. Conversely, bacterivores rose from 24% to 70% during the same time period. Total nematode population also fluctuated annually, with populations peaking at 773 individuals per 100 g dry soil in 2017 and low populations both in 2016 and 2018 (326 and 275 individuals per 100 g dry soil, respectively). Changes observed at the Post Farm may be due to the influence of more consistent tillage during the study than previously seen on the field than due to climatic and moisture variations.

Abundance of every functional guild declined during 2017 at the CARC relative to 2016 (Table 4.2), probably due to the lack of soil moisture in the former year (Fig. 4.1). Total population was 1179 individuals per 100 g dry soil during 2016, but only 657 individuals per 100 g dry soil the following year. This declining trend continued with only 416 individuals per 100 g dry soil by 2018, though differences in numbers between 2017 and 2018 were not detected. However, the percentage of cp 4 nematodes, largely comprised of omnivores, increased by late summer in 2017. The composition of the herbivore community also shifted more towards ectoparasitic nematodes (largely comprised of *Tylenchorhynchus* sp. and *Xiphinema* sp.), increasing from 34% at planting to 53% post-harvest in 2017. Even with the decrease in abundance, the Structure Index at CARC increased from 40 in 2016 to 57 in 2018. There was also a decrease in the percent abundance of *Tylenchus* sp. (from 32% to 24%). This, coupled with the increase in percent omnivores and Structure Index, suggests that the drought at CARC had a detrimental impact on lower cp value bacterivores and herbivores.

Agronomic data

Barley grain yields were not different across cropping systems at either location. Yields were higher at Post Farm due to higher yield potential, with an average grain yield of 4.0 Mg ha^{-1} across all three years, while CARC barley yields averaged 1.0 Mg ha^{-1} across all three years. Pea grain yields were different across years at each location. At CARC, pea yields were highest in 2016 (0.9 Mg ha^{-1}) followed by significant declines in 2017 and 2018 (averaging 0.5 Mg ha^{-1} in both years). At Post Farm, pea yields were highest in 2016 (2.5 Mg ha^{-1}) and 2018 (2.6 Mg ha^{-1}), with a decrease in yield in 2017 (1.9 Mg ha^{-1}). These variations are coincidental with the 2017 drought and, in the case of CARC during 2018 were a function of later planting (15 and 16 May 2018, the latest of the study) and below average precipitation during July and August.

By Cropping System

Post-harvest nematode populations tended to be higher under barley-pea manure and continuous barley compared to barley-fallow (Fig. 4.3). Total herbivores averaged across all three years and both sample timings were highest under barley-pea manure and continuous barley (130 and 114 individuals per 100 g dry soil, respectively) and reduced under barley-pea grain (67 individuals per 100 g dry soil) (Fig. 4.4).While both barley-pea manure and continuous barley systems had similar numbers of nematodes (Figs. 4.3 and 4.4), the composition of the herbivore community under each system varied (as was highlighted in Table 4.3), as did the way the nematode communities changed over time. For example, total population and semi-endoparasitic nematodes changed by cropping system during the growing season when averaged across locations (Table 4.3). Barley-fallow was less resilient to change than barley-pea manure, as evidenced by the greater change in total population under barley-fallow. Total herbivores decreased the most under continuous barley (-561 individuals per 100 g dry soil), with almost half of that *Tylenchus* spp. By comparison, total herbivores decreased by fewer than 260 individuals per 100 g dry soil under barley pea manure. *Eudorylaimus* spp. increased the most under the barley-pea grain system and the least under barley-pea manure. A higher percentage of cp 5 nematodes was observed under continuous barley than under barley-fallow, while both barley-pea systems were intermediate. This suggests a more amenable soil environment to cp 5 herbivores (such as *Xiphinema* spp.) under continuous barley than under barley-fallow systems.

Correlations of Nematode Data with Soils and Agronomic Data

Soil nitrate had relatively weak relationships with nematode parameters. The highest correlation at CARC was 0.36 ($p<0.001$, for the percentage of herbivores in the population, and 0.49 ($p<0.001$) for the percentage of fungivores in the non-herbivorous population at Post Farm. Similarly, barley grain yield correlations with nematode community parameters at Post Farm were relatively weak, with a correlation of 0.39 with the percentage of herbivores in the population ($p=0.003$). Barley grain yield at CARC had much higher correlation coefficients to nematode community structure. The total population and the total herbivore population both had positive correlations > 0.6, while herbivore footprint, fungivore footprint, total cp 2-5 nematodes, and total non-herbivorous nematodes all had correlations > 0.4. Conversely, the percentage of cp 4 nematodes, percent omnivores, and percent ectoparasites were negatively correlated to barley grain yield, with a weaker relationship ($r \leq |0.46|$). The correlations indicate that barley grain yield increased as did the percentage of herbivores in the nematode community at the Post Farm, while yield depression occurred as bacterivores comprised a greater percentage of the community. Similarly, barley yield increased as did the nematode population, including herbivores, though the composition of the herbivore component was important. For example, ectoparasitic nematodes, which included economically important PPNs, were associated with decreased yield at CARC.

Discussion

Research suggests that soil nematode communities can be indicators of soil health. However, few studies have assessed soil nematode community structure under agricultural systems in semi-arid regions such as the Northern Great Plains. We observed differences in nematode communities across time and cropping systems. The Post Farm location was characterized by a shift in dominant decomposer channels, from fungivorous nematodes to bacterivorous nematodes. The CARC location was characterized mostly by reductions in abundance and changes in composition due to soil moisture stress in 2017. The cropping systems themselves show that barley-pea manure is sustaining similarly high populations of herbivores to continuous barley. However, the composition of the herbivore community is different in those two systems; while herbivores are high in the barley-pea manure, the system is sustaining mostly non-economically important moss/lichen/algal feeding nematodes in the genus *Tylenchus*.

Differences in location

The community shift at the Post Farm from fungivores to bacterivores may be linked to the field history and its management. For the three years prior to the study, the field lay fallow and largely neglected, receiving one tillage operation each fall. This neglected fallow may have defined the nematode community prior to the establishment of the field experiment. We speculate that the more frequent tillage operations may have fundamentally shifted the soil biological community. The Post Farm tended to have larger changes in nematode composition rather than abundance. It is possible the community structure was less stable since tillage can have a stronger influence over nematode community structure than cultural practices like cropping system (Ito et al., 2015).

Prior field management was more stable at the CARC than the Post Farm. No-till, continuous cropping had been in place for several years prior to establishment of the field experiments at the CARC. No differences were observed between the experiments at the CARC and a 3-year cropping system study is likely too short to see any significant changes from the relatively stable and resilient nematode community already in place. In fact, the largest effect we observed at CARC over the three years was due to the persistent dry conditions that developed during 2017. The cp value nematodes, omnivores specifically, seemed to be more resilient than lower cp, basal indicating nematodes during and following with moisture deficit (Table 4.2). This speculation is supported by Landesman et al. (2011) who found that the family Qudsianematidae, which includes the omnivore genera detected in the present study, along with the family Cephalobidae, were the least sensitive to low soil moisture stress in a precipitation exclusion experiment Yan et al. (2018) noted that some genera of PPNs were less susceptible to drought than others, some of which overlap with genera observed at the CARC site. The changes observed at the CARC in Structure Index are also corroborated by Bakonyi et al. (2007). Their findings from an experiment on semiarid shrubland suggest that as soil dries and warms, a more structured community arises, increasing from an average of about 66 in their control, to about 74 in their dried soil treatment and 73 in the warmed soil treatment.

Variation due to cropping system

Differences among the cropping systems suggest that the barley-pea manure may sustain or increase the beneficial nematode population compared with barley-fallow. However, these increases also were observed in the herbivore component. A significant positive relationship between barley grain yield and total population and total herbivores at CARC, suggests that cropping systems with a higher nematode population may be inherently better suited for crop production than one with a low population. There was less of a reduction in the nematode community under barley-peas than barley-fallow, suggesting that inserting peas in barley-based cropping systems can maintain more nematodes, or at least sustain them longer under durations of high stress, such as periods of low moisture. Barley-pea systems also sustained more algal/lichen/moss feeding herbivores such as *Tylenchus* sp. and *Psilenchus* sp. and not more economically damaging PPNs such as *Pratylenchus* sp.

Most studies looking at nematode communities and crop yield have focused on control of herbivorous nematodes, but few have seen positive correlations between yield and herbivorous nematodes. Burkhardt et al. (in press) determined that a perennial legacy in dryland wheat-based systems led to higher cp value nematodes, including herbivores. Conversely, Zhang et al., 2017 determined that biofertilizers (derived from manure compost and inoculated with certain bacterial strains) in sugarcane production significantly increased the abundance of free-living nematodes while decreasing the abundance of PPNs. Other studies have looked at community structure due to the utilization of cover crops, indicating increased soil community structure and crop yield in cropping systems using cover crops (Wang et al., 2011; Leslie et al. 2017). We speculate that the incorporation of peas may lead to a more structured community, but our present study is too short to make these associations.

Conclusions

This study provides evidence further supporting the adoption of pulse crops into dryland barley systems. The few differences we observed in the cropping systems hint at longer-term changes in the nematode community. Cropping systems studies in semi-arid regions can often take several years before differences in soil properties are observed. That makes the few differences we did observe quite interesting. To be able to show in only three years at two geographically removed sites the same short-term changes occurring in the nematode community adds to our knowledge of the effect which crop rotations are having on soil health. By simply incorporating peas into a rotation with barley, we were able to mitigate the effects of drought on the nematode population without increasing abundance of economically important PPNs, and at least in the case of the barley-pea grain system, increase the abundance of omnivores. Moreover, while plant-water stress had significant negative impacts on the nematode community at CARC, it did significantly increase our Structure Index through the survival of more cp 4 omnivores on average. The differential response to environmental stresses of certain components of the nematode community would seem to be an important, if little studied, subject area.

Tables and Figures

Table 4.1: Mean values for fungivores and bacterivores averaged over four cropping systems for pre-plant and post-harvest for three years. The nematode community at Post Farm shifted from fungivore dominated in spring 2016 to bacterivore dominated in fall 2018.

Year (timing)	Fung‡	Bact
	--------------%-------------	
Post Farm		
2016 (pre)	75 a†	24 c
2016 (post)	41 b	60 b
2017 (pre)	45 b	53 b
2017 (post)	49 b	50 b
2018 (pre)	43 b	54 b
2018 (post)	29 c	70 a
CARC		
2016 (pre)	37	51
2016 (post)	42	52
2017 (pre)	40	37
2017 (post)	32	36
2018 (pre)	46	35
2018 (post)	43	30
	F ratio	
Year*timing	3.59 *	4.60 *

*Significant at $p<0.05$.

**Significant at $p<0.01$.

***Significant at $p<0.001$.

†Letters indicate significant differences by year and timing.

‡Fung = Fungivore, Bact= Bacterivore.

Table 4.2: Mean values for total population, Structure Index, and the composition of free-living cp 4 nematodes, ectoparasitic herbivores, and *Tylenchus* spp. averaged over four cropping systems. Drought significantly impacted responses at the CARC, causing nematode abundance to decrease, but some of the compositional percentages to increases, specifically ectoparasitic nematodes and omnivorous nematodes. These compositional changes were enough to increase the Structure Index over that same time period.

Location	Year (Timing)	Total population†	Structure Index	Free-living cp 4†	Herbivore composition	
					Ecto-parasites	*Tylenchus* spp. (cp 2)
		individuals per 100 g dry soil		--------------------%--------------------		
CARC	2016	1179 a	40 b	8 b	27 c	32 a
	2017	657 b	65 a	22 a	44 b	24 b
	2018	416 b	57 a	19 a	52 a	25 ab
Post Farm	2016	326 b	4	1	15	60
	2017	773 a	9	1	28	44
	2018	275 b	11	2	32	33
CARC	2016 (pre)	1177	35	10 d	26 b	29
	2016 (post)	1181	45	6 e	28 b	35
	2017 (pre)	859	61	18 bc	34 b	23
	2017 (post)	455	69	27 a	53 a	25
	2018 (pre)	461	54	16 c	51 a	20
	2018 (post)	371	61	23 ab	54 a	31

Post Farm	2016 (pre)	244	4	1	1	72
	2016 (post)	436	3	1	31	46
	2017 (pre)	896	10	1	29	34
	2017 (post)	667	9	2	26	53
	2018 (pre)	145	16	3	33	25
	2018 (post)	523	6	1	32	42
		F ratio				
	Year	11.49 ***	3.77 *	10.58 ***	8.05 ***	3.42 *
	Year*timing	0.28	0.78	5.94 **	3.18 *	0.12

*Significant at $p<0.05$.

**Significant at $p<0.01$.

***Significant at $p<0.001$.

†Back-transformed from $\ln(x+1)$

Table 4.3: Difference between pre-plant and post-harvest averaged over 3 yr and the difference between pre-plant 2016 and post-harvest 2018. Total population was reduced the least under barley-pea manure each season and the reduced the most under barley-fallow. Semi-endoparasites were reduced the most under continuous barley while they were increased on average under both barley-fallow and barley-pea grain. Total herbivores were reduced the least in the barley-pea systems and reduced the most in the continuous barley. *Tylenchus* spp. were the herbivores reduced the most in the continuous barley system. Among free-living nematodes, *Eudorylaimus* spp. were increased the most in the barley-pea grain system and the least in the barley-pea manure system.

Cropping System	Mean change over growing season		Difference between 2016 to 2018			
	Total pop.	Semi-endoparasites	Total Herbivores	*Tylenchus* sp. (Pp 2)	*Eudorylaimus* sp. (Om 4)	cp 5 herbivores
	individuals per 100 g dry soil	%	individuals per 100 g dry soil			%
BF‡	-217 b	1 a	-450 ab	-169 ab	7 ab†	0.5 b
BPG	-184 ab	1 ab	-343 ab	-84 ab	10 a	1.3 ab
BPM	-77 a	-1 bc	-257 a	-37 a	2 b	1.2 ab
CB	-178 ab	-3 c	-561 b	-234 b	3 ab	3.3 a
	F ratio					
cropping system	3.91 *	3.02 *	3.03 *	4.81 **	5 **	3.93 *
one df contrast	*t* ratio					
CB vs BPx	-0.13	1.82	-1.65	-2.19 *	-0.85	1.44

*Significant at p <0.05.

**Significant at p <0.01.

***Significant at p <0.001.

†Letters indicate significant differences among cropping systems, and among cropping systems at a specific location.

‡BF = Barley Fallow, CB = Continuous Barley, BPG = Barley-Pea Grain, BPM = Barley-Pea Manure, BPx = Barley-Peas

§Om = omnivore, Pp = herbivore

Table 4.4: Pearson's product-moment correlations for total soil nitrate (data from spring of each year and post-harvest 2018) and yield (post-harvest data from each year). The highest r estimates came from CARC for yield, showing where nematode populations were highest, yield was also high. At Post Farm, an opposite response was observed for fungivores and bacterivores from total soil nitrate. Where nitrate was highest, so too were fungivores, whereas bacterivores were reduced.

Response		Soil NO_3‡		Yield	
		Post Farm	CARC	Post Farm	CARC
Total Population		-0.14	0.13	0.10	0.62 ***
Total Free-living		-0.14	-0.06	-0.04	0.45 ***
Total cp 2-5		-0.15	-0.06	-0.01	0.47 ***
Total Herbivores		-0.11	0.25 ***	0.26 *	0.63 ***
Structure Index		-0.21 *	-0.18 **	-0.02	-0.37 ***
Herbivore Footprint		-0.07	0.21 **	0.19	0.53 ***
Fungivore Footprint		0.00	-0.01	-0.03	0.50 ***
% Total pop.	Herbivores	0.21 *	0.36 ***	0.39 **	0.27 **
	Fungivores	0.38 ***	-0.26 ***	-0.02	-0.10
	Bacterivores	-0.47 ***	-0.16 *	-0.36 **	0.18
	Omnivores	-0.19 *	-0.16 *	-0.01	-0.42 ***
% Free-living pop.	Fungivores	0.49 ***	-0.07	0.17	0.09
	Bacterivores	-0.47 ***	0.11	-0.15	0.37 ***
	Omnivores	-0.18	-0.04	0.07	-0.39 ***
	cp 2	0.07	0.13	0.15	0.31 **
	cp 3	-0.08	-0.23 ***	-0.07	0.17
	cp 4	-0.18	-0.05	0.07	-0.42 ***
Migratory Endoparasites		-0.05	0.06	0.10	0.36 ***
Ectoparasites		-0.36 ***	-0.05	-0.02	-0.46 ***
Algal/Lichen/Moss Feeders		0.39 ***	0.08	-0.03	0.16
	n	112	223	48	96

*Significant at p <0.05.

**Significant at p <0.01.

***Significant at p <0.001.

†Simpson's Reciprocal Diversity Index

‡Soil nitrate was transformed using $\ln(NO_3 + 1)$ to meet assumptions.

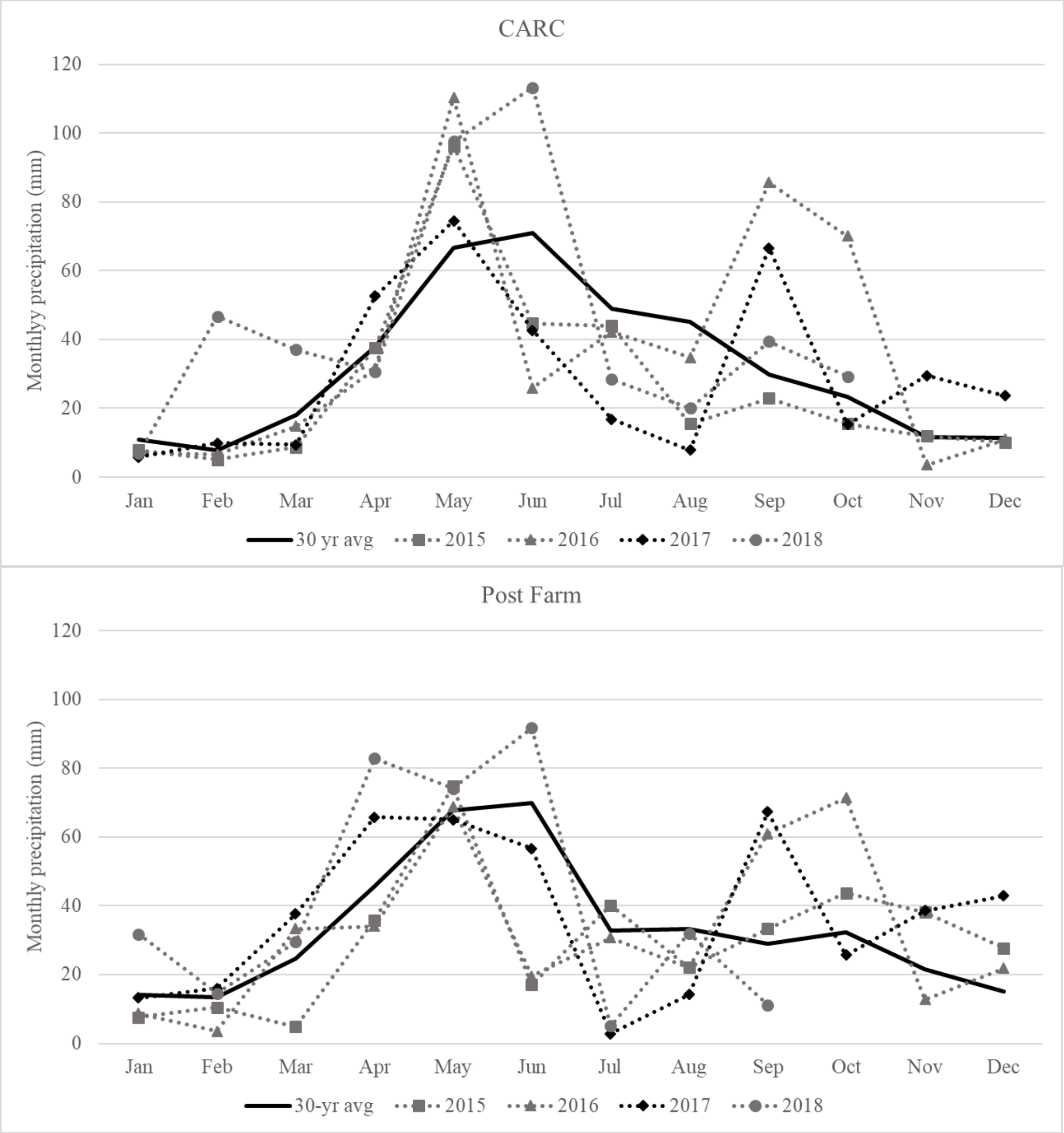

Figure 4.1: Weather data for the two locations. Post Farm had below average precipitation during the 2016 growing season (April-September). CARC had below average precipitation in 2017.

Figure 4.2: Photograph illustrating the Baermann funnel setup.

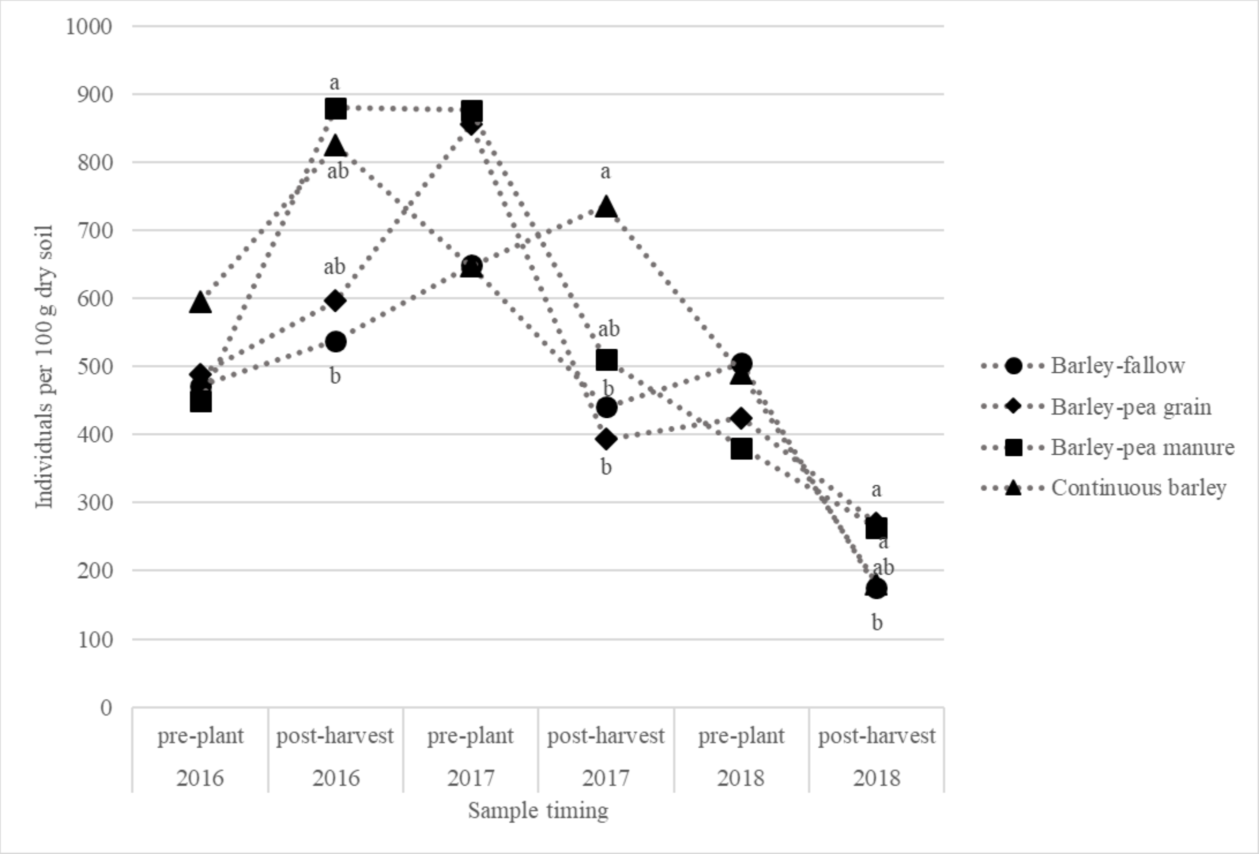

Figure 4.3: Total nematode population for cropping systems by year and sample timing. Letters indicate significant differences among cropping systems at the corresponding sample timing.

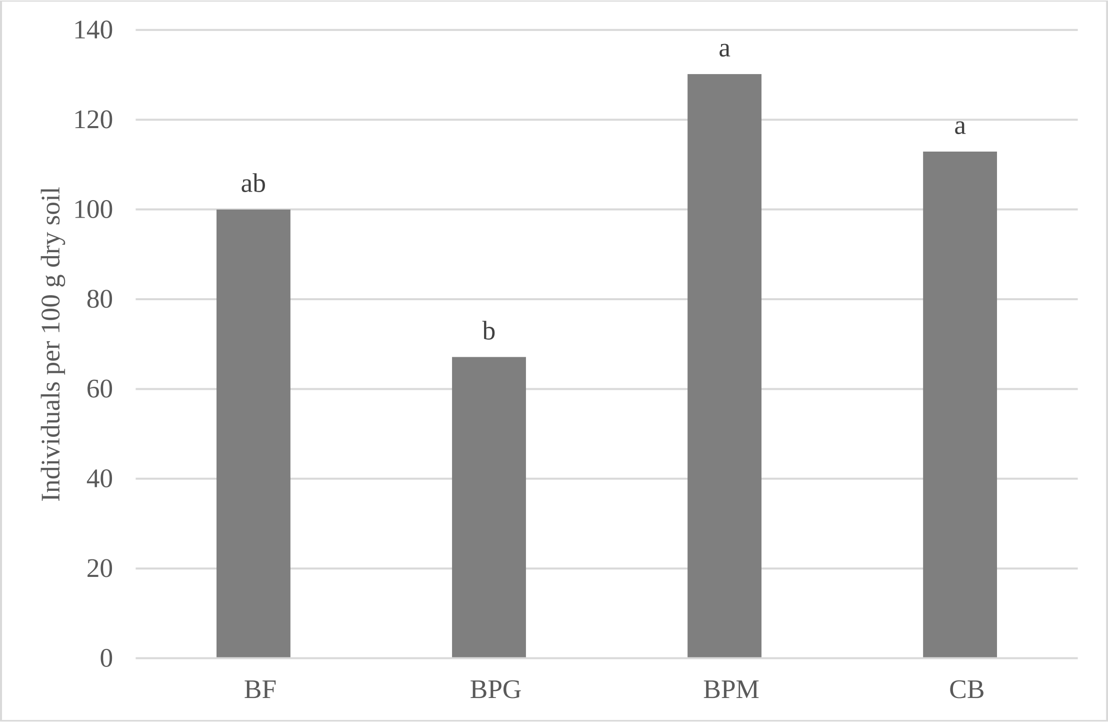

Figure 4.4: Total herbivores averaged over all three years and both sample timings. Barley-pea manure and continuous barley had significantly higher herbivore populations than barley-pea grain.

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