Applied Soil Ecology 170 (2022) 104263

Contents lists available at ScienceDirect

Applied Soil Ecology

journal homepage: www.elsevier.com/locate/apsoil

Ecological maturity and stability of nematode communities in response to precipitation manipulations in grasslands

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ARTICLE INFO

Keywords:
Drought
Indicator taxa
Soil fauna
Nematode indices
Climate change

ABSTRACT

Climate change is predicted to cause alterations in precipitation patterns in grasslands around the globe. The implications of these changes for soil biota and multiple key ecosystem functions that they regulate in grasslands is little known. We used soil nematodes as biological indicators in grassland ecosystems experiencing large shifts in precipitation in an arid, semiarid, and mesic grasslands. By calculating the nematode plant parasite index, maturity index, and its extensions: the enrichment, basal, channel, and structure index, we assessed grassland ecosystem response to five levels of manipulated precipitation over the course of two years. Nematode community structure described by these indices was sensitive enough to reflect community changes from the altered precipitation treatments and responded uniquely at each of the three sites. With increasing precipitation, nematode communities at the arid site became more enriched in species and switched to a more fungal-dominated decomposition pathway. The semiarid site showed a decline in nematode maturity, structure, and fungally dominated decomposition, but greater levels of enrichment, basal resources, and herbivory. In the mesic site increasing precipitation led to a nematode community with greater maturity and structure and shifted toward a fungal decomposition channel that also reflected a lower level of enrichment and plant parasites. We performed an indicator analysis to identify nematode genera representative of each grassland site and precipitation level. Nematode indicator composition was found to be significantly affected by the levels of applied precipitation and across sites, highlighting specific genera that may be affected by future precipitation regimes such as *Eucephalobus* in the arid site or *Trichodorus* from the mesic site. Nematode community analysis allowed for the detection of strong influences on the soil food web caused from extreme and moderate precipitation manipulations. This finding stresses the need for more genera level studies to be done to reflect specific ecosystem responses to climate change as well as the need for more cross site studies as site-specific differences must be accounted for ecological interpretations.

1. Introduction

Covering over a third of the Earth's land surface, grasslands have great economic and ecological value by supporting multiple ecosystem services such as providing food and forage and supporting biodiversity (Gibson and Newman, 2019; Wilsey, 2018). Grasslands, much like the

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https://doi.org/10.1016/j.apsoil.2021.104263
Received 23 March 2021; Received in revised form 11 September 2021; Accepted 6 October 2021
Available online 13 October 2021

rest of the planet, will experience changes in temperature and precipitation regimes due to increases in anthropogenic greenhouse gas emissions (Bradford et al., 2020). Climate models predict large shifts in precipitation patterns in the western United States, leading to an increased frequency of drought and intensity of rainfall events to the grasslands of the Great Plains (IPCC, 2013; Paschalis et al., 2020). Alterations in precipitation drive changes in both above and belowground communities. While increased received precipitation have positive effects especially in arid and semiarid environments by stimulating fine root growth (Zhang et al., 2019) or increasing microbial biomass (Zhang et al., 2013). In addition increased precipitation can negatively impact some soil properties by leading to more leaching and erosion (Austin and Vitousek, 1998). Thus for mesic sites an increase in precipitation may be stressful to soil communities, especially higher trophic groups that are sensitive to change (Bongers, 1990; Franco et al., 2017). While the response of vegetation to altered precipitation has been well documented (Fay et al., 2003; Felton et al., 2020; Heisler-White et al., 2008; Jentsch et al., 2011; Notaro et al., 2010), there has been less focus on effects on soil organisms. Soils are an essential component of grasslands and home to a wide range of belowground organisms that regulate multiple ecological functions such as decomposition, nutrient cycling, C sequestration, and disease suppression (Bach et al., 2020; Bender et al., 2016; Wall et al., 2015). When considering global change impacts on soil fauna communities, more emphasis has been on changes in temperature (Thakur et al., 2017) and nutrient gradients (Shaw et al., 2019; Yeates and Newton, 2009) than to alterations in precipitation. While there are some studies that focus on examining the effects of varied precipitation on soil nematodes most have primarily been based on a single field site (Darby et al., 2011; Landesman et al., 2011; Siebert et al., 2019), and thus cannot capture the potential variability of response across different ecosystems and those that do consider multiple sites (Sylvain et al., 2014) lack genera level data.

Soil nematodes, in particular, are known to influence multiple soil functions and have proven extremely useful as indicators of environmental response to stress and disturbance (Neher, 2001). Not only are soil nematodes one of the most diverse and abundant groups of soil organisms (Bardgett et al., 1999; van den Hoogen et al., 2019), they are a critical component of the soil environment, occupying multiple trophic levels and directly affecting primary production, nutrient cycling, decomposition, and influencing the turnover and activity of microbial populations (Cole et al., 2004; Freckman and Baldwin, 1990; Griffiths, 1994). Soil nematodes also span a wide range of life history strategies that allow for unique responses to stress and disturbance (Bongers and Ferris, 1999; Ney et al., 2019; Pattison et al., 2005; Yeates et al., 1993). Based on these characteristics and their vital role in multiple ecosystem processes, nematodes are an ideal model taxon for understanding how changes in precipitation can affect trophic complexity and energy or carbon pathways of soil communities as grasslands under climate change.

Ecological indices based on life history strategy and obligate feeding habits of different nematode genera can provide an assessment of how nematode community structure and function changes with environmental disturbances, and thus can offer valuable insight for understanding grassland ecosystem response to altered precipitation regimes (Bongers, 1990; Ferris et al., 2001). The maturity index (MI) has been utilized to show where the free living nematode community is positioned in ecological succession (Bongers, 1990) while the plant-parasite index (PPI) expresses the same ecological interpretation for plant parasites (Bongers and Bongers, 1998). Extensions of the MI; the enrichment (EI), basal (BI), structure (SI), and channel index (CI), indicate the complexity of the nematode soil food web as well as the main decomposition channel (Ferris et al., 2001). The high sensitivity of nematode communities that these indices provide can show a detailed status of the structure and function of soil food webs in response to altered precipitation (Landesman et al., 2011). Employing these indices across distinct grasslands experiencing manipulated droughts and increases in rainfall would provide valuable insight into the status of the soil food web as well as specific details of the nematode community.

With the present work, we tested the sensitivity of nematode ecological communities to climate change in three different grassland ecosystems experiencing five levels of manipulated precipitation. Our first hypothesis was that increased precipitation would result in a more mature and structured community that reflects a less enriched environment as indicated by increases in the MI, SI, and a decrease in PPI, BI, and EI. The rationale for our first hypothesis follows the finding of increased predator and omnivorous nematode abundances corresponding with increasing precipitation (Franco et al., 2019), which reflects a community composed of higher trophic groups with improved food web linkages, and thus a more resistant nematode community. Second, we hypothesized that greater precipitation would favor a fungal decomposition pathway. This is based on recent research suggesting bacteria abundance and diversity to be less responsive to water additions than fungi (Ochoa-Hueso et al., 2018). Third, we hypothesized that these changes in the nematode community would be more pronounced in the semiarid and mesic sites, compared to the arid site. The third hypothesis follows the findings of previous studies where short-lived changes to water availability in deserts had weak or no effect on nematode abundance and body traits (Andriuzzi et al., 2020; Freckman and Virginia, 1989; Sylvain et al., 2014; Vandegehuchte et al., 2015). Finally, we investigated the potential of individual nematode genera to be used as indicators of changes to precipitation that would complement the community indices mentioned above and provide more specific info about which taxa are driving the nematode community response.

2. Material and methods

2.1. Research sites

This experiment was conducted in three distinct North American grasslands: a desert grassland (Jornada Basin; JRN), a semiarid shortgrass steppe (Semiarid Grasslands Research Center; SGRC), and a mesic tallgrass prairie (Konza Prairie; KNZ). JRN is a long-term Ecological Research site (LTER) located in Southern New Mexico, with vegetation dominated by the perennial grass *Bouteloua eriopoda* (Havstad and Schlesinger, 2006). SGRC is located in northern Colorado, with the warm season perennial grass *Bouteloua gracilis* as the dominant cover (Lauenroth and Burke, 2008). KNZ is an LTER in eastern Kansas, with *Andropogon gerardii*, *Sorghastrum nutans*, and *Schizachyrium scoparium* as the dominant vegetation species (Knapp, 1998). Each grassland has distinct soil types, mean annual precipitation (MAP) and other climatic characteristics (Table 1).

2.2. Experimental design

In order to simulate altered precipitation conditions, we used automated rainfall manipulation systems consisting of rainout shelters paired with irrigation that allowed for reduction and increase of incoming rainfall at each site (Gherardi and Sala, 2013). Rainout shelters were constructed at each site in 2016 on relatively flat areas with vegetation representative of the site, and without cattle grazing. These shelters were maintained until 2017, thus allowing for the manipulations to occur for two growing seasons. Each year, the shelters were dismantled at the end of the growing season to avoid deterioration by snow and wind during the winter. The blocked incoming precipitation was stored in an accompanying tank that served as the source for water distribution via a solar-powered irrigation system (Gherardi and Sala, 2013). This design allowed for the implementation of five precipitation levels: extreme and moderate additions, extreme and moderate reductions, and a control (with no modifications to annual rainfall). Based on long-term historical precipitation extremes unique to each site, the first and 10th percentile of long-term precipitation for the rainfall reduction treatments and the 90th and 99th percentile of long-term

Table 1
Site characteristics for the Jornada Basin LTER, NM, Semiarid Grasslands Research Center, CO, and Konza Prairie LTER, KS. Mean annual precipitation and long-term mean for growing-season precipitation from NOAA climate data of nearby localities (Las Cruces [New Mexico], Nunn [Colorado], and Manhattan [Kansas]).

	Jornada Desert	Shortgrass Steppe	Konza Prairie
Grassland type	Arid	Semiarid	Mesic
Latitude	32°33′N	40°50′N	39°4′N
Longitude	106°49′W	104°45′W	96°34′W
Mean annual precipitation (mm)	245	321	835
Mean growing-season precipitation (mm)	105	204	428
Mean annual temperature (°C) a	14.7	8.4	12.5
Rainfall treatments (relative to ambient)			
Large reduction	−80%	−70%	−60%
Moderate reduction	−50%	−40%	−30%
Moderate addition	+50%	+40%	+30%
Large addition	+80%	+70%	+60%
Soil texture class	Fine sandy loam	Fine sandy loam	Silty clay loam
USDA soil type	Aridisols	Mollisols	Mollisols

Soil characteristics refer to the top 10 cm and are from the USDA Soil Survey.

precipitation for the rainfall addition treatments were distributed following the current manipulative experiment recommendations (Knapp et al., 2017). Thus, the reduction treatments relative to the control resulted in a reduction of 80 and 50% in the arid site, by 70 and 40% in the semiarid site, and 60 and 30% in the mesic site. The addition treatments added increases of 150 and 180%, 140 and 170%, and 130 and 160% in the three sites respectively (Table 1). The five treatments that received growing-season precipitation were randomly assigned to plots (5 × 2.5 m) with eight replications of each treatment resulting in 40 plots in total with the treatments being applied to the same plots during the growing seasons of 2016 and 2017. This research is one part of a larger experiment studying primary productivity, root herbivory, and soil nematode abundance and body size responses to precipitation (Andriuzzi et al., 2020; Ankrom et al., 2020; Franco et al., 2019).

2.3. Soil and nematode collection

Using a 2.5 cm diameter soil corer, four sub-samples were taken to a depth of 10 cm directly beneath the dominant vegetation of each plot at the end of the 2016 and 2017 growing seasons starting with the semiarid site, then the mesic, and finally the arid site, to be consistent with the rainfall patterns per site. The sub-samples were combined to form one composite sample for each plot within a site. To avoid cross-contamination, the soil corer was cleaned with 70% ethanol between plots. The soil samples were transported in coolers to Colorado State University for storage at 4 °C. Nematodes were extracted from soils within 5 days of arrival. Nematode abundances were calculated as the number of individuals per kg of dry soil; soil moisture was calculated by drying 50 g of soil for each sample at 105 °C for 48 h.

2.4. Nematode extraction and identification

Nematode extraction was conducted with the Baermann method, using approximately 100 g of soil per sample (Hooper, 1970). Solution samples (20 ml) were collected daily for 72 h and stored at 4 °C (total of 60 ml nematode solution per plot). Before counting and identification, the nematode solution was allowed to settle for 30 min so any nematodes would collect at the bottom, and excess water was vacuumed off until the remaining 5 ml of solution could be poured into lined counting dishes to be viewed with an inverted microscope (Olympus CKX41) at 200× magnification. The whole dish of nematode taxa was counted and identified to trophic groups (Yeates et al., 1993). For identification to genus, nematode solutions were preserved in 5% formalin (Southey, 1986). Total nematode population density was determined and the first 100 plant parasites and first 150 free living nematodes encountered were identified to genus and then adjusted to the absolute abundance per kg by adding up totals from each nematode genus identified.

The nematodes were classified according to their colonizer-persister (cp) scale to analyze community indices (Bongers, 1990). Life strategies are often categorized by a cp scale that ranges from 1 to 5, where nematodes deemed a '1' represent opportunists that recover quickly when stressed and reproduce rapidly, while those designated as a '5' are, broadly speaking, K-strategists that are intolerant to stress and have longer generation times (Ferris et al., 2001). Nematode genera were assigned to feeding groups based on Yeates et al. (1993).

Nematode genera data was then utilized to calculate the MI (Bongers, 1990), PPI (Bongers et al., 1997) as well as the EI, BI, SI, and CI (Ferris et al., 2001). The value of the MI denotes the disturbance level experienced by the environment; with a low value expressing a highly disturbed system (Bongers, 1990; Neher and Campbell, 1996). Plant parasite index is similar to the MI, but only considers nematodes feeding on higher plant forms. The EI reveals the flow of basal resources (i.e. carbon, nitrogen); wherein a high EI would indicate a large proportion on opportunistic bacterivores and fungivores which respond rapidly to increases in available resources. The BI measures the bacteria- and fungal-feeding nematodes in the cp grouping, thus a high value indicates poor ecosystem health. The SI denotes the food web complexity; where a high SI demonstrates a complex food web with greater representation of long-lived omnivores and predators, reflecting greater stability in the community as well as a more restored system. The CI expresses whether the decomposition pathway is dominated by bacteria (low CI) or fungi (high CI) (Ferris et al., 2001).

2.5. Statistical analysis

The effects of altered precipitation on nematode communities were determined by testing received growing-season precipitation, site, and their interaction on nematode ecological indices. The model did not include year as a factor as the variability in precipitation between the two experimental years and five rainfall manipulation treatments were combined to create ten levels of received precipitation to be used as continual explanatory variable without the distinction of years. Data were analyzed using linear mixed-effect models (LME) and plot identity was used as a random effect to account for repeated measurements in each plot, which justifies the lack of independence among years (Bates et al., 2015). All assumptions for homogeneity of variance and normality of residuals were met and visual inspection of predicted plots, Levene's test, QQ plots, Shapiro-Wilk test were done. Methods by Nakagawa and Schielzeth (2013) were used to determine the conditional r^2. These analyses were all conducted using R software, version 3.2.2 (R Core, 2014), with the following packages; "vegan"(Oksanen et al., 2019), "piecewiseSEM" (Bartoń, 2010), and package "ggplot2" was used for data visulization (Wickham, 2009). The effects of altered precipitation on nematode communities were determined by testing received growing-season precipitation, site, and their interaction on nematode ecological indices.

Indicator analysis was done using the "labdsv" package (Roberts, 2007) to identify genera that were characteristic of the three sites and the applied precipitation levels (Dufrêne and Legendre, 1997). This analysis calculates an indicator value for each genera, where "0" represents no indication and "1" represents the perfect indication of a habitat (site and applied precipitation level). The indicator value is based on the combination of abundance and relative frequency of occurrence of each genera (Dufrêne and Legendre, 1997). Nematode genera that were deemed indicators using this analysis (genera with a significant indicator value ≥0.3) were used in the Non-metric multidimensional scaling (NMDS) ordination using the Bray-Curtis distance coefficient and Permutational multivariate analysis of variance (PERMANOVA) analysis conducted in the "vegan" package (Oksanen et al., 2019) to determine dissimilarity among sites, precipitation treatments, and the nematode community. To better visualize the NMDS groupings the applied precipitation levels were grouped into "Reduction", "Control", and "Addition" categories.

3. Results

3.1. Precipitation effects on soil nematode ecological indices

Most nematode ecological metrics were significantly affected by changes in precipitation (Figs. 1 and 2). The MI was significantly influenced by both site and precipitation level as well as the interaction between the two ($P_{\text{Received precip.}} < 0.001$, $P_{Site} < 0.001$, $P_{\text{Interaction}} < 0.001$, $R^2 = 0.448$; Fig. 1A), such that MI increased with precipitation in the mesic site, but was negatively impacted by precipitation in the semiarid site and arid site. The opposite trend was found for the PPI ($P_{\text{Received precip.}} < 0.001$, $P_{Site} < 0.001$, $P_{\text{Interaction}} = 0.027$, $R^2 = 0.56.6$; Fig. 1B), where increased precipitation in the arid site resulted in a decrease in PPI, but increases in the semiarid and mesic sites. The EI varied with both site and precipitation ($P_{\text{Received precip.}} < 0.001$, $P_{Site} < 0.001$, $P_{\text{Interaction}} = 0.096$, $R^2 = 0.765$; Fig. 2A), generally decreasing in response to increased precipitation at the arid site and increasing at the semiarid site, with no effect of precipitation at the mesic site. The BI was significantly influenced by the interaction of received precipitation and site ($P_{\text{Received precip.}} < 0.001$, $P_{Site} < 0.001$, $P_{\text{Interaction}} < 0.001$, $R^2 = 0.384$; Fig. 1B), showing higher values with increased precipitation in the two drier sites, but lower values in the mesic site. The CI also responded to site and precipitation and displayed a significant interaction ($P_{\text{Received precip.}} = 0.002$, $P_{Site} < 0.001$, $P_{\text{Interaction}} = 0.001$, $R^2 = 0.687$; Fig. 1D), having values increase in both the arid and mesic sites in response to increasing precipitation, but decreased significantly in the semiarid site. The SI followed a similar trend to the MI, revealing an increase in the index only at the mesic site, but decreased in both the arid and semiarid sites with increasing precipitation ($P_{\text{Received precip.}} < 0.001$, $P_{Site} < 0.0001$, $P_{\text{Interaction}} < 0.001$, $R^2 = 0.310$; Fig. 1C).

The environmental gradient used in this study comprises three grassland types of large area cover (≈135 M ha combined) and represents the largest spatial scale in which belowground multitrophic responses to precipitation changes have been experimentally studied. It must be noted therefore that running the experiments over two years to produce a wide response surface (precipitation gradient) that increased statistical power may also have produced possible legacy effects (Supplementary Fig. S1). Further there were interannual differences in precipitation and nematode responses. For example, in KNZ the second year was much drier than the first, and nematode responses tended to be stronger in that year.

3.2. Description of indicator genera results

A total of 72 genera (20 bacterivore, 7 fungivore, 14 omnivore, 23 plant parasitic, and 8 predatory nematodes; Supplementary Table S1) from 35 families were identified from the three sites. Indicator species analysis identified 39 genera characteristic of the precipitation treatments; 22 genera associated with the arid site, three with the semiarid site, and fourteen with the mesic site. Some endemic genera to the mesic site were found by the analysis to be indicators such as *Trichodorus*. Indicator values (IndVal) were computed for each nematode genera and site, and tested by a Monte Carlo test. Table 2 summarizes all the values for the three sites from "IndVal". After 2 years of manipulated precipitation within the three grassland sites, testing based on the Bray-Curtis distance showed indicator nematode communities differed significantly based on site ($P_{Site} = 0.001$, $R^2 = 0.370$; Fig. 2). The NMDS also revealed that the applied precipitation treatments significantly affected nematode genera distribution, most easily discerned are the reduction treatments separating nematode genera known to be drought tolerant from the rest of the nematode community ($P_{\text{Recieved precip}} = 0.001$, $R^2 = 0.728$; Fig. 2).

4. Discussion

4.1. Ecological indices in the arid site

Our findings did not fully support our expectation that shifts in ecological indices would be absent from the arid site, as desert environments have previously shown little effect on nematode abundance or ecological makeup in response to altered available soil moisture (Freckman et al., 1987; Sylvain et al., 2014; Vandegehuchte et al.,

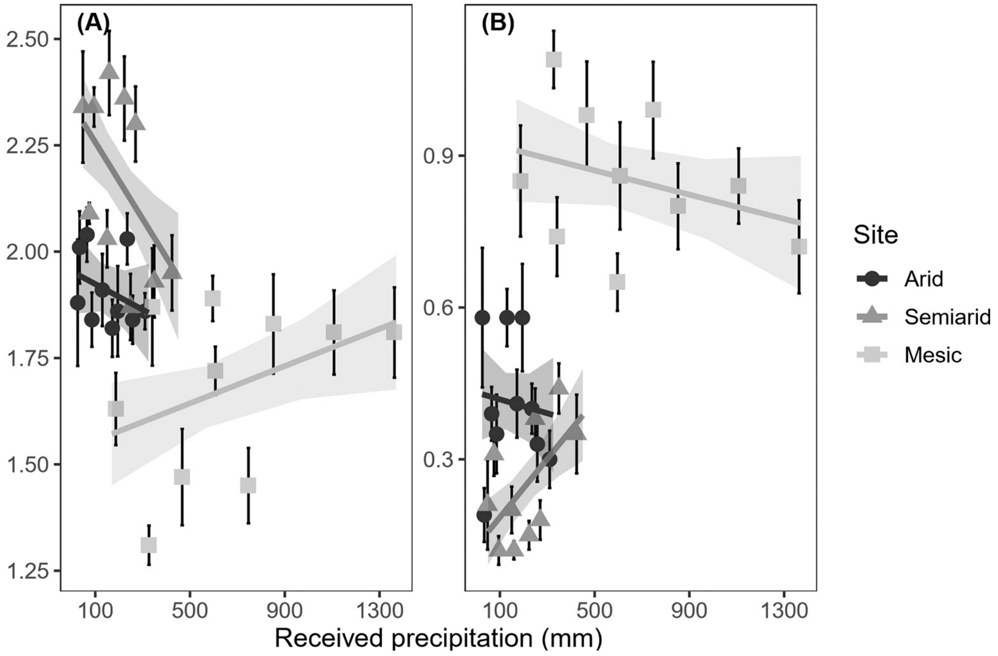

Fig. 1. Functional nematode indices (y axis) in response to precipitation treatments (x axis). Legend represents the grassland sites. Color- and shape-coded trend lines represent effects of manipulated precipitation (n = 8 per treatment in each site) predicted by mixed effects models for the three different sites. Shaded regions indicate 95% confidence limits. Points represent mean abundance of index per precipitation level (n = 16), and error bars represent standard error of the mean. (A) Maturity Index; (B) Plant Parasite Index. For all tests n = 240.

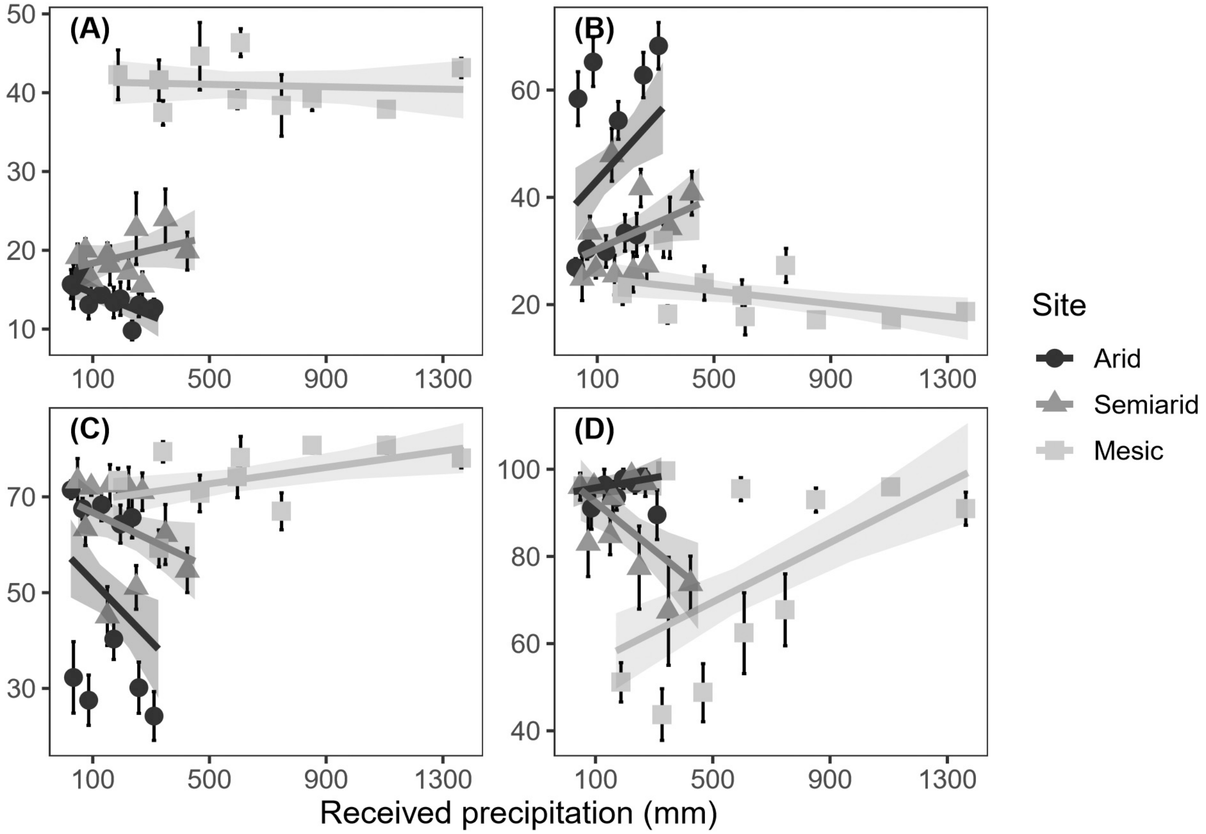

Fig. 2. Functional nematode indices (y axis) in response to precipitation treatments (x axis). Legend represents the grassland sites. Color- and shape-coded trend lines represent effects of manipulated precipitation ($n = 8$ per treatment in each site) predicted by mixed effects models for the three different sites. Shaded regions indicate 95% confidence limits. Points represent mean abundance of index per precipitation level ($n = 16$), and error bars represent standard error of the mean. (A) Enrichment Index; (B) Basal Index; (C) Structure Index; (D) Channel Index. For all tests $n = 240$.

2015). Contrary to our hypotheses, increased precipitation at the arid site resulted in reduced maturity, enrichment, and structure of the nematode communities, as shown by decreases in MI, EI, and SI. This finding indicates a nematode assemblage that is experiencing a disturbed environment and is part of a less complex food web (Ney et al., 2019), a finding bolstered by the increase in BI. In response to greater precipitation the arid site displayed a lower PPI, largely driven by the lower abundances of *Pratylenchus* and *Tylenchorhynchus*, both genera extremely sensitive to moisture (Kandel et al., 2013; Ruan et al., 2012). A lower EI in response to greater precipitation suggests that fewer opportunistic nematodes are present (Ferris et al., 2001); mainly due to the decreases in *Rhabditis* nematodes; a cp-1 bacterivore, (Ferris and Bongers, 2006) deemed an indicator genus in the arid site (Table 2). Despite the decline of enrichment opportunists the BI increased with increasing precipitation, showing a soil food web sensitive to received precipitation (Ferris et al., 2001). This finding contrasts with previous findings from this same site focused on nematode trophic levels (Franco et al., 2019) that showed little change in abundance of nematode trophic groups in response to increased precipitation. The CI did increase slightly with received precipitation, indicating a shift toward the fungal decomposition pathway. This was surprising, given the slight negative response of fungivores to increased precipitation observed at this site (Franco et al., 2019). The lower EI and higher CI indicates that in response to more precipitation more organic matter will be decomposed through the fungal energy channel (Sánchez-Moreno et al., 2010). As no predators were found in the arid site (Franco et al., 2019), the decreases in the MI and SI are driven mostly by the decline of important omnivore genera such as *Eudorylaimus*, which had its greatest abundances in the control and drought treatments (Supplementary Table S1). The decline in SI (decreased higher trophic nematodes) and slight rise in the CI (decrease in opportunist bacterivores) in response to increased precipitation indicates a food web that is severely disrupted (Yeates and Bongers, 1999). Bacterivores deemed to be enrichment-opportunist are very efficient in nutrient mineralization, especially N (Freckman, 1988), while omnivorous and predatory nematodes are often correlated with concentrations of many other soil nutrients (Ferris and Matute, 2003). Thus, the loss of these groups in the arid grassland due to increased precipitation has consequences for plant health as well as the stability of the ecosystem. Namely, that in the long-term plant parasites without predator pressure could decrease plant health (Franco et al., 2019).

Our results from the arid site contrast with previous work where applying water pulses to a desert grassland, resulted in no change in nematode community at the broad trophic-group level, suggesting that such nematodes are resistant and can remain stable despite environmental variability; likely due to survival strategies for dehydration (Freckman, 1986). The arid site findings do partially align with results from a climatically similar desert steppe in Inner Mongolia by Zhang et al. (2020), where a switch from the bacterial to fungal decomposition channel occurred when precipitation increased. However; this same study also showed increasing precipitation led to a more connected soil food web with greater food chain lengths (Zhang et al., 2020), whereas our results show an inverse relationship between SI and precipitation. The changes of the nematode community in response to varied precipitation also differs from previous results from this same arid site that showed no response from nematode trophic groups (Sylvain et al., 2014) and a study that only showed a positive response from plant parasites and omnivores (Vandegehuchte et al., 2015). Nematodes from the arid site may be more tolerant to water stress (Freckman et al., 1987; Vandegehuchte et al., 2015), but with increased precipitation these communities will be less structured in terms of trophic interactions, which

Table 2
Indicator values for nematode genera for the three grassland sites. The displayed values range from 0 (no indication) to 1 (perfect indicator).

Site	Seasonal precipitation	Genera	Indicator value	*P* value	Abbreviation
Mesic	Control	*Achromadora*	0.567	0.005	Ach
Arid	Control	*Acrobeles*	0.338	0.005	Abe
Arid	Reduction	*Acrobeloides*	0.323	0.01	Abo
Arid	Reduction	*Anaplectus*	0.513	0.005	Ana
Arid	Reduction	*Aphelenchoides*	0.305	0.005	Apl
Arid	Reduction	*Aphelenchus*	0.371	0.04	Aph
Semiarid	Addition	*Aporcelaimellus*	0.318	0.04	Apo
Mesic	Addition	*Basiria*	0.440	0.005	Bas
Arid	Addition	*Cephalobus*	0.391	0.005	Cep
Arid	Addition	*Cervidellus*	0.366	0.005	Cer
Arid	Addition	*Chiloplacus*	0.398	0.01	Chi
Mesic	Control	*Coslenchus*	0.520	0.005	Cos
Mesic	Addition	*Criconema*	0.341	0.01	Cyl
Arid	Reduction	*Diphtherophora*	0.457	0.005	Dip
Arid	Reduction	*Dorydorella*	0.366	0.005	Dor
Arid	Reduction	*Ecumenicus*	0.468	0.005	Ecu
Mesic	Addition	*Epidorylaimus*	0.427	0.015	Epi
Arid	Addition	*Eucephalobus*	0.333	0.01	Euc
Arid	Reduction	*Eudorylaimus*	0.420	0.005	Eud
Mesic	Control	*Eumonhystera*	0.419	0.005	Eum
Mesic	Addition	*Gracilacus*	0.332	0.05	Gra
Mesic	Addition	*Helicotylenchus*	0.320	0.01	Hel
Mesic	Addition	*Longidorus*	0.449	0.005	Lon
Mesic	Addition	*Mesocriconema*	0.532	0.005	Mec
Mesic	Control	*Mylonchulus*	0.461	0.005	Myl
Semiarid	Addition	*Panagrolaimus*	0.437	0.005	Pan
Semiarid	Reduction	*Panagrellus*	0.528	0.005	Pag
Arid	Control	*Paraphelenchus*	0.338	0.035	Pap
Mesic	Reduction	*Paratrophorus*	0.480	0.005	Pat
Mesic	Addition	*Paratylenchus*	0.336	0.03	Par
Arid	Control	*Paraxonchium*	0.492	0.005	Pax
Arid	Addition	*Plectus*	0.450	0.005	Ple
Arid	Addition	*Pratylenchus*	0.302	0.045	Pra
Mesic	Addition	*Prismatolaimus*	0.414	0.005	Pri
Arid	Reduction	*Rhabditis*	0.325	0.03	Rha
Arid	Addition	*Rhabdolaimus*	0.338	0.025	Rhd
Arid	Control	*Subanguina*	0.327	0.005	Sub
Arid	Reduction	*Thonus*	0.314	0.005	Tho
Arid	Addition	*Torumanawa*	0.442	0.005	Tor
Mesic	Control	*Trichodorus*	0.435	0.005	Tri
Arid	Control	*Tylenchorhynchus*	0.432	0.005	Tyl
Arid	Reduction	*Wilsonema*	0.321	0.03	Wil

may have long-term consequences for nutrient losses in the system as nematode predation releases excess for nutrients, primarily as plant available amino acids, NH_4^+ and PO_4^{-3} (Ingham et al., 1985). The evidence from our arid site, where nematode community composition was modified by a reduction in omnivorous nematodes with increasing precipitation (Franco et al., 2019), suggests that these systems are more susceptible to environmental stress (Bongers and Bongers, 1998). This differential response of ecological indices to trophic groups highlights the value of generic level descriptions for gaining insight to the broader community response to climate change and outlining a more likely scenario for the nematode community that will result from altered precipitation. This insight can lead to more specific management strategies as it could be necessary to manage the cp-1 nematodes in the arid site by applying labile inputs frequently to avoid the shifts in EI, BI, and CI (Ferris and Matute, 2003) that would potentially lower mineralization and lead to lower levels of soil fertility in an already stressed system (Fig. 3).

4.2. Ecological indices in the semiarid site

In contrast to our first hypothesis, the semiarid site exhibited a nematode community that was less mature, more enriched, less structured, and shifted toward a bacterial decomposition pathway when exposed to increasing precipitation. The rise in PPI in response to greater precipitation aligns with previous studies (Ruan et al., 2012; Zhang et al., 2020) and is reflected in our study by enhanced abundances of *Paratylenchus* and *Helicotylenchus* which represented a large proportion of the total plant parasite population (Ankrom et al., 2020) as well as higher cp plant parasite *Hoplolaimus*. The increase in EI and BI could be associated with the decrease in CI, as both a greater population of cp-1 bacterivore *Acrobeloides* and a lower population of cp-2 fungivore *Aphelenchoides* were found under increased precipitation in the semiarid site. This finding supports previous work from Sohlenius (1985) that found high densities of *Acrobeloides* and a low density of *Aphelenchoides* under wet conditions explaining the different response to be due to a change in the food supply as both genera respond rapidly to increased food availability (Forge et al., 2005; Sohlenius, 1985). Soil bacteria are generally resilient in response to drought and precipitation treatments (Cole et al., 2019; Cruz-Martínez et al., 2009; Zhang et al., 2016), while fungi are relatively sensitive to drought in less arid sites (Ochoa-Hueso et al., 2018), which could also help explain the increase in the aforementioned bacterivores in the wetter treatments. The increase in EI and BI and decrease in CI with increasing precipitation aligns with work in the Inner Mongolian Steppe that reported greater abundances of bacterivores in response to water additions (Ruan et al., 2012). The decrease in SI with increased precipitation reflects a community with fewer omnivores and predators, aligning with findings that showed a lack of response in omnivores and decrease in predators within this same site (Franco et al., 2019). The negative response of the MI and SI to increasing precipitation seems to be driven solely by the abundance of *Aporcelaimellus*, a cp 5 omnivore that declined in abundance under the addition treatments (Supplementary Table S1). The semiarid nematode

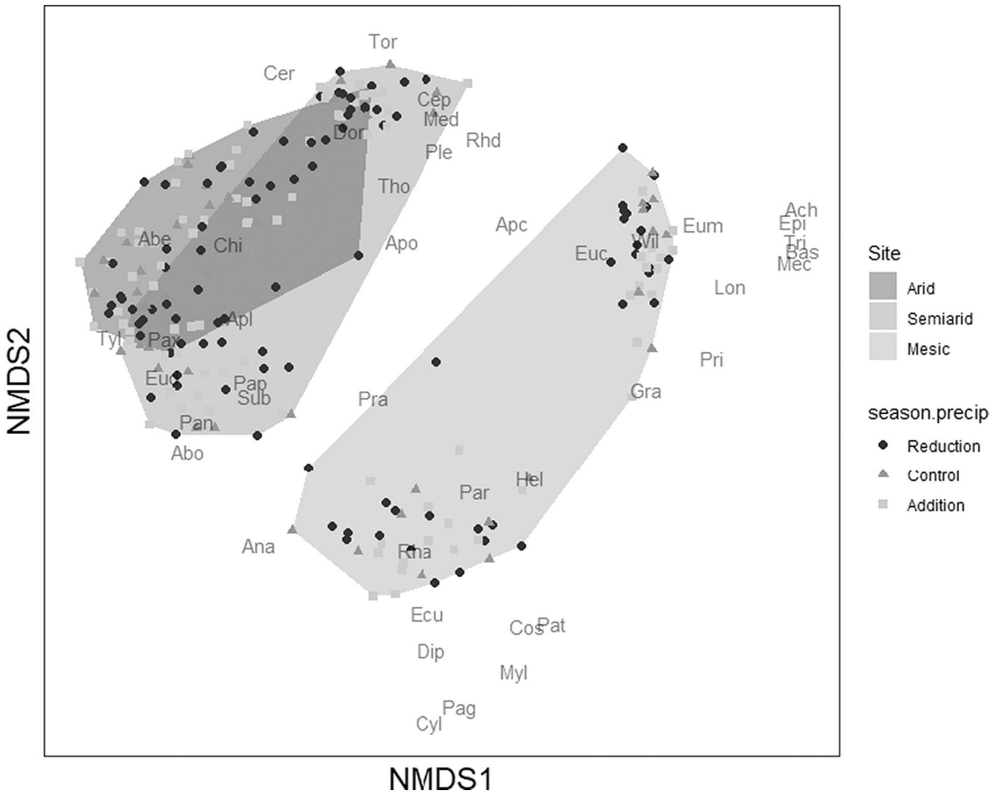

Fig. 3. Nonmetric multidimensional scaling plot of nematode genera as a function of received growing season across the three sites. Each point reflects the community found in each plot (n = 240) from both years of the study (2016 and 2017). Points that are close together have more similar communities than points.

community, seeing a reduction in MI and SI with increased precipitation, may actually continue to increase the EI; these higher cp nematodes feed on and regulate the abundance of opportunist nematodes (Ferris, 2010) leading to a positive feedback loop where the decrease in SI increases the EI.

4.3. Ecological indices in the mesic site

As predicted, the mesic nematode community became more mature and structured, and shifted toward a fungal decomposition channel when precipitation was increased. Increased precipitation led to a decrease in PPI in the mesic site which opposes a finding in the same site that saw large increases in plant parasites with increased soil moisture (Todd et al., 1999); however, this difference is certainly driven by the lowered abundances *Trichodorus*, *Xiphinema* and, *Longidorus*. The weak effect seen in the EI and BI is likely due to the low populations of *Panagrolaimus* and *Panagrellus* as well as the slight alterations in *Rhabditis* populations in response to any precipitation treatments. The mesic nematode community exhibited a greater MI and SI in response to increasing precipitation, indicating an environment that supports enhanced soil food web complexity, and suggests a more stable and resilient soil ecosystem (Bongers, 1990; Neher, 2001). Additionally, increases in abundance of long-lived and higher cp omnivores *Eudorylaimus* and *Paraxonchium*, as well as predatory *Discolaimium* (Supplementary Table S1) nematodes further point to increased ecosystem stability and resilience. This marked shift in ecological indices at the mesic site is likely due to multiple trophic interactions, associated with the greater abundance of omnivorous and predacious nematodes feeding on lower cp nematodes. Water additions having positive effects on the stability and maturity of the mesic soil food web does align with a study from an agroecosystem with comparable mean annual precipitation (704.2 mm) in China that showed severe drought to decrease MI and SI (Yan et al., 2018). The decomposition channel switch from bacterial to fungal dominance is also supported by *Aphelenchoides* having a greater abundance in the water addition treatments (Supplementary Table S1).

4.4. Nematode indicators response to precipitation treatments across sites

In this study we found differences in nematode indicator composition between levels of applied precipitation and grassland sites, revealing that specific grasslands will see shifts in certain genera that are characteristic of each site with changing precipitation regimes, which may lead to altered decomposition, nutrient cycling, and even C sequestration. A study focused on the link between nematodes and microorganisms in mediating SOC turnover in soil macroaggregates found that an increase in bacterivores led to greater grazing pressure on microorganisms resulting in microbial-derived SOC turnover (Jiang et al., 2018). This finding of bacterivore driven C dynamics places importance on the indicator results from the arid site; as both *Eucephalobus* and *Acrobeloides* are known to be adapted to dry climates (Griffiths et al., 1995; Bakonyi and Nagy, 2000) and *Plectus* has shown variable responses to precipitation, by being enhanced with drought in an agroecosystem (Yan et al., 2018) and by wetter conditions in a citrus field (Porazinska et al., 1998). The indicator bacterivores had their greatest abundance under drought treatments (Table 2; Supplementary Table S1) and as this arid site is likely to experience more intense rainfall patterns, any decline in important bacterivores would affect C metabolism shifting it toward the fungal channel even more. An indicator omnivore, *Aporcelaimellus*, declined in both drought and addition treatments, a variable response that that aligns with previous work (Porazinska et al., 1998; Yan et al., 2018) and shows its sensitivity to altered precipitation. When *Aporcelaimellus* decreases in abundance the maturity and structure for the semiarid community also decreases; and with its reduction the PPI increases as top down control is lessened (Franco et al., 2019). *Pratylenchus* an indicator genus for the mesic site declined under addition treatments, with this grassland expected to experience greater drought it's likely the rise in PPI associated with greater *Pratylenchus* populations will lower the nematode community stability.

As for site effects on nematode genera there was a clear separation of the mesic site community from the drier grasslands. This finding contrasts with our hypothesis that the arid site would respond uniquely to altered precipitation, and appear to differentiate more from the wetter grasslands. However the arid nematode community and the semiarid nematode community share many more genera as displayed by a large overlapping polygon seen in the NMDS (Fig. 2). There are more unique genera that were found in the mesic site. It is these genera such as *Trichodorus*, a plant parasite known to be sensitive to abiotic factors (Bor and Kuiper, 1966) that drive this separation from our other sites displayed in the NMDS.

4.5. Conclusion

This experiment as part of a larger collaboration study has now revealed the response of nematode predator-prey interactions (Franco et al., 2019), those nematodes tightly linked to decomposition (Andriuzzi et al., 2020), and herbivory (Ankrom et al., 2020) to climate change across three grasslands. Our current observation shows that altered precipitation affected nematode assemblages as well as nematode indices suggesting key ecosystem functions influenced by these nematodes (e.g., nutrient mineralization, herbivory, C cycling) will also be affected. With more extreme precipitation events likely to occur across these grasslands (Reidmiller et al., 2017), changes in nematode community dynamics and functionality may result in cascading effects for host plants and the soil ecosystem at large. The greater drought periods predicted for the mesic grassland showed an overwhelming effect on the soil nematode community resulting in altered energy channels, simplified food web structures, and a general decrease in maturity. Through nematode community analysis we observed strong influences on the soil food web caused from extreme and moderate precipitation manipulations. This finding features the importance of genera level resolution and suggests that the sensitivity of these indices allows for ecological interpretation of belowground function and status, which is especially pertinent as these grasslands will not respond to precipitation alterations similarly and will therefore require unique mitigation strategies. Including long term observational studies of nematodes at regional grassland sites such as in this study can also be linked to how plant health will respond to nematodes with future climate changes.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2021.104263.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This work was supported by the National Science Foundation under grant number DEB-1456631 and DEB-1456597 to Diana H. Wall and Osvaldo E. Sala. This work was supported by funding from the National Science Foundation for the Jornada Basin Long-Term Ecological Research Program DEB 2025166. We thank the staff at the Jornada Basin LTER, Semi-arid Grassland Research Center, Central Plains Experimental Range, and Konza Prairie Biological Station for site-based assistance.

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