SOIL ORGANISMS 97 (3) · 2025
pp. 281–290
https://doi.org/10.25674/453

Aporrectodea earthworms respond to salt and organic matter levels in captive and free-choice mesocosms

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Received 5 February 2025 | Accepted 2 July 2025 | Published online 1 December 2025

Abstract

Earthworms play a role as soil health indicators, including for saline soils. Salinity influences soil chemistry, structure, hydrology, and biological activity. To better understand the response of *Aporrectodea* earthworms to salinity, we conducted experiments in captive mesocosms that ranged in soil salinity ($EC_{1:1}$ = 1 – 4.5 dS/m) and soil organic matter content (3.4% – 10%), and split-bin mesocosms that offered earthworms contrasting combinations of salt and organic matter levels. We observed that in no-choice situations, adult *Aporrectodea* earthworms survived in soils at all salinity and organic matter levels for at least 60 days. When given a choice between salinity and organic matter levels, more adult *Aporrectodea* earthworms selected non-saline soils compared to saline soils, and elevated organic matter only alleviated the aversion to salinity when the alternative soil had less organic matter content. Based on these experiments, we conclude that earthworms prefer to reside in high organic matter, non-saline soils and prefer to avoid saline soils unless they are augmented with organic matter. The utility of earthworms as soil health indicators in saline soils depends on their ability to select and move into more favorable environments, rather than their tolerance to salt ions.

Keywords Endogeic | Electrical Conductivity | Lumbricidae | Northern Great Plains | Salinity

1 Introduction

Soil salinity is an important environmental factor influencing soil function throughout the world (Daliakopoulos et al. 2016, Wu et al. 2019). Saline soils impact biological communities, including plants, microbes, and fauna (Boyrahmadi & Raiesi 2018, Owojori et al. 2009, Zörb et al. 2019). In some ecosystems, soil salinity is caused by human activities, but in the Northern Great Plains soils of North America, salinity occurs naturally due to the parent material and shallow hydrology. High evaporative demand, along with the discharge and recharge system in the soil profile bring salts to the surface and maintain surface salt concentrations (Keller et al. 1986). Land management practices, such as deep tillage and sub-surface tile drainage, can facilitate downward salt movement (Li et al. 2025), but the effectiveness of these practices depends on local hydrology. The saline soils in the Northern Great Plains are unique in that they are dominated by sulfate and carbonate salts as opposed to chloride salts common in other regions (Gasch et al. 2021, Keller et al. 1986). The salt ion composition is relevant because different ions directly and indirectly impact soil biological activities in varied ways, ultimately influencing

ISSN 1864-6417 · eISSN 2509-9523

toxicity, nutrient availability, and habitat suitability (Keller et al., 1986, Raiesi et al., 2020). Soil salinity is relevant to land use and management, including for crop production. Agriculture is a vital part of the economy in the Northern Great Plains, and salinity has resulted in significant crop yield losses (Hadrich 2012). As a result, previous research in the region has focused on crop response to salinity (Bilski et al. 1988, Butcher et al. 2018, Thapa et al. 2017). Belowground impacts of elevated salt concentrations, including for soil organisms, have received less attention.

Earthworms are an indicator of soil health (Edwards & Bohlen 1996, Hirano & Tamae 2011), and they play roles in soil structure, cycling nutrients (Shutenko et al. 2022), facilitating nitrification (Van Vliet et al. 2007), sequestering carbon (Angst et al. 2017), remediating pollution (Wu et al. 2019), and providing cultural services (examples in archaeology, education, and recreation, Blouin et al. 2013, Edwards & Bohlen 1996). Many of these earthworm roles accompany, complement, and correlate with soil organic matter (OM) content. Most earthworm species accomplish these tasks by contributing vermicasts (fecal waste) to the environment and creating burrows. Vermicasts are rich in nutrients that can be used by microorganisms and plants (Sharif et al. 2016). Their burrows and castings create nutrient-rich areas that support roots and microbial growth; this, in turn, allows mineralization to occur at a faster rate (Carpenter et al. 2008, Edwards & Bohlen 1996). Furthermore, the ability of the earthworms to aggregate and change the porosity of the soil influences the flow of water through the soil (Bottineli et al. 2010, Hendrix 1995).

Past research focused on earthworm responses to salinity indicates that increasing salinity generally negatively affects earthworms and their activities (Sharif et al. 2016, Gasch et al. 2021, Karimi et al. 2020, Wu et al. 2019). Salt ions can influence osmotic processes and related energetics in earthworms, damaging the neurosecretory system, and reducing their ability to produce casts and lay cocoons (Sharif et al. 2016). One experiment noted that an electrical conductivity (EC) of 8 dS/m reduced the survivability of the *Eisenia fetida* earthworm species in the presence of other environmental toxins, such as zinc and copper (Karimi et al. 2020). While *Eisenia fetida* is a common species used in earthworm-salinity studies (see also Owojori et al. 2009, 2014), it does not occur naturally in Northern Great Plains soils. The *Aporrectodea* genus, however, is commonly found in the region, although it is not native (Schwert et al. 1991). *Eisenia fetida* is epigeic (residing in organic matter on the soil surface), while *Aporrectodea* spp. in the Northern Great Plains are endogeic (burrowing into the soil). Given the niche differences between the genera, knowledge about *Eisenia fetida* and salinity does not inform *Aporrectodea* responses to salts. Furthermore, naturally occurring salinity in Northern Great Plains soils is dominated by sulfate-based salts rather than chloride-based salts, which are also commonly used in earthworm salinity studies (Owojori et al. 2009, 2014; Karimi et al. 2020; Raiesi et al. 2020). Gasch et al. (2021) examined *Aporrectodea* earthworm abundance and growth stages in a naturally occurring salinity gradient in a field soil in North Dakota, USA. While adults and cocoon numbers were even across salinity gradients, juveniles declined in plots with an EC in a 1:1 soil: water slurry ($EC_{1:1}$) of over 4 dS/m (Gasch et al. 2021). In the field study, soil OM content decreased with increasing salt concentration from about 7% in the non-saline soil plots to about 3% in the saline plots. These natural field conditions did not allow insight into the opposing influences of salts and OM on earthworm habitat quality. The decline in earthworm abundance in field soils may result from increased salt concentration, reduced OM content, or both, warranting further studies to delineate the effects of salt concentrations and OM content in saline soils. In addition to its potential role as a food source, soil OM content fundamentally influences soil physical properties (temperature, water holding capacity, aeration, aggregation) and biochemical properties (nutrient and energy for soil life) that improve the quality of the soil as an earthworm habitat. High salt concentrations in soil can also influence soil structure, water dynamics, and the osmotic environment, which may reduce earthworm habitat quality.

Given that plant productivity declines with increasing salinity, leading to reduced OM inputs and poor soil habitat quality, it is reasonable to assume that increasing salt concentration interferes with the positive feedback between earthworms, OM, and soil health. To better understand earthworm responses to salinity, and the potential roles that earthworms play in indicating soil health in the presence of salts, we conducted mesocosm experiments to assess *Aporrectodea* earthworm survival and habitat selection in different combinations of salt concentrations and OM levels. Our specific questions were: When mobility is restricted, do earthworms survive increasing salt concentrations in soil and does OM level influence this response? When given a choice and the ability to move, do earthworms avoid saline soils, and does OM level influence this response? We expected that increasing salt concentrations would reduce earthworm survival and occurrence and that increasing OM levels would alleviate aversion to salinity. These experiments can inform soil health assessments and *Aporrectodea* ecology in saline soils.

2 Materials and Methods

We used two lab mesocosm approaches to investigate earthworm responses to salinity and OM levels. We collected soil for all experiments from western Minnesota, USA (Glyndon series); it is a coarse-silty, mixed, superactive, frigid Aeric Calciaquoll (Soil Survey Staff 2024). We collected the top 15 cm of soil, the 'Ap' horizon, where the *Aporrectodea* species typically reside (Edwards & Bohlen 1996). According to the official soil description, this soil is primarily used for farming small grain crops, sugar beets, and potatoes but is historically home to native tall grass prairies (Soil Survey Staff 2024). We air-dried and sieved the soil to 2 mm and measured initial EC and pH on a 1:1 soil: water slurry (Rhoades 1996, Thomas 1996) and OM via loss-on-ignition (Combs & Nathan 2011). Initial $EC_{1:1}$ was 0.4 dS/m, pH was 8.15, and OM was 3.4 %.

To modify soils for the experimental treatments, we homogenized the salt and organic matter materials into the soils by hand (for mesocosms) or with a mechanical soil mixer (for split bins). To elevate salt concentrations in the soil, we added a mixture of salt, created to match the regional field salt composition: 5 % KCl, 15 % $CaCO_3$, 25 % Na_2SO_4, 20 % $CaSO_4$, and 35 % $MgSO_4$ (reported in Gasch et al., 2021). To elevate OM levels in soil, we added corn (*Zea mays*) husks collected from a farm near Fargo, North Dakota, USA, dried and ground to pass a 2 mm sieve.

We collected earthworms for the experiments from a farm near Rutland, North Dakota, USA and allowed them to acclimate to the lab setting for a few months. Prior to the experiments, earthworms were housed in tubs containing a mixture of the untreated test soil and composted cattle manure. We stored the tubs in the dark at approximately 14 deg. C and fed and watered earthworms twice a week or as needed. Food consisted of dried, finely ground grass clippings, sprinkled on the surface and replenished as they disappeared (twice per week).

The individual earthworms used in the experiments were members of the *Aporrectodea* species complex, a grouping of morphologically similar species, including those common in the Northern Great Plains (Pérez-Losada et al. 2009). The complex includes *Aporrectodea caliginosa*, *trapezoides*, and *tuberculata* (Edwards 2004, Edwards & Bohlen 1996). Adult earthworms were identified and selected for the experiment based on a prominent tubercula pubertatis, markings used as indicators of *Aporrectodea* complex membership and sexual maturity (Edwards & Bohlen 1996). We did not separate ore select test subjects by species for these experiments, so all results reflect the behavior of the *Aporrectodea* complex to treatments.

In the first experiment, we evaluated earthworm survival in increasing salinity concentrations within small mesocosm containers. We supplemented the salt mixture to the test soil to achieve the following $EC_{1:1}$ values: 1, 2.6, 3.3, 3.5, and 4.5 dS/m. We chose these values because they are likely to exist in soil in the region, and they fall within the range of salinity levels where plants experience stress. For each salt level, we added 20 g of corn husk material to 200 g of salt-amended soil to achieve a 10 % soil OM level, then manually mixed each sample to homogenize. We then placed the homogenized mixture into a small plastic container with drainage holes. Each treatment had three replicates across two factors: salinity concentration and baseline or elevated OM content, totaling 30 mesocosm units (Fig. 1). We added approximately 100 ml of water to the containers, allowing them to drain and chill in the dark incubator at 14 deg. C. We then added three adult *Aporrectodea* earthworms to each container and covered them with perforated lids. We added water as needed throughout the experiment to maintain the approximate starting soil water content. After six weeks, we deconstructed mesocosms and recorded living adults, dead earthworms, and cocoons in each container. We chose this duration to allow sufficient time for adults to lay cocoons, for cocoons to hatch, and for sensitive earthworms to die from salt exposure (Bart et al., 2019b). *Aporrectodea* species are reported to have reduced cocoon production, cocoon health, body weight, and survival in response to high concentrations of other toxins (soil pesticides and heavy metals) (Bart et al. 2019a, Holmstrup 2000, Khalil et al. 1996). In *Eisenia fetida*, these reproductive and health metrics collectively decline with increasing exposure to salt concentrations (Fischer & Molnár 1997, Owojori et al. 2008). We assume cocoons indicate the presence of healthy, reproductively active earthworms in *Aporrectodea*. The captive mesocosm experiment was conducted twice.

In the second experiment, we evaluated earthworm response when they were allowed to move between different soil conditions in split bin mesocosms. We created different combinations of soil for the split bins, using the same materials as in the first experiment. Soil conditions included non-saline soil (field soil, $EC_{1:1}$ = 0.4 dS/m) or saline soil (field soil with supplemental salt mixture to $EC_{1:1}$ = 6 dS/m), and field level OM (3.4 %) or elevated OM (10 %). Each split bin held approximately 30 kg of soil material, with 15 kg on each side (approximately 15 cm deep); sides were separated with a thin plastic sheet during bin construction. The combinations of soil mixtures are illustrated in Fig. 2. Each bin was replicated three times. After construction, we added water to the bins until we observed drainage and allowed settling. The divider was removed, and 30 adult earthworms from the *Aporrectodea*

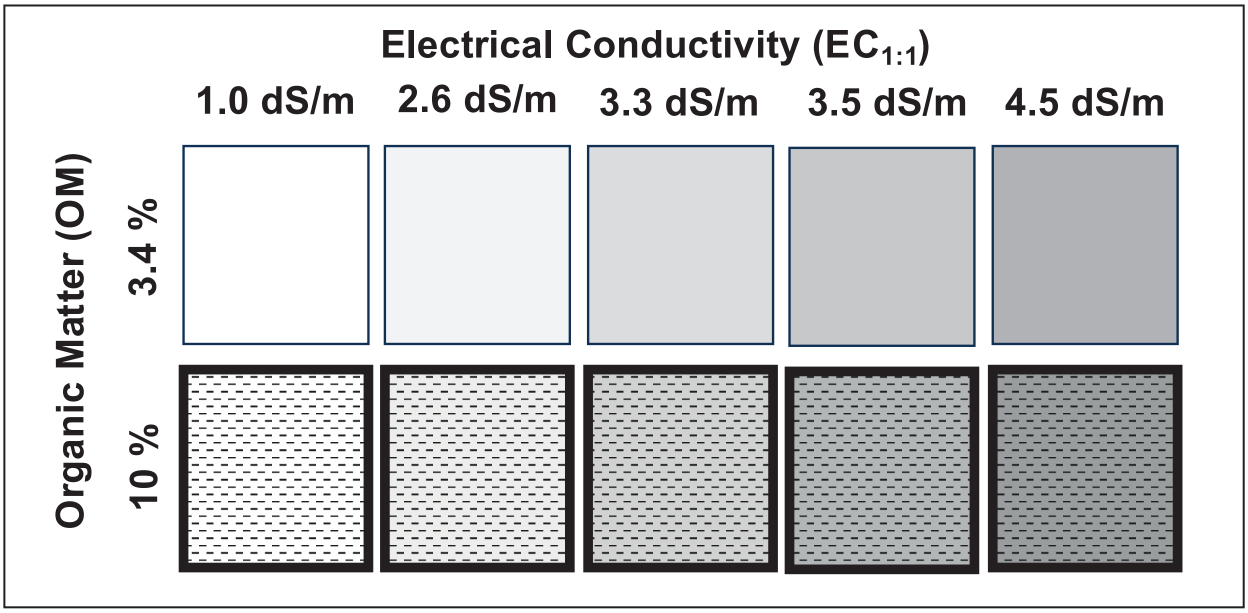


Figure 1. Design of captive mesocosm experiment. Containers held combinations of salt concentrations and OM content and hosted three adult earthworms.

complex were placed in the center of each bin. Bins were lightly watered to the approximate starting water condition (assessed by eye and touch) as needed for the duration of the experiment. After 30 days, the divider was replaced, and mesocosms were deconstructed. In each side, we counted living adult earthworms, juveniles, and cocoons. We assumed all cocoons were deposited and all juveniles hatched during the 30-day experiment.

For the captive mesocosm experiment, we combined the replicates from the two experimental rounds for each mesocosm treatment (n = 6). We used a two-factor analysis of variance to separately compare mean live earthworm, cocoon, and dead earthworm counts across treatments. For the split bin mesocosm experiment, we did not construct all possible combinations of soil conditions in split bins. To evaluate the earthworm response across this unbalanced design, we used paired T-tests to compare the mean counts of cocoons, juveniles, and adults between soil treatments within bins. This comparison focused on within-bin movement and soil condition preference. In order to understand if the counts in each side differed from the control, we used standard T-tests to compare mean counts between each treatment side and the control. We used RStudio (Posit Team 2024) to conduct all statistical analyses and visualizations in R (R Core Team 2024) using 'ggplot2' (Wickham 2016) and 'Hmisc' (Harrell 2024) packages.

3 Results

In the captive mesocosm experiment, average adult earthworm, cocoon, and dead earthworm counts after 60 days were similar across all salinity concentrations and OM levels (Table 1). While seven mesocosms hosted between one and three dead earthworms, the average adult count was not statistically different to the initial number of earthworms in all treatments, and all but one treatment held cocoons. The ANOVA indicated that OM level was a significant factor for adult earthworm count (Table 2), with fewer adult earthworms at the higher OM level. Otherwise, counts of adults, cocoons, and dead were not statistically different across treatments.

In the split-bin choice experiment, earthworms occurred in higher abundance in non-saline soils than in saline soils and preferred soil with elevated OM content, as indicated by cocoon deposition (Fig. 3A) and adult counts (Fig. 3C). Juvenile earthworm counts were generally low across all bins and mean juvenile earthworm counts were not different across soil treatments and were not different from the control bins (Fig. 3B). Cocoon deposition closely followed adult abundance in the split bins. When given the choice between non-saline and saline soil, both adult and cocoon counts were higher in non-saline soil, except in one set of treatments (non-saline with baseline OM content versus saline with elevated OM content), which had very low cocoon counts and equal adult earthworm counts. This treatment comparison was also the exception when comparing earthworm selection between soils with baseline and elevated OM content. Cocoon counts were higher in elevated OM non-saline soils, but were very

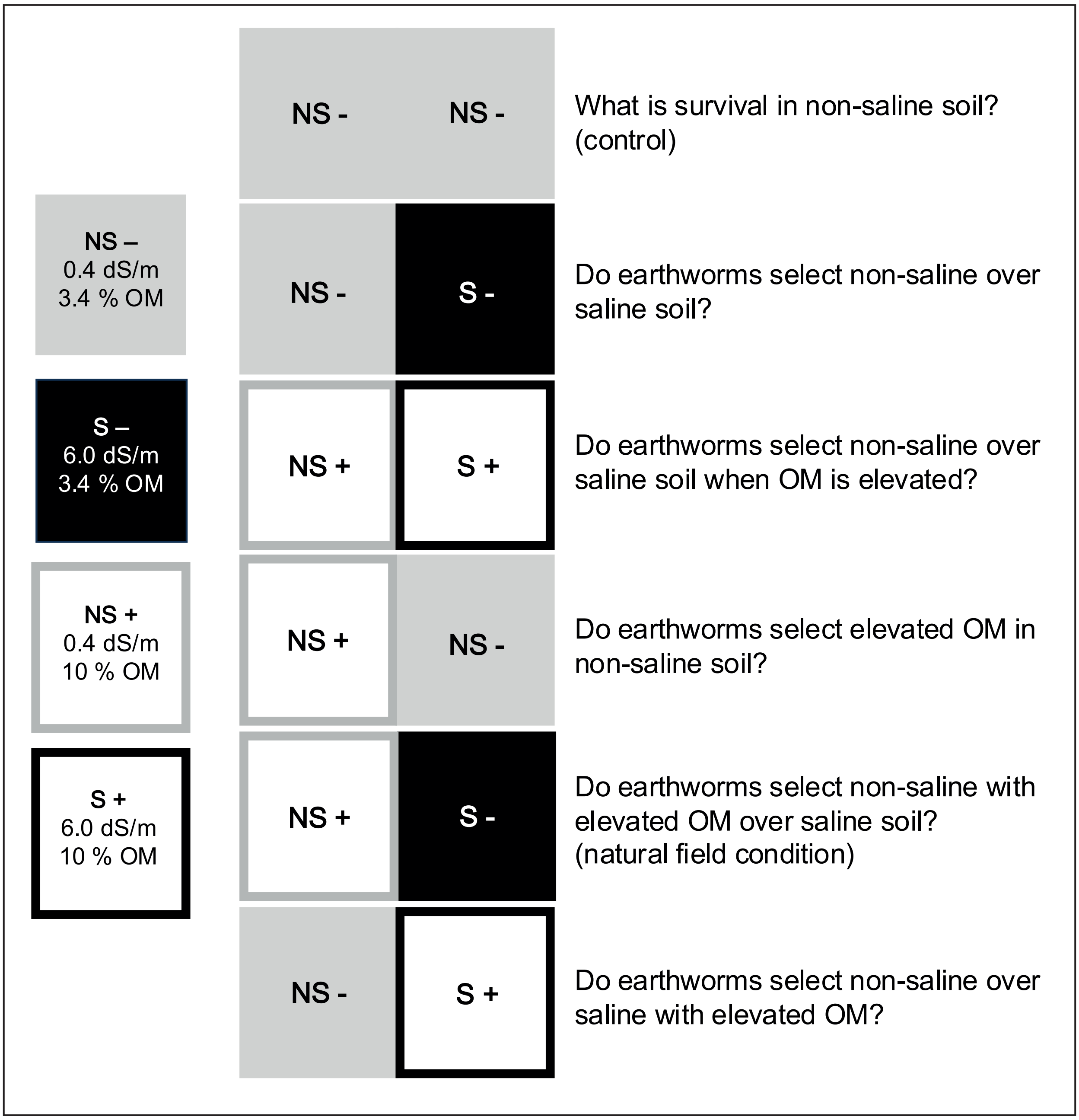


Figure 2. Design of split bin mesocosm experiment. Containers held combinations of salinity concentration (**NS** and **S**) and OM (+ and -) and hosted 30 adult earthworms.

low in saline soils with elevated OM content. Adult counts were also generally higher in non-saline soils with elevated OM content, but were not higher in saline soils with elevated OM content.

4 Discussion

In the captive mesocosm experiment, *Aporrectodea* earthworms tolerated levels of salinity at concentrations that exceed plant tolerance ($EC_{1:1}$ up to 4.5 dS/m) for 60 days without experiencing mortality. In addition to surviving these conditions, the earthworms also deposited cocoons and produced living juveniles during the experiment duration. Further studies will need to define *Aporrectodea* threshold salinity levels since our study did not achieve this. In a North Dakota field study, saline soils had low earthworm counts (Gasch et al. 2021), but it wasn't clear if the absence was due to avoidance or mortality. While salinity alters soil structure by reducing porosity and increasing soil plasticity, OM

Table 1. Average counts of living and dead earthworms and cocoons, with standard deviation in parentheses (n = 6), for a captive mesocosm experiment.

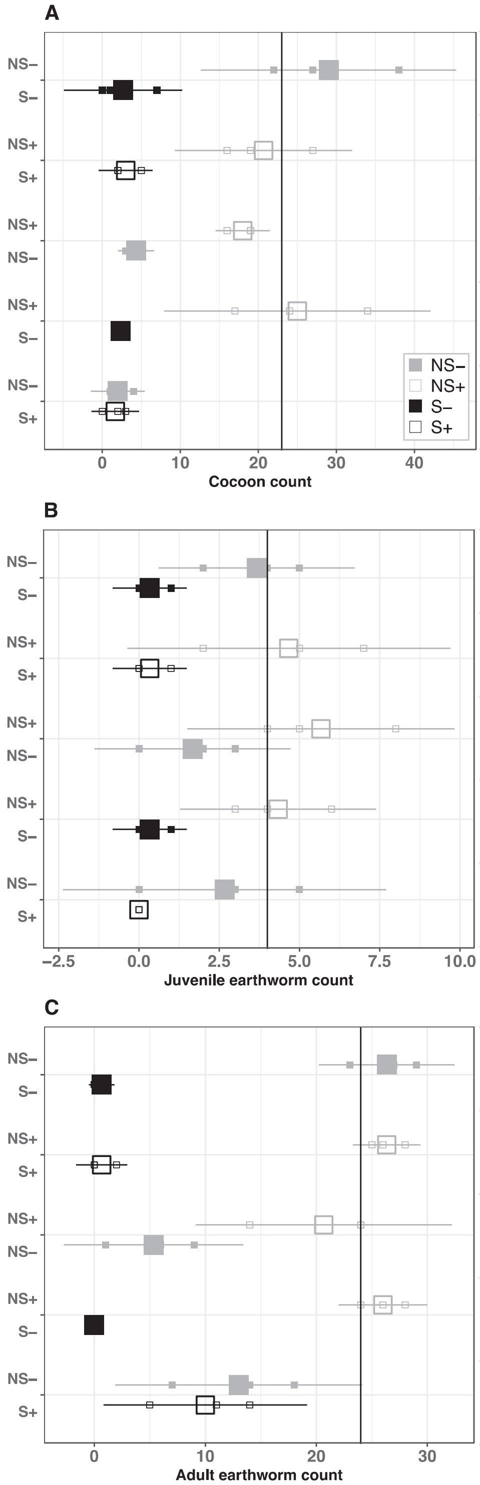
Electrical Conductivity (EC1:1)	Organic matter	Adults	Cocoons	Dead
1 dS/m	3.4%	3.0 (0.0)	0.2 (0.4)	0.0 (0.0)
	10%	3.0 (0.0)	1.0 (1.3)	0.0 (0.0)
2.6 dS/m	3.4%	2.8 (0.4)	0.8 (1.6)	0.2 (0.4)
	10%	2.3 (1.2)	0.5 (0.6)	0.7 (1.2)
3.3 dS/m	3.4%	3.0 (0.0)	0.3 (0.5)	0.0 (0.0)
	10%	2.5 (0.6)	0.3 (0.5)	0.0 (0.0)
3.5 dS/m	3.4%	2.8 (0.4)	0.5 (0.8)	0.2 (0.4)
	10%	3.0 (0.0)	1.0 (0.9)	0.0 (0.0)
4.5 dS/m	3.4%	3.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	10%	2.3 (0.8)	0.2 (0.4)	0.7 (0.8)

Table 2. Two factor analysis of variance (ANOVA, n = 6) table for living and dead earthworm and cocoon counts for a captive mesocosm experiment. P-values < 0.05 are indicated in bold.

		Df	Sum Sq	Mean Sq	F value	Pr (>F)
Adults	Electrical conductivity	4	1.433	0.3583	1.295	0.285
	Organic matter	1	1.350	1.3500	4.880	**0.032**
	EC x OM	4	1.567	0.3917	1.416	0.242
	Residuals	50	13.833	0.2767		
Cocoons	Electrical conductivity	4	3.57	0.89	1.305	0.281
	Organic matter	1	0.82	0.81	1.195	0.280
	EC x OM	4	2.43	0.61	0.890	0.477
	Residuals	50	34.17	0.68		
Dead	Electrical conductivity	4	1.833	0.4583	1.858	0.132
	Organic matter	1	0.600	0.600	2.432	0.125
	EC x OM	4	1.567	0.3917	1.588	0.192
	Residuals	50	12.333	0.2467		

influences structure by increasing porosity, aggregation, air flow, and water storage. Many studies have shown that adding OM can improve earthworm habitat and provide earthworms with much-needed carbon and nitrogen in harsh soil ecosystems (Angst et al. 2017; Van Vliet et al. 2007). In our experiment, mean adult counts were reduced in containers with elevated OM content. We attribute this to the high water content and fungal growth in the elevated OM containers, which may have directly or indirectly aggravated the captive earthworms. We can conclude from this experiment that earthworms tolerate saline soils (up to 4.5 dS/m), regardless of OM level; therefore, we presume that the absence of *Aporrectodea* earthworms in saline soils of the Northern Great Plains is due to avoidance rather than mortality.

In the split bin mesocosm experiment, we observed that adult earthworm and cocoon abundance was consistently higher in non-saline soils than in saline soils when the non-saline soil had equal or higher OM content. In one set comparing saline soil with elevated OM content and non-saline soil with baseline OM content, adult earthworm and cocoon counts were equal, albeit lower than the control, because earthworms were more equally distributed across the two treatments. We also observed that adult



	Across Treatment	Treatment vs Control	Interpretation
A	**0.039**	0.331 **0.004**	S- < NS- = C
A	**0.017**	0.56 <**0.001**	S+ < NS+ = C
A	**0.011**	**0.032** <**0.001**	NS- < NS+ < C
A	**0.039**	0.738 **0.002**	S- < NS+ = C
A	0.667	<**0.001** <**0.001**	S+ = NS- < C
B	0.063	0.831 0.077	S- = NS- = C
B	0.069	0.739 0.077	S+ = NS+ = C
B	0.184	0.374 0.189	NS+ = NS- = C
B	0.074	0.831 0.077	S- = NS+ = C
B	0.208	0.514 0.074	S+ = NS- = C
C	**0.006**	0.600 **0.014**	S- < NS- = C
C	**0.003**	0.575 **0.012**	S+ < NS+ = C
C	0.104	0.458 **0.008**	NS- = NS+ NS+ = C NS- < C
C	**0.002**	0.642 **0.015**	S- < NS+ = C
C	0.612	0.061 **0.023**	S+= NS- NS- = C S+ < C

Figure 3. Earthworm cocoon (**A**), juvenile (**B**), and live adult (**C**) counts in soil within split bin mesocosms. Small points are counts per soil condition in each bin (n = 3), larger symbols represent averages, and whiskers represent standard deviation. The vertical lines on each plot indicate the average counts in the control bins. Point symbols and colors represent soil condition (filled gray = **NS-** = non-saline with baseline OM, filled black = **S-** = saline with baseline OM, open gray = **NS+** = non-saline with elevated OM, and open black = **S+** = saline with elevated OM). P-values on the right-hand side of the figure are for paired t-tests across treatments within bins and for t-tests between each treatment side and the control bins. P-values < 0.05 are indicated in bold. Average counts and p-values are interpreted to rank earthworm occurrence across treatments.

earthworms do not necessarily occupy non-saline soil with elevated OM content in higher abundance than non-saline soil with baseline OM content. However, we did see higher cocoon counts in high OM non-saline soil. Based on these observations, we can conclude that *Aporrectodea* earthworms prefer non-saline over saline soil, and that elevated OM content may alleviate salinity avoidance when the alternative environment has lower OM content. Based on this set of soil treatment comparisons and resulting earthworm counts, *Aporrectodea* earthworms prefer soil conditions in the following order: non-saline with elevated OM > non-saline > saline with elevated OM > saline.

This set of experiments clarified how *Aporrectodea* earthworms respond to different levels of salt and OM content, as measured by abundance and cocoon deposition. It did not address the specific mechanisms resulting in these observations. For example, high concentrations of salt ions can influence soil porosity, aggregation, and tilth (Hanson et al. 1999). During mesocosm deconstruction, we observed that saline soil had a more plastic behavior (detected by feel) compared to non-saline soil. Such physical characteristics of the saline soil may influence earthworm movement independent of direct salt ion effects. Additionally, we did not measure earthworm body size or weights, earthworm activity, feeding patterns, or burrowing patterns in these mesocosms, which are important aspects that inform earthworm ecology and function (Curry & Schmidt 2007), and which may vary across members of the *Aporrectodea* complex. We created OM treatments with one type of plant material (corn husk), and earthworms likely have a range of preferences for different OM substrates, which may also influence physical and chemical properties in the soil in different ways. These are all potential avenues for further study, in addition to extending the duration of exposure to different soil conditions and including more combinations of treatments for choice experiments. Despite the limitations of these experiments, they have provided information on earthworm reactions to different salt and OM levels, *Aporrectodea* ecology, and salt compositions typical in the Northern Great Plains.

As earthworms continue to serve as popular soil health indicators, it is important to relate their occurrence and behavior to soil function. We know that salinity creates unique soil ecosystems that differ in chemistry, structure, hydrology, and biological activity compared to non-saline soil. We also know that earthworm activity in soil reflects responses to complex interactions between the physico-chemical environment, and their occurrence is context-dependent. Based on our observations, earthworm occurrence across salinity levels can indicate soil health if earthworms are free to migrate — they will likely reside in non-saline soils. However, if earthworms are present, movement is restricted, and soils have elevated salinity, they may not necessarily indicate the health status of soils or favorable plant growth conditions. Therefore, earthworm presence in this region does not necessarily indicate a soil suitable for plant production, which is important for a land manager to recognize. In practice, agricultural land managers can consider supplementing saline soils with organic amendments, which may attract earthworms to saline areas. The combination of OM additions and earthworm activities may initiate soil health improvements such as increasing porosity and infiltration, thereby facilitating salt leaching from the rooting zone and supporting plant growth. We must continue to explore how different species of earthworms behave across the vast diversity of soil conditions to understand and recognize their ecological roles and value as indicators.

Acknowledgments

This research was supported by funding from the North Dakota Corn Utilization Council, the North Dakota Soybean Council, the North Dakota Agriculture Experiment Station, and the School of Natural Resource Sciences at North Dakota State University. The authors also express gratitude to Joe Breker for supplying field-collected earthworm populations, Sophia Portner, Joel Bell, Rodney Utter, Katherine Kral-O'Brien, Jose Pablo Castro Chacon, and Michael McKenna for assistance in the field and lab. We also dedicate this paper to our co-author, the late Dr. Brian Darby, who spent his career furthering our knowledge and appreciation of soil organisms in all that they do. He selflessly gifted us with his ecology knowledge, critical mind for scientific rigor, and compassion. We collectively acknowledge that we gather at NDSU, a land grant institution, on the traditional lands of the Oceti Sakowin (Dakota, Lakota, Nakoda) and Anishinaabe Peoples in addition to many diverse Indigenous Peoples still connected to these lands. We honor with gratitude Mother Earth and the Indigenous Peoples who have walked with her throughout generations. We will continue to learn how to live in unity with Mother Earth and build strong, mutually beneficial, trusting relationships with Indigenous Peoples of our region.

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