Soil enzyme activity as affected by land-use, salinity, and groundwater fluctuations in wetland soils of the prairie pothole region

Shayeb Shahariar (shayeb.shahariar@usask.ca)
University of Saskatchewan College of Agriculture and Bioresources https://orcid.org/0000-0001-6559-0548
Bobbi Helgason
University of Saskatchewan College of Agriculture and Bioresources
Raju Soolanayakanahally
Agriculture and Agri-Food Canada
Angela Bedard-Haughn
University of Saskatchewan College of Agriculture and Bioresources

Research Article

Keywords: extracellular enzyme activities (EEAs), land-use practice, shallow groundwater table fluctuations, salinity, wetland soils, prairie pothole region (PPR)

Posted Date: June 18th, 2021

DOI: https://doi.org/10.21203/rs.3.rs-214304/v1

Version of Record: A version of this preprint was published at Wetlands on February 25th, 2021. See the published version at https://doi.org/10.1007/s13157-021-01431-8.

Abstract

Land-use change and climatic variability are significant drivers for the loss of ecosystem services and soil quality in the prairie pothole region (PPR) wetland systems. Land-use induced changes in groundwater table and salinity may influence biogeochemical processes facilitated by extracellular enzymes (EEs) involved in soil organic matter (SOM) decomposition. The effects of changing groundwater table and salinity on β-glucosidase (BG), N-acetyl glucosaminidase (NAG), and alkaline phosphatase (AP) activities were assessed in wetland soils collected from three different adjacent riparian land-use practices in the PPR. In a microcosm study conducted over ten weeks, soils were treated with groundwater salinity (control, 6 mS cm^{-1}, and 12 mS cm^{-1}) and declining groundwater table depths. Extracellular enzyme activities (EEAs) differed significantly ($p < 0.05$) among soils from different land-uses and between groundwater table depths. The impact of groundwater salinity on soil EEAs were non-significant ($p > 0.05$). Soil EEAs were significantly higher in soils from pasture, suggesting that the land-use effects resulted from background SOC and TN. Soil EEAs significantly ($p < 0.05$) reduced under a deeper groundwater table depth, except reverse for BG in site B, indicated that the lowered groundwater table could lead to transitory drought stress for SOM decomposers.

Highlights

- Wetland riparian zone land-use practices significantly impacted soil EEAs
- Land-use effects ranked PA > AC = SRW resulted from background SOC and TN in soil
- Elevated groundwater salinity decreased soil EEAs, but not significantly
- EEAs censored with declined water table showing the drying effects in soil
- Shallow groundwater table fluctuation has a significant impact on soil EEAs

1. Introduction

Extracellular enzymes (EEs) facilitated by microorganisms to acquire energy and nutrients (Sinsabaugh et al. 2009; Wallenstein and Burns 2011), are the primary mediators of biogeochemical cycling through soil organic matter (SOM) decomposition (Sinsabaugh et al. 2008; Burns et al. 2013; Luo et al. 2017). Soil hydrolytic extracellular enzyme activities (EEAs) can be used as indicators of change in soil function due to land-use practices (Trasar-Cepeda et al. 2008) and climate-linked environmental stresses (Schimel et al. 2007; Henry 2012); their activity can detect changes sooner than other soil analyses (Acosta-Martínez et al. 2007). Numerous studies have shown that EEAs were sensitive to changes in soil characteristics due to change in land-use practices (Bandick and Dick 1999; Acosta-Martínez et al. 2003a; Acosta-Martínez et al. 2003b; Wallenius et al. 2011; Stauffer et al. 2014; Tischer et al. 2015), fluctuating groundwater table depths (Pulford and Tabatabai 1988; Freeman et al. 1996; Wiedermann et al. 2017), and variations in salinity (Frankenberger and Bingham 1982; García et al. 1994; García and Hernández 1996; Pan et al. 2013; Shi et al. 2019). Therefore, EEAs have been suggested as potential indicators of soil quality, useful for understanding soil ecosystem functioning (Bandick and Dick 1999).

Wetland soils can serve as a reservoir of water, carbon, and nutrients, with fluctuations in water levels influencing the type and intensity of biogeochemical processes. The prairie pothole region (PPR) contains millions of small wetlands that support prairie grasses, habitat for migratory birds, productive agricultural land, and many further ecosystem services (Richardson and Arndt 1989; Mitsch and Gosselink 2000). With its semi-arid climate, the PPR is composed of a hydrologically distinct and highly sensitive wetland ecosystem that is vulnerable to land-use and climate change (Johnson et al. 2005; Johnson et al. 2010; Werner et al. 2013). Soils of this region experience both drought and deluge (Winter and Rosenberry 1998; Johnson et al. 2004). There is potential for future drier climatic conditions (Millett et al. 2009), jeopardizing the ecosystem services provided by the PPR due to the alteration of shallow groundwater induced by rapid evaporation and increased transpiration through wetland riparian zone land-use practices (Poiani and Johnson 1991; Poiani and Johnson 1993). Intensive agricultural land-use practices, including wetland drainage, have disturbed the native vegetation and soils throughout the PPR (Guntenspergen et al. 2002; Bartzen et al. 2010; McCauley et al. 2015). Hence, stresses related to land-use can diminish the functionality and capability of wetland ecosystems to sustain soil health and environmental quality (Rosen et al. 1995). Furthermore, hydrology research in Prairie wetlands suggests that surrounding land-use changes can significantly affect the water balance due to greater potential evapotranspiration vs. precipitation (Conly and van der Kamp 2001).

Short rotation willow (SRW) is a high biomass producing crop that was introduced in Canada during the early 1990's as an environmentally sustainable land-use practice fulfilling multiple ecological benefits including the sustainable supply of bioenergy feedstock (Amichev et al. 2014b); however, this practice is relatively new to the PPR of Saskatchewan (Amichev et al. 2014a). Establishing fast-growing SRW within the riparian zones can impact shallow groundwater hydrology and the soil water balance (Mercau et al. 2016; Caldwell et al. 2018). During the growing season, shallow groundwater can be depleted by speedy evapotranspiration from the wetland vegetation in the riparian zones (Hayashi et al. 2016), which might become critical for agricultural production and wetland management in this region and globally (Fan et al. 2013).

Land-use practices that supply elevated levels of crop residues can significantly increase the soil EEAs (Jordan et al. 1995; Bandick and Dick 1999). In cultivated soil systems, EEAs were higher where organic residues were added as compared to treatments without organic amendments (Bandick and Dick 1999); and showed that the soil β-glucosidase (BG) activities best reflect the management effects on soil quality. Soil EEAs (except α- and β-glucosidase, and α- and β-galactosidase) remained higher in the adjacent pasture (PA) compared to annual crop (AC) production (Bandick and Dick 1999). In a study with SRW compared to forestry, pasture, and agroecosystem, high laccase and phosphatase activities were observed in the forest soil compared to the other land-uses and did not significantly differ between the SRW and the other land-uses (Stauffer et al. 2014).

Salinization is a pressing environmental challenge globally (Rengasamy 2006) and a significant threat to agricultural productivity across the PPR (Eilers et al. 1997; Nachshon et al. 2014). Precipitation events contribute to shallow groundwater fluctuations and dilution of soil salinity (LaBaugh et al. 1995), whereas drought periods can concentrate salts in riparian soils (Levy et al. 2018). This oscillation in salinity (Euliss and Mushet 1996; LaBaugh et al. 2018) can also

potentially affect soil biogeochemical cycling (Holloway et al. 2011; Evenson et al. 2018) through nutrient imbalances and the lower osmotic potential of the soil solution.

Elevated soil salinity can reduce EEAs directly via the effects of osmotic potential and specific ions on enzymes and indirectly by lowering microbial biomass (Rath and Rousk 2015). For example, in a laboratory experiment, Frankenberger and Bingham (1982) found that soil β-glucosidase, phosphatase, sulfatase, amylase, and dehydrogenase activity decreased with increasing electrical conductivity (EC); however, the degree of inhibition varied among the EEAs, and the nature and amounts of salts added. Egamberdieva et al. (2011) observed that soil glucosidase, alkaline phosphatase (AP), phosphodiesterase, urease, and protease activity were inhibited by higher soil salinity treatments (5.6 and 7.1 mS cm^{-1}) compared to non-saline soil (1.3 mS cm^{-1}). Additionally, high salt concentrations are often combined with low availability of soil water and have different effects on microorganisms (Kakumanu and Williams 2014).

During drought conditions, water is held more tightly to soil aggregates as matric potential decreases (Kakumanu et al. 2013). Drought conditions created due to the decline in water table depth have shown to affect soil EEAs. For instance, β-glucosidase and phenol oxidase activities decreased with declining water table depth in a mesocosm experiment with alpine wetland (Wang et al. 2017). In a mesocosm experiment with peat monoliths in Michigan, USA, Wiedermann et al. (2017) measured hydrolytic EEAs at intermediate depth and found the reduced activity of β-glucosidase, N-acetyl glucosaminidase (NAG), alkaline phosphatase, and sulfatase except for cellulase. However, there are also conflicting results exist in literature with the water table drawdown experiment. In a field-based experiment in Welsh peatland Freeman et al. (1996) found a 31 to 67% increase in β-glucosidase, phosphatase, and sulphatase activities upon water table drawdown, suggesting that drought condition increased mineralization rate through direct stimulation of enzymes.

Understanding the interactions among climatic conditions, shallow groundwater hydrology, salinity, and biogeochemical cycling associated with prevailing land-use practices within the PPR is complex and vital. Individual effects of land-use, salinity, and groundwater table variation due to climatic variability on soil EEAs have been well documented in the literature. However, their combined effects on soil hydrolytic EEAs, especially in mineral wetlands, has not been studied before. We conducted a microcosm experiment with controlled groundwater table levels at two levels of salinity with intact soil cores collected from three adjacent riparian land-use practices from the PPR to evaluate the effects on three hydrolytic soil EEAs, i.e., β-glucosidase, N-acetyl glucosaminidase, and alkaline phosphatase. We hypothesized that soil EEAs would be: 1) higher in soils from pasture compared to annual crop and short rotation willow land-use practices, irrespective of groundwater table depths or salinity levels; 2) lower under higher salinity (groundwater EC = 12 mS cm^{-1}) due to microbial stress from increased osmotic potential; 3) lower under a reduced groundwater table level because of slower SOM decomposition resulting from a decrease in soil moisture.

2. Materials And Methods

2.1.1. Site Description and Collection of Intact Soil Cores

For the microcosm incubation experiment, 54 intact soil cores (9 cores per land-use × 3 land-uses × 2 sites; 0 to 30 cm depth) were collected from riparian zones of PPR wetlands within three different adjacent land-use areas at each of two neighboring PPR wetland sites (site A and site B) at Indian Head, Saskatchewan, Canada (N 50° 30.605'; W 103° 43.011'; 605 m in elevation) (Supplementary Fig. 1). The three contrasting land-uses included: short rotation willow = SRW, annual crop = AC, and pasture = PA. The soils of both sites are non-calcareous Black Chernozems of the Oxbow Association, with level to gentle rolling (0–10% slopes) topography formed on loamy glacial till (Saskatchewan Soil Survey Staff 1986). At both sites, short rotation willow variety *Salix dasyclados* Wimm. (cultivar 'India') was planted in June 2013 side-by-side with pasture (established 10–12 years before with alfalfa (*Medicago sativa*) and bromegrass (*Bromus madritensis*) mixture, and annual crop (cultivated oats, *Avena sativa*). All the soil cores were collected in mid-August (during the Summer of 2015) following sufficient natural warming with peak microbial activities. Intact soil cores were collected in order to avoid disturbance effects in soils produced by sieving (Reichstein et al. 2005). Cores were made with a transparent PVC-cylinder of 9 cm diameter and 30 cm height with a sharpened bottom and capped on both ends. Cores were collected with a truck-mounted hydraulic corer (Giddings Machine Company Ltd., Windsor, CO, USA) based on the landscape position and distance from the wetland basin (riparian zones under each land-use practice). Collected soil cores were transported back to Saskatoon in coolers and preserved frozen at -20 °C until the incubation experiment. One additional soil core was also collected from the same micro-location under each land-use practice from both sites for soil physiochemical properties measurements.

2.1.2. Microcosm Experimental Setup

A microcosm incubation experiment following a nested design (Schielzeth et al. 2013; Krzywinski et al. 2014) was carried out for ten weeks in the greenhouse of the University of Saskatchewan, Canada, to understand the effect of preceding land-use practices and its associated change in groundwater table depths and salinity on soil EEAs related to C, N, and P cycles. For this purpose, total 54 (2 sites × 3 land-use × 3 salinity levels × 3 replicates) intact soil cores were used from two PPR wetland sites under three land-use practices (SRW, AC, and PA), with three groundwater salinity levels (control = 0.3 mS cm^{-1}, S1 = 6 mS cm^{-1}, and S2 = 12 mS cm^{-1}) with three (n = 3) replicates (Supplementary Fig. 2).

2.1.3. Groundwater Table Manipulation and Salinity Treatments

Each experimental unit (Fig. 1) consisted of a PVC bucket (height 38.1 cm and width 30.48 cm, with 19 L capacity) to house a single intact soil core. The bottom of each bucket was layered with approximately 2.5 cm of gravel. The bottom portion of each soil core was wrapped with a piece of fiberglass screen of 1 mm (mesh size 18) opening to hold the soil securely. The top portion of the cores was kept open. The PVC cylinders casing the soil cores were punched with a uniform series of holes (with 3 cm horizontal by 7 cm vertical distance using a 3 mm diameter needle) to facilitate water movement into the core. Declining groundwater table depths were maintained from 0 cm (from the soil surface) to 29 cm (the bottom of the soil cores) depths over 10 weeks period. The groundwater table was dropped by stepping down the water table level from the surface (at 0 cm in week 0) to a depth of 2 cm (i.e., high water table) in

the first week, and then 3 cm each week for 10 weeks when it reached at the bottom of the cores at 29 cm (i.e., low water table). The water table dropdown was controlled manually by removing saline water from the container to a pre-specified depth for each week.

Groundwater salinity levels for the treatments of S1 and S2 were attained by mixing Na_2SO_4: KCl: $CaCl_2$: $MgSO_4$ salts at the ratio of 5:2:12:14 with distilled water. All these salts were chosen because they are composed of dominant cations and anions that are commonly present in the soil and groundwater in the Prairie region of Canada and the northern United States (Last and Ginn 2005). The control salinity treatment was distilled water without any salts. EC of the water was monitored weekly to maintain the groundwater salinity at the desired level. In-core soil volumetric soil water content (VSWC) and EC were also measured at the time of soil samples collection for enzyme activity analyses using a digital soil moisture meter (HydroSense II, Campbell Scientific Inc., Logan, UT, USA). The temperature and relative humidity of the greenhouse chamber used for microcosm incubation experiments were controlled at 20 ± 1 °C and an average 44%, respectively.

2.1.4. Collection of Soils for Enzyme Activity

Soils for EEAs were collected from each intact soil core at week-1 and week-10 (Fig. 1). Surface soil samples (0–10 cm depth) were collected without disturbing the soil cores as much as possible using a small stainless-steel tube. Soil samples were transferred instantly in plastic Ziploc bags to preserve the field moisture conditions and were kept on ice for transport into the laboratory immediately. All the soil samples were kept frozen at -20 °C until analyses. Gravimetric water content was calculated from a 5-g sub-sample (Topp and Ferre 2002).

2.1.5. Extracellular Soil Enzyme Activity Analyses

The activities of three soil EEs involved in the hydrolysis of organic compounds (Hydrolase group) important to soil C, N, and P cycling were carried out: β-glucosidase (EC 3.2.1.21), N-acetyl glucosaminidase (EC 3.2.1.30), and alkaline phosphatase (EC 3.1.3.1) using a MUB (4-methylumbelliferone) based high-throughput fluorometric microplate assay (Bell et al. 2013; Hargreaves and Hofmockel 2015). EEAs were determined in triplicate on 1 g of field moist/fresh soil, mixed with 125 mL Tris buffer (also known as modified universal buffer) adjusted to pH 8 (Deng et al. 2013); mixing was done in a blender at high speed for 30 s to make a homogenous slurry. While stirring on a magnetic stirrer, 1800 µL of soil slurry was taken into a 5 mL centrifuge tube where it received one of the three synthetic C-, N-, and P- rich substrates bound with 4-Methylumbelliferyl (MUF) fluorescence dye solutions (4-Methylumbelliferyl β-D-glycopyranose for BG, 4-Methylumbelliferyl N-acetyl-β-D-glucosaminide for NAG, and 4-Methylumbelliferyl phosphate for AP). Substrate amended soils were incubated for 3 hours at 24 °C at 140 rpm on a mechanical shaker. All the samples were centrifuged for 5 minutes at 2000 rpm, and 10 µL 1 M NaOH were added before centrifugation to enhance fluorescence. With an electronic pipette, 250 µL of the centrifuged solution was dispensed into each well of a black 96 well microplate. Fluorescence was determined using a FilterMax F5 Microplate Reader (Molecular Devices, USA) at the wavelengths for excitation light of 360 nm and emission light of 465 nm. The fluorescence readings of the substrate wells were converted to MUF units using a series of 4-methylumbelliferone standards in concentrations ranging from 0-100 µM (0, 2.5, 5, 10, 25, 50, 100 µM). For the correction of different quenching and autofluorescence properties of the samples, all standards were prepared with three analytical replicates in each soil suspension. Specific enzyme activity refers to the enzyme activity divided by the SOC content for each of the soils.

2.1.6. Analyses of Soil Physiochemical Properties

Each of the additional soil core collected for soil physiochemical properties were divided into three subsamples according to analysis requirements. The first subsample was air-dried, ground, and passed through 2 mm sieve for particle size distribution, cation exchange capacity (CEC), pH, electrical conductivity, ammonium acetate extractable N, and P. The second was air-dried and ground finely with a ball mill grinder for organic C, total C, and N. The third was frozen until analysis for water extractable organic carbon (WEOC) and water extractable organic nitrogen (WEON). During core sampling, soil samples for bulk densities were also collected in the field using hand-held core sampler (diameter = 5.4 cm, height = 3 cm), which were then weighed and oven-dried at 105 °C for 24 hours (Hao et al. 2008). Particle size distribution was determined by the modified pipette method (Kroetsch and Wang 2008). Soil CEC was measured by the ammonium acetate methods at pH 7 (Hendershot et al. 2008a). Soil pH was determined in 20 mL deionized water with 10 g air-dried soil samples (2 : 1 ratio) by digital pH meter (PC700 pH/mV/conductivity, Oakton, Vernon Hills, IL, USA) (Hendershot et al. 2008b). Soil EC determined in the same extract used for pH measurement after 1 hour shaking with an end-over-end shaker, then filtered (No. 42, Whatman Inc., Piscataway, NJ), and measured using digital EC meter (PC700 pH/mV/conductivity, Oakton, Vernon Hills, IL, USA) (Miller and Curtin 2008). Ammonium (NH_4-N) and nitrate (NO_3-N) were determined using 2.0M KCl (Maynard et al. 2008), and phosphate (PO_4-P) were measured using a 1M ammonium acetate (buffered at pH 7) extraction and colorimetric analysis using a Technicon Auto-Analyzer (Technicon Industrial Systems, Tarrytown, NY, USA) (Simard 1993). Total soil carbon (TSC) and soil organic carbon (SOC) were measured by dry combustion (model Leco-2000, Leco Corporation, St. Joseph, MI) (Skjemstad and Baldock 2008); carbonates were removed by HCl acid fumigation in a desiccator (Bisutti et al. 2004) for SOC measurements. Total nitrogen (TN) was determined by dry combustion with a CNS analyzer (model C632, Leco Corporation, St. Joseph, MI) (Rutherford et al. 2008). WEOC and WEON determined with fresh soil (20 ± 1 g) gently mixed with 30 mL 5 mM $CaCl_2$, then filtered through 0.45 µm polycarbonate membrane filter (Whatman Inc., Piscataway, NJ), and measured using a TOC-VCPN analyzer (Shimadzu Scientific Instruments, Kyoto, Japan) (Chantigny et al. 2008).

2.1.7. Statistical Analyses and Data Visualization

Visualization of soil enzyme data and statistical analyses were performed using R version 3.4.4 for Windows (R Core Team 2018) and the following packages “car” (Fox et al. 2018), “corrplot” (Wei et al. 2017), “ggplot2” (Wickham 2016; Wickham et al. 2018), “lmerTest” (Kuznetsova et al. 2017), “TukeyC” (Faria et al. 2018), “vegan” (Oksanen et al. 2017), and “HH” (Heiberger 2017). Linear mixed-effects models (Bolker et al. 2009; Zuur et al. 2009; Schielzeth et al. 2013) for nested design (Krzywinski et al. 2014) were used to find the difference among treatments or factors. The Shapiro-Wilk test and histogram were used to test the normality of obtained EEAs data. Homogeneity of variances or homoscedasticity was tested by Levene’s test using “car” package. For both univariate and multivariate analyses, the square root transformation was performed to improve the assumption of normality and homoscedasticity. The relationship among soil enzymes and physiochemical properties were assessed by Spearman’s rank-order correlation test and visualized using “corrplot” package. A linear

regression model was used to recognize the general relationship between applied groundwater table depths and groundwater salinity treatments using “ggplot2” package. Analysis of variance (ANOVA) with a nested design and linear mixed-effects models was used from “lmerTest” to assess significant difference (hypothesis testing) of individual EEA. The permutation multivariate ANOVA (PERMANOVA) was used to assess the significant difference of EEAs combinedly among land-use practices, groundwater salinity treatments, and between groundwater table depths. Tukey Honest Significant test (Tukey HSD) used for univariate multiple comparisons of means among treatments in case of significant effects found in ANOVA using the “TukeyC” package. Unconstrained ordination (with Bray-Curtis matrix of dissimilarities), non-metric multidimensional scale (NMDS) was used to plot the original position in multidimensional space with a reduced number of dimensions to visualize the difference between sites, among groundwater table depths, among land-use practices and groundwater salinity treatments along with soil EEAs. The linear relationship between soil physiochemical properties and EEAs were analyzed by redundancy analysis (RDA) through the development of multiple linear regression to reflect variables in the same Cartesian coordinate system. The proportional contribution of land-use practices, groundwater salinity, and water table depth to variation in soil EEAs were determined by variation partitioning analysis (VPA). The NMDS, RDA, and VPA analyses were carried out using “vegan” package. All statistical tests were statistically significant at p-values ≤ 0.05.

3. Results

3.1. Soil EEAs

3.1.1. Differences in Soil EEAs Following the Effects of Land-use Practices

The mean values of soil EEAs (BG, NAG, AP), and post-hoc multiple comparison procedure (Tukey HSD test) results are presented in Table 1. All EEAs were significantly higher ($p < 0.001$) from PA compared to the soils from AC and SRW land-use practices in both sites (Tables 1 and 2, Supplementary Fig. 3). Soil BG, NAG, and AP activities across the soils from different land-use practices were in the order of PA > SRW = AC. Compared to AC and SRW, the soils from PA are twice as high for BG, five times greater for NAG, and three times greater for AP (Table 1).

Table 1
Mean (± SE) soil EEAs, VSWC, and soil EC measured under different groundwater table levels and salinity treatments in the soil cores collected from different land-use practices at two field sites.

	Site A					Site B				
	BG	NAG	AP	VSWC	EC	BG	NAG	AP	VSWC	EC
	(nmol activity g^{-1} C h^{-1})			(%)	(mS cm^{-1})	(nmol activity g^{-1} C h^{-1})			(%)	(mS cm^{-1})
Land-use										
AC	69 ± 3.0 b	5.20 ± 0.38 b	27 ± 1.2 b	47 ± 1.11 a	3.3 ± 0.10 a	78 ± 3.1 b	5.7 ± 0.73 b	37 ± 2.8 b	47 ± 1.01 b	3.2 ± 0.08 b
PA	171 ± 15.0 a	31.10 ± 3.20 a	96 ± 10.8 a	47 ± 0.87 a	3.2 ± 0.08 a	190 ± 5.8 a	41.0 ± 3.58 a	113 ± 5.5 a	49 ± 0.90 a	3.4 ± 0.08 a
SRW	55 ± 5.0 b	4.20 ± 0.53 b	26 ± 2.7 b	47 ± 1.18 a	3.3 ± 0.11 a	98 ± 7.8 b	6.1 ± 0.52 b	33 ± 1.9 b	50 ± 0.54 a	3.5 ± 0.07 a
Salinity										
S0	92 ± 15.0 a	12.00 ± 3.00 b	53 ± 11.4 a	42 ± 0.89 c	2.8 ± 0.04 c	114 ± 13 a	20.0 ± 5.0 a	71 ± 11.4 a	46 ± 1.10 c	3.0 ± 0.05 c
S1	107 ± 17.0 a	18.00 ± 4.60 a	51 ± 10.2 a	49 ± 0.40 b	3.3 ± 0.03 b	134 ± 16 a	13.0 ± 2.0 a	61 ± 9.5 a	49 ± 0.48 b	3.4 ± 0.03 b
S2	97 ± 15.0 a	10.00 ± 2.30 b	47 ± 8.9 a	50 ± 0.11 a	3.7 ± 0.04 a	118 ± 10 a	20.0 ± 5.6 a	51 ± 7.2 a	51 ± 0.20 a	3.7 ± 0.03 a
Groundwater table										
High	127 ± 14.6 a	16.00 ± 3.50 a	69 ± 9.9 a	49 ± 0.53 a	3.3 ± 0.07 a	112 ± 11.5 b	19.0 ± 4.0 a	69 ± 4.0 a	51 ± 0.29 a	3.4 ± 0.05 a
Low	70 ± 6.6 b	11.00 ± 1.90 b	31 ± 3.4 b	46 ± 0.99 b	3.2 ± 0.09 b	132 ± 9.3 a	16.0 ± 3.3 b	53 ± 3.3 b	47 ± 0.79 b	3.3 ± 0.07 b

[a] Means within a column for land-use, salinity, and groundwater table followed by the same letter are not significantly different ($p > 0.05$) using Tukey HSD.

[b] SE = standard error, EEAs = extracellular enzyme activities, BG = β-glucosidase, NAG = N-acetyl glucosaminidase, AP = alkaline phosphatase, VSWC = volumetric soil water content, EC = electrical conductivity, AC = annual crop, PA = pasture, SRW = short rotation willow, S0 = control, S1 = 6 mS cm^{-1}, S2 = 12 mS cm^{-1}.

Table 2
Analysis of variance (ANOVA) for EEAs, VSWC, and soil EC under different groundwater salinity and water table levels in soil cores collected from three different land-use practices at two field sites.

			BG		NAG		AP		VSWC		EC	
	Sources of variation	df	F stat	p - value	F stat	p - value	F stat	p - value	F stat	p - value	F stat	p - value
Site A	Land-use	2	147.35	< 0.001 ***	80.65	< 0.001 ***	148.25	< 0.001 ***	0.08	0.930 ns	1.67	0.541 ns
	Salinity	2	3.09	0.095 ns	4.93	0.036 *	0.58	0.563 ns	122.74	< 0.001 ***	250.62	< 0.001 ***
	Groundwater table	1	122.70	< 0.001 ***	11.61	0.002 **	103.42	< 0.001 ***	49.42	< 0.001 ***	12.96	< 0.001 ***
Site B	Land-use	2	71.63	< 0.001 ***	41.52	< 0.001 ***	90.37	< 0.001 ***	7.41	0.013 *	24.63	< 0.001 ***
	Salinity	2	1.78	0.223 ns	0.22	0.809 ns	3.98	0.058 ns	30.27	< 0.001 ***	240.51	< 0.001 ***
	Groundwater table	1	21.53	< 0.001 ***	4.15	0.047 *	117.92	< 0.001 ***	62.52	< 0.001 ***	33.39	< 0.001 ***

[a] *, **, *** Indicate there is a statistically significant difference at $p \leq 0.05$, $p \leq 0.01$ and $p \leq 0.001$ level of significance, respectively; ns, is not significantly different ($p > 0.05$).

[b] EEAs = extracellular enzyme activities, VSWC = volumetric soil water content, EC = electrical conductivity, BG = β-glucosidase, NAG = N-acetyl glucosaminidase, AP = alkaline phosphatase.

The unconstrained NMDS ordination showed a robust clustering of soil EEAs based on PA land-use practice in both sites, except for AC and SRW (Fig. 2A, B, D, and E). The stress values for NMDS from both sites were less than 0.05, which provides an excellent representation of data in a reduced dimension. The NMDS analysis of soil EEAs differed considerably among land-use practices in both sites, suggesting that land-use was a key factor driving variability (Fig. 2A, B, D, and E). The multivariate permutation analysis of variance (PERMANOVA) test confirmed the significant difference among the land-use practices (p = 0.001) in both sites (Table 3). The VPA test showed that the land-use practice alone has the greatest contribution to the variation of soil EEAs in both sites (site A = 66.7%, and site B = 85.9%) (Supplementary Fig. 4).

Table 3
Permutation multivariate analysis of variance (PERMANOVA) test for EEAs under different groundwater salinity and water table levels in soil cores collected from three different land-use practices at two field sites.

		Site A			Site B		
Sources of variation	df	Pseudo-F	R^2	Pr (> F)	Pseudo-F	R^2	Pr (> F)
Land-use	2	28.13	0.53	0.001 ***	19.07	0.43	0.001 ***
Salinity	2	2.85	0.10	0.061 ns	1.17	0.04	0.317 ns
Groundwater table	1	11.27	0.18	0.001 ***	10.23	0.16	0.001 ***

[a] *, **, *** Indicate there is a statistically significant difference at $p \leq 0.05$, $p \leq 0.01$, and $p \leq 0.001$ level of significance, respectively; [ns], is not significantly different ($p > 0.05$).

[b] EEAs = extracellular enzyme activities.

3.1.2. Differences in Soil EEAs Under Groundwater Salinity Levels

The univariate ANOVA test showed no significant difference ($p > 0.05$) in soil EEAs in both sites except for NAG ($p = 0.036$) activity in site A (Tables 1 and 2). Similarly, both the NMDS and PERMANOVA tests did not show any distinct grouping or significant difference ($p > 0.05$) among the groundwater salinity treatments in both sites (Fig. 2A and D; Table 3), suggested the soil EEAs were not affected by the imposed elevated salinity levels. Groundwater salinity only accounted for 0.4% and 2.7% contribution to the variation of soil EEAs in site A and site B, respectively (Supplementary Fig. 4).

3.1.3. Differences in Soil EEAs Under Groundwater Table Depths

Overall, significantly higher ($p < 0.05$) soil EEAs were observed under higher (at week 1 = 2 cm) vs. lower groundwater table depth (at week 10 = 29 cm), suggesting that the groundwater table depth was an influencing factor driving the variability in soil EEAs (Table 2). Higher mean values for all EEAs were observed under the high water table, except for soil BG activity in site B, where the response to the water table was the opposite (Table 1), indicating that the effect of water table drawdown affected each of the enzymes differently.

The NMDS ordination showed a notable group difference between high and low groundwater table treatments (Fig. 2B and E). The PERMANOVA test indicated that the soil EEAs were significantly affected ($p = 0.001$) by groundwater table depths in both sites (Table 3). The VPA showed that the groundwater table

depth contributed 20.9% in site A and 3.4% in site B, suggesting the water table contributed to the variation of soil EEAs after the land-use practices (Supplementary Fig. 4).

3.2. Physiochemical Properties of Experimental Soil

The physiochemical properties of soils used for the microcosm experiment are presented in Table 4. No significant differences were observed in soil physicochemical properties among land-use practices and between sites except SOC, TN, SO_4^{2-} content (ANOVA results are not shown here). The SOC and TN were significantly ($p < 0.05$) higher in soils from PA compared to other land-use practices in the order of PA > SRW = AC in both sites (Table 4). However, no significant differences ($p > 0.05$) were found in SOC and TN content between sites. The SO_4^{2-} the content was approximately eight times higher in soils from site B than site A (Table 4). In the order of land-use practices, the soil SO_4^{2-} contents were SRW > PA = AC in site A, and SRW = AC > PA in site B, suggesting no observed consistent land-use patterns between sites.

Table 4
Physiochemical properties of soils used for microcosm study

Site	Land-use practice	pH	EC (mS cm^{-1})	Soil texture	Clay (%)	Bulk density (g cm^{-3})	CEC ($cmol_c$ kg^{-1})	TSC (%)	SOC (%)	WEOC (mg C kg^{-1})	TN (%)	NH_4^+-N (mg kg^{-1})	NO_3^--N (mg kg^{-1})	WEON (mg N kg^{-1})	C/N ratio	PO_4^{3-}-P (mg kg^{-1})	SO_4^{2-}-S (mg kg^{-1})
Site A	AC	8.4	1.4	CL	33.0	1.4	36.7	4.1	2.2	3.5	0.2	4.3	25.1	8.1	11.3	24.9	82.1
	PA	7.8	0.6	CL	34.0	1.3	43.9	3.4	2.9	5.2	0.3	6.7	7.0	3.7	11.6	28.5	98.2
	SRW	8.0	1.9	SCL	27.0	1.3	37.4	3.7	2.2	5.2	0.2	6.0	12.5	5.1	10.8	21.3	641.5
Site B	AC	7.8	1.0	CL	33.0	1.3	48.7	3.1	2.5	5.9	0.2	6.0	17.0	4.5	9.8	30.0	2353.2
	PA	8.0	2.6	CL	32.0	1.2	42.5	4.9	2.7	4.6	0.3	5.2	33.4	8.1	10.8	31.2	274.4
	SRW	7.8	2.8	CL	30.0	1.4	45.9	2.8	2.4	6.2	0.3	6.3	13.9	4.3	9.4	37.8	3496.2

[a] AC = annual crop, PA = pasture, SRW = short rotation willow, EC = electrical conductivity, CL = clay loam, SCL = sandy clay loam, CEC = cation exchange capacity, TSC = total soil carbon, SOC = soil organic carbon, WEOC = water-extractable organic carbon, TN = total nitrogen, WEON = water-extractable organic nitrogen, C/N ratio = carbon and nitrogen ratio.

3.2.1. Relationships of EEAs with Soil Physiochemical Properties

The relationships between soil EEAs (BG, NAG, and AP) with soil clay content, SOC, and TN were significantly ($p < 0.05$) positive, whereas for bulk density it was significantly ($p < 0.05$) negative (Fig. 3). Besides, soil EEAs were positively correlated with VSWC, EC (due to the salinity treatment), CEC, NH_4^+, NO_3^-, C/N ratio, and PO_4^{3-}, whereas negatively correlated with pH, background EC, WEOC, WEON, and SO_4^{2-}, however, not significantly ($p > 0.05$) (Fig. 3).

3.2.2. Redundancy Analysis (RDA) Between Soil Physiochemical Properties and EEAs

Redundancy analysis (RDA) was performed to explore the relationship of soil physiochemical properties with EEAs shown (Fig. 2C and F). The first two component axes explained 67.87% and 0.29% of site A (Fig. 2C), and 81.36% and 2.33% (Fig. 2F) of site B of soil EAAs, respectively. The vector lines of SOC, VSWC, EC from site A, and SOC, TN, EC from site B were statistically significant ($p < 0.05$), showing that SOC played a better role in explaining soil EEAs in both sites. Significant positive correlations ($p < 0.05$) observed between SOC and soil EEAs in both sites A and B (Fig. 2C and F). The relationship between TN and soil EEAs were positive and significant ($p < 0.05$) in site B, but not significant ($p > 0.05$) in site A.

3.2.3. Relationships of Soil EEAs with VSWC and EC Measured During the Microcosm Experiment

Groundwater salinity manipulation resulted in a statistically significant difference ($p < 0.05$) in soil EC among different salinity treatment levels (in S1 and S2 compared to control) in both sites (Tables 1 and 2). Similarly, water table manipulation resulted in a significant difference ($p < 0.05$) in observed VSWC between high and low groundwater table depths in both sites. We did not find any significant difference ($p > 0.05$) in VSWC or EC among land-use practices from site A ($p > 0.05$); however, we found a significant difference ($p < 0.05$) in site B because of groundwater salinity and water table manipulation (Tables 1 and 2). We also observed a significant ($p < 0.05$) positive relationship between soil EC and VSWC in both sites (Fig. 3 and Supplementary Fig. 5) during the incubation experiment.

4. Discussion

4.1. Land-use, Groundwater Salinity, and Water Table Effects on Soil EEAs

4.1.1. Land-use

In this experiment, the highest soil EEAs were observed in soils from PA land-use practice compared to AC and SRW, suggesting higher microbial activity in grassland soil. Soils from PA land-use practice have the highest SOC, TN, and overall PO_4-P contents, and reflected the highest soil EEAs in our study, perhaps due to the faster SOC alteration and balanced substrate availability in PA soils that differ from other land-use practices. Similarly, a three-fold increase in microbial biomass was observed, indicating increased catalytic efficiency and faster turnover of substrates along a land-use sequence from forest to young

(20-years) pasture (Tischer et al. 2015). We observed a clear grouping for PA from the NMDS ordination plot in both sites and significant linear relationships between EEAs with SOC and TN from RDA analysis. Wallenius et al. (2011) observed decreased EEAs activity in the order of forest organic layer ≈ forest mineral layer > meadow grassland > crop field in a plot-scale study. Likewise, the microbial community structure is highly specific to land-use practices, and SOM content is the primary reason for the variation of both structural and functional properties of soil microorganisms (Wallenius et al. 2011). In a regional-scale study, Cenini et al. (2016) observed a positive relationship between SOC content and BG activity, and L-leucine amino-peptidase (LAP) + NAG activity with a soil N content of grassland soils. Kuramae et al. (2012) found that soil factors (SOC, TN, PO_4-P, and pH) had a more robust impact on soil bacteria than the land-use practices. At the metabolic scale, the proportionality constant that connects C:N:P stoichiometry of organic matter and enzymatic activities controls the elasticity of extracellular enzymatic reactions (Sinsabaugh et al. 2014). However, over large geographic areas where different land-uses has resulted from the difference in inherent soil characteristics, predictably have more influence on soil properties over land-use practices itself.

We found highly significant effects of land-use practices on soil EEAs. Yet, it can be said that the specific soil properties that resulted from different land-use practices influenced these differences (Bowles et al. 2014). In general, the type of land-use practice indicates soil use that can influence SOC content and thus the effects on soil EEAs through the breakdown process of SOM and the loss of labile organic carbon (Trasar-Cepeda et al. 2008). In a field experiment, Bandick and Dick (1999) found higher EEAs in the continuous grass field than in cultivated fields except for α- and β-glucosidase. A global-scale meta-analysis in soils from 40 ecosystems Sinsabaugh et al. (2008) observed increased activities of β-glucosidase, N-acetyl glucosaminidase, and phosphatase with increased SOM content. Consequently, it indicated that hydrolyzing capability of the SOM depends on enzymatic stoichiometry, which links the elemental stoichiometry of microbial biomass and detrital organic matter to microbial nutrient assimilation and growth (Sinsabaugh and Follstad Shah 2012).

In addition to land-use practice, tillage can impact different biological attributes including soil microbial biomass, soil organic C, and N. We used intact soil cores from the cultivated AC with conventional tillage, which might be the most likely reason for relatively lower SOC content, and lower EEAs compared to pasture land-use. For instance, Gupta and Germida (1988) compared soil EEAs between cultivated and adjacent native PA soil in Canadian Prairie and found that tillage suppressed 49% phosphatase and 65% arylsulphatase activity. Acosta-Martínez et al. (2003a) found lower EEAs in continuous cropland than reserve grassland and native rangeland, and a strong relationship with SOC and TN. In semi-arid agricultural land of west Texas, Acosta-Martínez et al. (2003b) observed increased soil β-glucosidase, β-glucosaminidase, alkaline phosphatase, and arylsulfatase activities under general crop rotation and conservation tillage compared to a single crop and conventional tillage. Hence, it suggested that the production of EEs and C turnover rapidly occur in particulate organic matter fractions, thus increased by physical disruption of soil structure associated with tillage Allison and Jastrow (2006).

Soil EEAs were not significantly different between AC and SRW, and significantly lower compared to PA land-use practices from both sites in our experiment, most probably because of observed non-distinguishable variabilities in SOC and TN content. However, several studies on SRW suggested conflicting results regarding SOC accumulation compared to other land-use practices. For example, the topsoil SOC increased under SRW plantation, on former agricultural land compared to conventional AC (Dimitriou et al. 2012), adjoining agricultural fields (Lafleur et al. 2015); not increased significantly compared to grassland (Harris et al. 2017), after re-conversion to arable land (Toenshoff et al. 2013); and no significant change after conversion to SRW compared to no-till alfalfa field and buckwheat field (Lockwell et al. 2012). Three years after the conversion of arable land to the SRW promoted fungal abundance; however, soil alkaline phosphatase, cellobiohydrolase, and phenoloxidase were higher than AC soils but lower than forest and PA soils (Stauffer et al. 2014).

4.1.2. Salinity

We did not find any significant effects of groundwater salinity treatments during our experiment. Previous studies have reported that salinity can suppress soil EEAs, and all enzymes are not equally sensitive to the salinity (Pan et al. 2013). For example, García and Hernández (1996) observed a higher degree of hydrolase (β-glucosidase and phosphatase) inhibition by salinity compared to oxidoreductases (dehydrogenase and catalase). The reduction of EEAs in saline soil is primarily due to the lower microbial biomass, osmotic potential, and specific ion effects of the salts present (Rath and Rousk 2015). Shi et al. (2019) found that the addition of organic amendments can increase microbial biomass and EEAs in saline-alkaline soil, suggesting that SOM can improve SOC and nutrient conditions for microbial activity due to higher substrate availability. Likewise, the addition of readily decomposable substrate can improve microbial salt tolerance (Wong et al. 2008; Mavi and Marschner 2013). We observed relatively high enzyme activity in site B, despite a slightly higher mean background soil salinity than site A; however, none of our sites can be classified as saline soil as the average EC was < 4 mS cm^{-1}.

4.1.3. Water Table

Soil EEAs were significantly reduced by lowered groundwater table depth (i.e., higher depth to GWT) compared to shallower water tables, except for BG in site B, which was opposite, which suggested that the lowered groundwater table can lead to transitory drought stress for SOM decomposers. In a mesocosm experiment with peat soil, Wiedermann et al. (2017) observed a similar result with the greatest groundwater table drawdown effect shown by the phosphatase enzyme. In a mesocosm experiment with declining water table depth from 0 to 20 cm in Alpine wetland soil, Wang et al. (2017) found a significant decrease in β-glucosidase and phenol oxidase activities. In a field-based water table drawdown experiment with peat soil, Freeman et al. (1996) found that β-glucosidase and phosphatase activities were raised between 31 to 67% with a water table drawdown without a corresponding increase in microbial respiration. Therefore, the authors suggested a direct stimulation of existing enzymes rather than stimulation of new enzyme synthesis as the cause. Henry (2012) proposed three hypothetical models to predict the variation of EEAs with soil moisture gradients (poorly-drained, a well-drained, arid) that suggested in a poorly-drained water-saturated (anaerobic) soil; initial water table drawdown can stimulate enzyme activity, whereas further drying can reduce EEAs through the restriction of water. Perhaps a similar response explained the quadratic response of EEAs to water table drawdown and consequent changes in moisture status in our experiment. Three roles of water have been suggested: 1) as a resource to maintain water potential, 2) as a solvent, and 3) as a transport medium. Thus depending on conditions, water as a resource might be the least important regulator of soil biogeochemical processes (Schimel 2018). Roles as both a solvent and a transport medium are critical as the majority of organic substances are water-soluble, and the movement of chemicals in solution from sources to microorganisms regulate metabolism (Schimel and Schaeffer 2012).

The effects of physiochemical properties of *in situ* soil are not discrete. Even under ideal conditions, one individual factor seldom solely drives soil biogeochemical processes because of interactions among soil properties. However, one particular factor might dominate the soil's ecological processes, such as SOM decomposition. Specific management practices within agroecosystems, such as the addition of plant residues, can also interact with soil moisture and affect EEA. Geisseler et al. (2011) found that the addition of crop residues in a combination of higher soil moisture likely increase protease, β - glucosidase, glucosaminidase, and exocellulase activities, whereas EEAs were less affected by higher soil moisture when no residues were added. As a result, it was hypothesized that the presence of the substrate potential of EEAs might be decoupled from microbial biomass size and respiration under dry moisture conditions. The total soil water potential is the result of both osmotic and matric potential in soil (Kakumanu and Williams 2014). Likewise, low soil water content with lower matric potential and low osmotic potential due to salinity in the soil is typical in semi-arid regions (Chowdhury et al. 2011). However, it is tough to differentiate the distinct effect of water potential and osmotic potential (Chowdhury et al. 2011) as microbes have a similar mechanism to react to drought and for high salt concentrations in soil (Schimel et al. 2007).

4.2. Soil Physiochemical Properties and EEAs

The relationships were variable among all EEAs with physiochemical properties of the experimental soils. Soil EEAs were positively correlated with clay content, even though there was no significant variation among land-use practices or sites. Clay content has little explanatory power to reflect the SOM cycling compared to other physiochemical properties in the soil (Rasmussen et al. 2018). A significant negative correlation observed between soil EEAs with bulk density, and a positive correlation with initial SOC and TN content, which agrees with the findings of Dick et al. (1988) and Xie et al. (2017) indicating that direct and/or indirect links with microbial functions for continuing the soil enzymatic activities (Sinsabaugh et al. 2008; Allison et al. 2011). Soil pH can affect soil nutrients availability, decomposition of SOC, and activity and diversity of microorganisms that are involved in soil biochemical reactions, including soil EEAs (Dick et al. 2000). We observed a minor non-significant variation in initial experimental soil texture and pH. According to Sinsabaugh et al. (2008), soil hydrolytic enzymes are more stable under conditions of small pH variation compared to oxidative soil EEAs. None of the remaining soil properties were correlated significantly with soil EEAs except soil NH_4-N and PO_4-P with BG activity. The microbial economic theory suggests that microbes produce extracellular enzymes that target essential macronutrients only if they are deficient (Allison et al. 2011). It has been suggested that soil physiochemical properties, as well as microorganisms, are highly heterogeneous, which may vary significantly over temporal and spatial scales (Baker et al. 2009). However, contrasting land-use practices within a single PPR wetland system is more likely to influence soil physicochemical properties, especially C, N, and P, from similar soil characteristics.

5. Conclusions

The results of this study suggest that land-use practice had the most significant impact on soil EEAs. Significantly higher EEAs in soils from PA point to the higher SOC turnover from the past land-use practices, while no significant difference was observed between AC and SRW due to non-distinguishable variabilities background SOC and TN content of our experimental soil. We found a significant effect of groundwater drawdown on soil EEAs. However, no significant effects were distinguished for salinity treatments recommended that EEAs (BG, NAG, and AP) in soil feasibly respond to the differences in resource availability attributable to land-use and metabolic limitation as a result of interacting effects of shifting groundwater tables and salinity.

Subsequently, under all land-use practices, SOC content was the primary parameter that influences all biological activity and is highly correlated with all soil EEAs. Significant differences in SOC, TN, and nutrients were indicative of possible alterations in soil microbial activities and could mediate the variation in EEAs among land-use practices. However, using *in-situ* enzyme activity as an indicator of land-use practices can be challenging as they can vary between different soil and different enzymes as well as at a spatial scale. Therefore, interrelating effects of land-use practices in combination with fluctuating shallow groundwater table and salinity on the structure and functioning of the soil microbial community in a field setting is required to enhance our understanding of the PPR wetland soils.

Declarations

Funding: This work was financially supported by a Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant to ABH (RGPIN-2017-05909); and Agriculture and Agri-Food Canada (AAFC) A-Base research funding to RS (LOI 1231). Also, SS received funding support from AAFC's Research Affiliate Program. The funding agency had no role in study design, data collection and analysis, the decision to publish, or preparation of the manuscript.

Conflicts of interest/Competing interests: The authors declare no conflict of interest/competing interests.

Ethics approval: This article does not contain any studies with human or animal subjects performed by the any of the authors.

Consent to participate: Not applicable

Consent for publication: Not applicable

Availability of data and material: All relevant data and materials from this experiment are included in the supplementary materials.

Code availability (software application or custom code): Not applicable

Authors' contributions: SS conceptualized; designed and performed the experiment - methodology; formal analysis and investigation; wrote original draft; reviewed and edited the manuscript. BH contributed to methodology - enzyme analysis; resources; reviewed and edited the manuscript. RS contributed to

funding acquisition; resources; reviewed and edited the manuscript. ABH contributed to supervision; resources; funding acquisition; reviewed and edited the manuscript. All authors read and approved the final manuscript

References

1. Acosta-Martínez V, Cruz L, Sotomayor-Ramírez D, Pérez-Alegría L (2007) Enzyme activities as affected by soil properties and land use in a tropical watershed. Appl Soil Ecol 35:35–45. http://doi.org/10.1016/j.apsoil.2006.05.012
2. Acosta-Martínez V, Klose S, Zobeck TM (2003a) Enzyme activities in semiarid soils under conservation reserve program, native rangeland, and cropland. J Plant Nutr Soil Sci 166:699–707. http://doi.org/10.1002/jpln.200321215
3. Acosta-Martínez V, Zobeck TM, Gill TE, Kennedy AC (2003b) Enzyme activities and microbial community structure in semiarid agricultural soils. Biol Fertil Soils 38:216–227. http://doi.org/10.1007/s00374-003-0626-1
4. Allison SD, Jastrow JD (2006) Activities of extracellular enzymes in physically isolated fractions of restored grassland soils. Soil Biol Biochem 38:3245–3256. http://doi.org/10.1016/j.soilbio.2006.04.011
5. Allison SD, Weintraub MN, Gartner TB, Waldrop MP (2011) Evolutionary-Economic Principles as Regulators of Soil Enzyme Production and Ecosystem Function. In: Shukla G, Varma A (eds) Soil Enzymology. Springer, Berlin Heidelberg, pp 229–243. http://doi.org/10.1007/978-3-642-14225-3_12
6. Amichev BY, Hangs RD, Bélanger N, Volk TA, Vujanovic V, Schoenau JJ, Van Rees KCJ (2014a) First-Rotation Yields of 30 Short-Rotation Willow Cultivars in Central Saskatchewan, Canada. BioEnergy Research:1–15. http://doi.org/10.1007/s12155-014-9519-4
7. Amichev BY, Hangs RD, Konecsni SM, Stadnyk CN, Volk TA, Bélanger N, Vujanovic V, Schoenau JJ, Moukoumi J, Van Rees KCJ (2014b) Willow Short-Rotation Production Systems in Canada and Northern United States: A Review. Soil Sci Soc Am J 78:S168–S182. http://doi.org/10.2136/sssaj2013.08.0368nafsc
8. Baker KL, Langenheder S, Nicol GW, Ricketts D, Killham K, Campbell CD, Prosser JI (2009) Environmental and spatial characterisation of bacterial community composition in soil to inform sampling strategies. Soil Biol Biochem 41:2292–2298. http://doi.org/10.1016/j.soilbio.2009.08.010
9. Bandick AK, Dick RP (1999) Field management effects on soil enzyme activities. Soil Biol Biochem 31:1471–1479. http://doi.org/10.1016/S0038-0717(99)00051-6
10. Bartzen BA, Dufour KW, Clark RG, Caswell FD (2010) Trends in agricultural impact and recovery of wetlands in prairie Canada. Ecol Appl 20:525–538. http://doi.org/10.1890/08-1650.1
11. Bell CW, Fricks BE, Rocca JD, Steinweg JM, McMahon SK, Wallenstein MD (2013) High-throughput Fluorometric Measurement of Potential Soil Extracellular Enzyme Activities. Journal of Visualized Experiments: JoVE:50961. http://doi.org/10.3791/50961
12. Bisutti I, Hilke I, Raessler M (2004) Determination of total organic carbon – an overview of current methods. TrAC Trends Anal Chem 23:716–726. http://doi.org/10.1016/j.trac.2004.09.003
13. Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MH, White JS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol Evol 24:127–135. http://doi.org/10.1016/j.tree.2008.10.008
14. Bowles TM, Acosta-Martínez V, Calderón F, Jackson LE (2014) Soil enzyme activities, microbial communities, and carbon and nitrogen availability in organic agroecosystems across an intensively-managed agricultural landscape. Soil Biol Biochem 68:252–262. http://doi.org/10.1016/j.soilbio.2013.10.004
15. Burns RG, DeForest JL, Marxsen J, Sinsabaugh RL, Stromberger ME, Wallenstein MD, Weintraub MN, Zoppini A (2013) Soil enzymes in a changing environment: current knowledge and future directions. Soil Biol Biochem 58:216–234. http://doi.org/10.1016/j.soilbio.2012.11.009
16. Caldwell PV, Jackson CR, Miniat CF, Younger SE, Vining JA, McDonnell JJ, Aubrey DP (2018) Woody bioenergy crop selection can have large effects on water yield: A southeastern United States case study. Biomass Bioenerg 117:180–189. http://doi.org/10.1016/j.biombioe.2018.07.021
17. Cenini VL, Fornara DA, McMullan G, Ternan N, Carolan R, Crawley MJ, Clément J-C, Lavorel S (2016) Linkages between extracellular enzyme activities and the carbon and nitrogen content of grassland soils. Soil Biol Biochem 96:198–206. http://doi.org/10.1016/j.soilbio.2016.02.015
18. Chantigny MH, Angers DA, Kaiser K, Kalbitz K (2008) Extraction and Characterization of Dissolved Organic Matter. In Carter MR and Gregorich EG (eds.), Soil Sampling and Methods of Analysis, Second Edition. CRC Press. http://doi.org/10.1201/9781420005271.ch48
19. Chowdhury N, Marschner P, Burns R (2011) Response of microbial activity and community structure to decreasing soil osmotic and matric potential. Plant Soil 344:241–254. http://doi.org/10.1007/s11104-011-0743-9
20. Conly FM, van der Kamp G (2001) Monitoring the hydrology of Canadian prairie wetlands to detect the effects of climate change and land use changes. Environ Monit Assess 67:195–215. http://doi.org/10.1023/A:1006486607040
21. Deng S, Popova IE, Dick L, Dick R (2013) Bench scale and microplate format assay of soil enzyme activities using spectroscopic and fluorometric approaches. Appl Soil Ecol 64:84–90. http://doi.org/10.1016/j.apsoil.2012.11.002
22. Dick RP, Myrold DD, Kerle EA (1988) Microbial Biomass and Soil Enzyme Activities in Compacted and Rehabilitated Skid Trail Soils. Soil Sci Soc Am J 52:512–516. http://doi.org/10.2136/sssaj1988.03615995005200020038x
23. Dick WA, Cheng L, Wang P (2000) Soil acid and alkaline phosphatase activity as pH adjustment indicators. Soil Biol Biochem 32:1915–1919. http://doi.org/10.1016/S0038-0717(00)00166-8
24. Dimitriou I, Mola-Yudego B, Aronsson P, Eriksson J (2012) Changes in Organic Carbon and Trace Elements in the Soil of Willow Short-Rotation Coppice Plantations. BioEnergy Research 5:563–572. http://doi.org/10.1007/s12155-012-9215-1

25. Egamberdieva D, Renella G, Wirth S, Islam R (2011) Enzyme Activities in the Rhizosphere of Plants. In: Shukla G, Varma A (eds) Soil Enzymology. Springer, Berlin Heidelberg, pp 149–166. http://doi.org/10.1007/978-3-642-14225-3_8
26. Eilers R, Eilers W, Fitzgerald M (1997) A salinity risk index for soils of the Canadian Prairies. Hydrogeol J 5:68–79. http://doi.org/10.1007/s100400050118
27. Euliss NH, Mushet DM (1996) Water-level fluctuation in wetlands as a function of landscape condition in the prairie pothole region. Wetlands 16:587–593. http://doi.org/10.1007/BF03161350
28. Evenson GR, Golden HE, Lane CR, McLaughlin DL, D'Amico E (2018) Depressional wetlands affect watershed hydrological, biogeochemical, and ecological functions. Ecol Appl 28:953–966. http://doi.org/10.1002/eap.1701
29. Fan Y, Li H, Miguez-Macho G (2013) Global Patterns of Groundwater Table Depth. science, 339:940. http://doi.org/10.1126/science.1229881
30. Faria JC, Jelihovschi EG, Allaman IB (2018) R Package "TukeyC": Conventional Tukey Test. Version 1.3-0. https://cran.r-project.org/web/packages/TukeyC/index.html
31. Fox J, Weisberg S, Price B, Adler D, Bates D, Baud-Bovy G, Bolker B, Ellison S, Firth D, Friendly M, Gorjanc G, Graves S, Heiberger R, Laboissiere R, Maechler M, Monette G, Murdoch D, Nilsson H, Ogle D, Ripley B, Venables W, Walker S, Winsemius D, Zeileis A (2018) R Package "car": Companion to Applied Regression. Version 3:0–2. https://cran.r-project.org/web/packages/car/index.html
32. Frankenberger WT, Bingham FT (1982) Influence of Salinity on Soil Enzyme Activities. Soil Sci Soc Am J 46:1173–1177. http://doi.org/10.2136/sssaj1982.03615995004600060011x
33. Freeman C, Liska G, Ostle NJ, Lock MA, Reynolds B, Hudson J (1996) Microbial activity and enzymic decomposition processes following peatland water table drawdown. Plant Soil 180:121–127. http://doi.org/10.1007/BF00015418
34. García C, Hernández T (1996) Influence of salinity on the biological and biochemical activity of a calciorthird soil. Plant Soil 178:255–263. http://doi.org/10.1007/bf00011591
35. García C, Hernández T, Costa F (1994) Microbial activity in soils under Mediterranean environmental conditions. Soil Biol Biochem 26:1185–1191. http://doi.org/10.1016/0038-0717(94)90142-2
36. Geisseler D, Horwath WR, Scow KM (2011) Soil moisture and plant residue addition interact in their effect on extracellular enzyme activity. Pedobiologia 54:71–78. http://doi.org/10.1016/j.pedobi.2010.10.001
37. Guntenspergen GR, Peterson SA, Leibowitz SG, Cowardin LM (2002) Indicators of wetland condition for the Prairie Pothole Region of the United States. Environ Monit Assess 78:229–252. http://doi.org/10.1023/A:1019982818231
38. Gupta VVSR, Germida JJ (1988) Distribution of microbial biomass and its activity in different soil aggregate size classes as affected by cultivation. Soil Biol Biochem 20:777–786. http://dx.doi.org/10.1016/0038-0717(88)90082-X
39. Hao X, Ball BC, Culley JLB, Cater MR, Parkin GW (2008) Soil Density and Porosity. In Carter MR and Gregorich EG (eds.), Soil Sampling and Methods of Analysis, Second Edition. CRC Press. http://doi.org/10.1201/9781420005271.ch57
40. Hargreaves SK, Hofmockel KS (2015) A modified incubation method reduces analytical variation of soil hydrolase assays. European Journal of Soil Biology 67:1–4. http://doi.org/10.1016/j.ejsobi.2014.12.002
41. Harris ZM, Alberti G, Viger M, Jenkins JR, Rowe R, McNamara NP, Taylor G (2017) Land-use change to bioenergy: grassland to short rotation coppice willow has an improved carbon balance. GCB Bioenergy 9:469–484. http://doi.org/10.1111/gcbb.12347
42. Hayashi M, van der Kamp G, Rosenberry DO (2016) Hydrology of Prairie Wetlands: Understanding the Integrated Surface-Water and Groundwater Processes. Wetlands 36:237–254. http://doi.org/10.1007/s13157-016-0797-9
43. Heiberger RM (2017) R Package "HH": Statistical Analysis and Data Display: Heiberger and Holland. Version 3.1–34. https://cran.r-project.org/web/packages/HH/index.html
44. Hendershot WH, Lalande H, Duquette M (2008a) Ion Exchange and Exchangeable Cations. In Carter MR and Gregorich EG (eds.), Soil Sampling and Methods of Analysis, Second Edition. CRC Press. http://doi.org/10.1201/9781420005271.ch18
45. Hendershot WH, Lalande H, Duquette M (2008b) Soil Reaction and Exchangeable Acidity. In Carter MR and Gregorich EG (eds.), Soil Sampling and Methods of Analysis, Second Edition. CRC Press. http://doi.org/10.1201/9781420005271.ch16
46. Henry HAL (2012) Soil extracellular enzyme dynamics in a changing climate. Soil Biol Biochem 47:53–59. http://doi.org/10.1016/j.soilbio.2011.12.026
47. Holloway JM, Goldhaber MB, Mills CT (2011) Carbon and nitrogen biogeochemistry of a Prairie Pothole wetland, Stutsman County, North Dakota, USA. Appl Geochem 26:S44–S47. http://doi.org/10.1016/j.apgeochem.2011.03.025
48. Johnson WC, Boettcher SE, Poiani KA, Guntenspergen G (2004) Influence of weather extremes on the water levels of glaciated prairie wetlands. Wetlands 24:385–398. http://doi.org/10.1672/0277-5212(2004)024[0385:IOWEOT]2.0.CO;2
49. Johnson WC, Millett BV, Gilmanov T, Voldseth RA, Guntenspergen GR, Naugle DE (2005) Vulnerability of northern prairie wetlands to climate change. Bioscience 55:863–872. http://doi.org/10.1641/0006-3568(2005)055[0863:VONPWT]2.0.CO;2
50. Johnson WC, Werner B, Guntenspergen GR, Voldseth RA, Millett B, Naugle DE, Tulbure M, Carroll RWH, Tracy J, Olawsky C (2010) Prairie Wetland Complexes as Landscape Functional Units in a Changing Climate. Bioscience 60:128–140. http://doi.org/10.1525/bio.2010.60.2.7
51. Jordan D, Kremer RJ, Bergfield WA, Kim KY, Cacnio VN (1995) Evaluation of microbial methods as potential indicators of soil quality in historical agricultural fields. Biol Fertil Soils 19:297–302. https://doi.org/10.1007/BF00336098
52. Kakumanu ML, Cantrell CL, Williams MA (2013) Microbial community response to varying magnitudes of desiccation in soil: A test of the osmolyte accumulation hypothesis. Soil Biol Biochem 57:644–653. https://doi.org/10.1016/j.soilbio.2012.08.014

53. Kakumanu ML, Williams MA (2014) Osmolyte dynamics and microbial communities vary in response to osmotic more than matric water deficit gradients in two soils. Soil Biol Biochem 79:14–24. https://doi.org/10.1016/j.soilbio.2014.08.015
54. Kroetsch D, Wang C (2008) Particle Size Distribution. In Carter MR and Gregorich EG (eds.), Soil Sampling and Methods of Analysis, Second Edition. CRC Press. https://doi.org/10.1201/9781420005271.ch55
55. Krzywinski M, Altman N, Blainey P (2014) Nested designs. Nat Methods 11:977–978. http://doi.org/10.1038/nmeth.3137
56. Kuramae EE, Yergeau E, Wong LC, Pijl AS, van Veen JA, Kowalchuk GA (2012) Soil characteristics more strongly influence soil bacterial communities than land-use type. FEMS Microbiol Ecol 79:12–24. https://doi.org/10.1111/j.1574-6941.2011.01192.x
57. Kuznetsova A, Brockhoff PB, Christensen RHB (2017) lmerTest Package: Tests in Linear Mixed Effects Models. J Stat Softw, 82. http://doi.org/10.18637/jss.v082.i13
58. LaBaugh JW, Rosenberry DO, Mushet DM, Neff BP, Nelson RD, Euliss NH (2018) Long-term changes in pond permanence, size, and salinity in Prairie Pothole Region wetlands: The role of groundwater-pond interaction. Journal of Hydrology: Regional Studies 17:1–23. https://doi.org/10.1016/j.ejrh.2018.03.003
59. LaBaugh JW, Rosenberry DO, Winter TC (1995) Groundwater contribution to the water and chemical budgets of Williams Lake, Minnesota, 1980–1991. Can J Fish Aquat Sci 52:754–767. https://doi.org/10.1139/f95-075
60. Lafleur B, Labrecque M, Arnold AA, Belanger N (2015) Organic Carbon Accumulation in Topsoil Following Afforestation with Willow: Emphasis on Leaf Litter Decomposition and Soil Organic Matter Quality. Forests 6:769–793. https://doi.org/10.3390/f6030769
61. Last WM, Ginn FM (2005) Saline systems of the Great Plains of western Canada: an overview of the limnogeology and paleolimnology. Saline Systems 1:10. http://doi.org/10.1186/1746-1448-1-10
62. Levy ZF, Rosenberry DO, Moucha R, Mushet DM, Goldhaber MB, LaBaugh JW, Fiorentino AJ, Siegel DI (2018) Drought-induced recharge promotes long-term storage of porewater salinity beneath a prairie wetland. J Hydrol 557:391–406. https://doi.org/10.1016/j.jhydrol.2017.12.005
63. Lockwell J, Guidi W, Labrecque M (2012) Soil carbon sequestration potential of willows in short-rotation coppice established on abandoned farm lands. Plant Soil 360:299–318. https://doi.org/10.1007/s11104-012-1251-2
64. Luo L, Meng H, Gu JD (2017) Microbial extracellular enzymes in biogeochemical cycling of ecosystems. J Environ Manage 197:539–549. http://doi.org/10.1016/j.jenvman.2017.04.023
65. Mavi MS, Marschner P (2013) Salinity affects the response of soil microbial activity and biomass to addition of carbon and nitrogen. Soil Research 51:68. https://doi.org/10.1071/sr12191
66. Maynard DG, Kalra YP, Crumbaugh JA (2008) Nitrate and Exchangeable Ammonium Nitrogen. In Carter MR and Gregorich EG (eds.), Soil Sampling and Methods of Analysis, Second Edition. CRC Press. http://doi.org/10.1201/9781420005271.ch6
67. McCauley LA, Anteau MJ, van der Burg MP, Wiltermuth MT (2015) Land use and wetland drainage affect water levels and dynamics of remaining wetlands. Ecosphere 6:1–22. https://doi.org/10.1890/ES14-00494.1
68. Mercau JL, Nosetto MD, Bert F, Giménez R, Jobbágy, EG (2016) Shallow groundwater dynamics in the Pampas: Climate, landscape and crop choice effects. Agric Water Manag 163:159–168. https://doi.org/10.1016/j.agwat.2015.09.013
69. Miller JJ, Curtin D (2008) Electrical Conductivity and Soluble Ions. In Carter MR and Gregorich EG (eds.), Soil Sampling and Methods of Analysis, Second Edition. CRC Press. http://doi.org/10.1201/9781420005271.ch15
70. Millett B, Johnson WC, Guntenspergen G (2009) Climate trends of the North American prairie pothole region 1906–2000. Clim Change 93:243–267. http://doi.org/10.1007/s10584-008-9543-5
71. Mitsch WJ, Gosselink JG (2000) The value of wetlands: importance of scale and landscape setting. Ecological economics 35:25–33. https://doi.org/10.1016/S0921-8009(00)00165-8
72. Nachshon U, Ireson A, van der Kamp G, Davies SR, Wheater HS (2014) Impacts of climate variability on wetland salinization in the North American prairies. Hydrol Earth Syst Sci 18:1251–1263. https://doi.org/10.5194/hess-18-1251-2014
73. Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2017) R Package "vegan": Community Ecology Package. Version 2.4-6. https://cran.r-project.org/web/packages/vegan/index.html
74. Pan C, Liu C, Zhao H, Wang Y (2013) Changes of soil physico-chemical properties and enzyme activities in relation to grassland salinization. European Journal of Soil Biology 55:13–19. http://doi.org/10.1016/j.ejsobi.2012.09.009
75. Poiani KA, Johnson WC (1991) Global warming and prairie wetlands. Bioscience 41:611–618. http://doi.org/10.2307/1311698
76. Poiani KA, Johnson WC (1993) A Spatial Simulation Model of Hydrology and Vegetation Dynamics in Semi-Permanent Prairie Wetlands. Ecol Appl 3:279–293. https://doi.org/10.2307/1941831
77. Pulford ID, Tabatabai MA (1988) Effect of waterlogging on enzyme activities in soils. Soil Biol Biochem 20:215–219. http://doi.org/10.1016/0038-0717(88)90039-9
78. R Core Team (2018) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/
79. Rasmussen C, Heckman K, Wieder WR, Keiluweit M, Lawrence CR, Berhe AA, Blankinship JC, Crow SE, Druhan JL, Hicks Pries CE, Marin-Spiotta E, Plante AF, Schädel C, Schimel JP, Sierra CA, Thompson A, Wagai R (2018) Beyond clay: towards an improved set of variables for predicting soil organic matter content. Biogeochemistry 137:297–306. https://doi.org/10.1007/s10533-018-0424-3
80. Rath KM, Rousk J (2015) Salt effects on the soil microbial decomposer community and their role in organic carbon cycling: A review. Soil Biol Biochem 81:108–123. https://doi.org/10.1016/j.soilbio.2014.11.001

81. Reichstein M, Subke J-A, Angeli AC, Tenhunen JD (2005) Does the temperature sensitivity of decomposition of soil organic matter depend upon water content, soil horizon, or incubation time? Glob Change Biol 11:1754–1767. http://doi.org/10.1111/j.1365-2486.2005.001010.x
82. Rengasamy P (2006) World salinization with emphasis on Australia. J Exp Bot 57:1017–1023. https://doi.org/10.1093/jxb/erj108
83. Richardson JL, Arndt JL (1989) What use prairie potholes? Journal of soil water conservation 44:196–198. https://doi.org/10.1016/S0065-2113(08)60623-9
84. Rosen BH, Adamus P, Lal H (1995) A conceptual model for the assessment of depressional wetlands in the prairie pothole region. Wetlands Ecol Manage 3:195–208. https://doi.org/10.1007/BF00179836
85. Rutherford PM, McGill WB, Arocena JM, Figueiredo CT (2008) Total Nitrogen. In Carter MR and Gregorich EG (eds.), Soil Sampling and Methods of Analysis, Second Edition. CRC Press. http://doi.org/10.1201/9781420005271.ch22
86. Saskatchewan Soil Survey Staff (1986) Soil Survey Reports for Saskatchewan: The Soils of Indian Head, Rural Municipalty no 156 Saskatchewan. Saskatchewan Institute of Pedology Publication S202, Saskatoon, Saskatchewan http://sis.agr.gc.ca/cansis/publications/surveys/sk/sks202/index.html
87. Schielzeth H, Nakagawa S, Freckleton R (2013) Nested by design: model fitting and interpretation in a mixed model era. Methods Ecol Evol 4:14–24. http://doi.org/10.1111/j.2041-210x.2012.00251.x
88. Schimel J, Balser TC, Wallenstein M (2007) Microbial stress-response physiology and its implications for ecosystem function. Ecology 88:1386–1394. http://doi.org/10.1890/06-0219
89. Schimel JP (2018) Life in Dry Soils: Effects of Drought on Soil Microbial Communities and Processes. Annu Rev Ecol Evol Syst 49:409–432. https://doi.org/10.1146/annurev-ecolsys-110617-062614
90. Schimel JP, Schaeffer SM (2012) Microbial control over carbon cycling in soil. Front Microbiol 3:348. https://doi.org/10.3389/fmicb.2012.00348
91. Shi S, Tian L, Nasir F, Bahadur A, Batool A, Luo S, Yang F, Wang Z, Tian C (2019) Response of microbial communities and enzyme activities to amendments in saline-alkaline soils. Appl Soil Ecol 135:16–24. http://doi.org/10.1016/j.apsoil.2018.11.003
92. Simard RR (1993) Ammonium Acetate-Extractable Elements. In Carter MR (ed.), Soil Sampling and Methods of Analysis, First Edition. Lewis Publishers
93. Sinsabaugh RL, Belnap J, Findlay SG, Shah JJF, Hill BH, Kuehn KA, Kuske CR, Litvak ME, Martinez NG, Moorhead DL, Warnock DD (2014) Extracellular enzyme kinetics scale with resource availability. Biogeochemistry 121:287–304. http://doi.org/10.1007/s10533-014-0030-y
94. Sinsabaugh RL, Follstad Shah JJ (2012) Ecoenzymatic Stoichiometry and Ecological Theory. Annual Review of Ecology, Evolution Systematics 43:313–343. http://doi.org/10.1146/annurev-ecolsys-071112-124414
95. Sinsabaugh RL, Hill BH, Follstad Shah JJ (2009) Ecoenzymatic stoichiometry of microbial organic nutrient acquisition in soil and sediment. Nature 462:795–798. http://doi.org/10.1038/nature08632
96. Sinsabaugh RL, Lauber CL, Weintraub MN, Ahmed B, Allison SD, Crenshaw C, Contosta AR, Cusack D, Frey S, Gallo ME, Gartner TB, Hobbie SE, Holland K, Keeler BL, Powers JS, Stursova M, Takacs-Vesbach C, Waldrop MP, Wallenstein MD, Zak DR, Zeglin LH (2008) Stoichiometry of soil enzyme activity at global scale. Ecology Lettters 11:1252–1264. http://doi.org/10.1111/j.1461-0248.2008.01245.x
97. Skjemstad JO, Baldock JA (2008) Total and Organic Carbon. In Carter MR and Gregorich EG (eds.), Soil Sampling and Methods of Analysis, Second Edition. CRC Press. http://doi.org/10.1201/9781420005271.ch21
98. Stauffer M, Leyval C, Brun JJ, Leportier P, Berthelin J (2014) Effect of willow short rotation coppice on soil properties after three years of growth as compared to forest, grassland and arable land uses. Plant Soil 377:423–438. http://doi.org/10.1007/s11104-013-1986-4
99. Tischer A, Blagodatskaya E, Hamer U (2015) Microbial community structure and resource availability drive the catalytic efficiency of soil enzymes under land-use change conditions. Soil Biol Biochem 89:226–237. http://doi.org/10.1016/j.soilbio.2015.07.011
100. Toenshoff C, Stuelpnagel R, Joergensen RG, Wachendorf C (2013) Carbon in plant biomass and soils of poplar and willow plantations-implications for SOC distribution in different soil fractions after re-conversion to arable land. Plant Soil 367:407–417. https://doi.org/10.1007/s11104-012-1481-3
101. Topp GC, Ferre PA (2002) Water Content. In: Dane JH, Topp CG (eds) Methods of Soil Analysis: Part 4 Physical Methods. Soil Science Society of America, Madison, pp 417–545. http://doi.org/10.2136/sssabookser5.4.c19
102. Trasar-Cepeda C, Leirós MC, Gil-Sotres F (2008) Hydrolytic enzyme activities in agricultural and forest soils. Some implications for their use as indicators of soil quality. Soil Biol Biochem 40:2146–2155. http://doi.org/10.1016/j.soilbio.2008.03.015
103. Wallenius K, Rita H, Mikkonen A, Lappi K, Lindström K, Hartikainen H, Raateland A, Niemi R (2011) Effects of land use on the level, variation and spatial structure of soil enzyme activities and bacterial communities. Soil Biol Biochem 43:1464–1473. https://doi.org/10.1016/j.soilbio.2011.03.018
104. Wallenstein MD, Burns RG (2011) Ecology of Extracellular Enzyme Activities and Organic Matter Degradation in Soil: A Complex Community-Driven Process. p. 35–55. In Dick RP (ed.), Methods of Soil Enzymology. Soil Science Society of America. http://doi.org/10.2136/sssabookser9.c2
105. Wang Y, Wang H, He JS, Feng X (2017) Iron-mediated soil carbon response to water-table decline in an alpine wetland. Nat Commun 8:15972. http://doi.org/10.1038/ncomms15972
106. Wei T, Simko V, Levy M, Xie Y, Jin Y, Zemla J (2017) R Package "corrplot": Visualization of a Correlation Matrix. Version 0.84. https://cran.r-project.org/web/packages/corrplot/index.html
107. Werner BA, Johnson WC, Guntenspergen GR (2013) Evidence for 20th century climate warming and wetland drying in the North American Prairie Pothole Region. Ecology Evolution 3:3471–3482. https://doi.org/10.1002/ece3.731
108. Wickham H (2016) ggplot2-Elegant Graphics for Data Analysis. Springer, New York, USA. http://doi.org/10.1007/978-3-319-24277-4
109. Wickham H, Chang W, Henry L, Pedersen TL, Takahashi K, Wilke C, Woo K (2018) R Package "ggplot2": Create Elegant Data Visualisations Using the Grammar of Graphics. Version 3.0.0. https://cran.r-project.org/web/packages/ggplot2/index.html

110. Wiedermann MM, Kane ES, Potvin LR, Lilleskov EA (2017) Interactive plant functional group and water table effects on decomposition and extracellular enzyme activity in Sphagnum peatlands. Soil Biol Biochem 108:1–8. http://doi.org/10.1016/j.soilbio.2017.01.008
111. Winter TC, Rosenberry DO (1998) Hydrology of prairie pothole wetlands during drought and deluge: a 17-year study of the Cottonwood Lake wetland complex in North Dakota in the perspective of longer term measured and proxy hydrological records. Clim Change 40:189–209. https://doi.org/10.1023/A:1005448416571
112. Wong VNL, Dalal RC, Greene RSB (2008) Salinity and sodicity effects on respiration and microbial biomass of soil. Biol Fertil Soils 44:943–953. https://doi.org/10.1007/s00374-008-0279-1
113. Xie X, Pu L, Wang Q, Zhu M, Xu Y, Zhang M (2017) Response of soil physicochemical properties and enzyme activities to long-term reclamation of coastal saline soil, Eastern China. Sci Total Environ 607–608:1419–1427. http://doi.org/10.1016/j.scitotenv.2017.05.185
114. Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed Effect Models and Extensions in Ecology with R.. Springer. http://doi.org/10.1007/978-0-387-87458-6

Figures

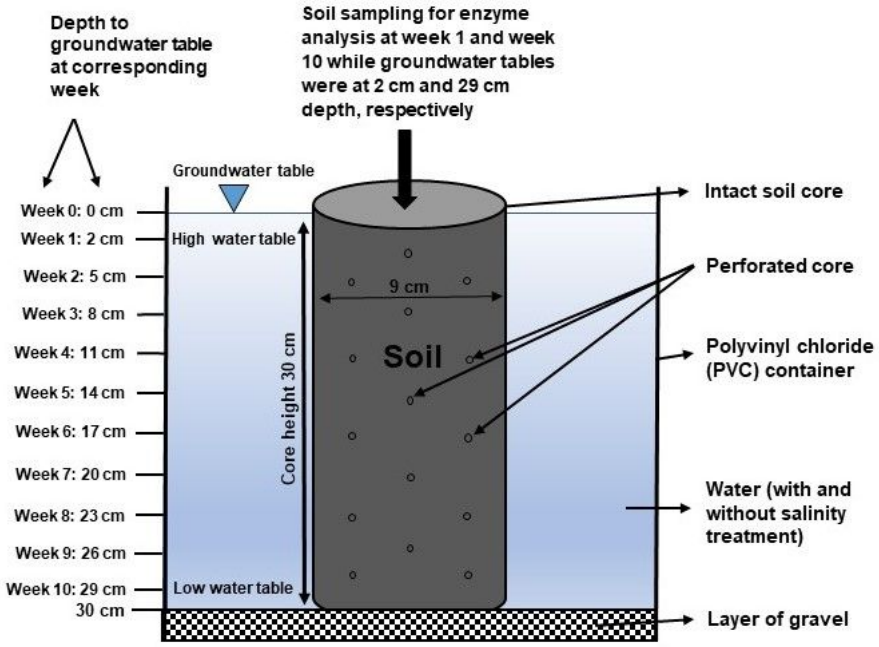

Figure 1

Illustration of an individual experimental unit with intact soil core used for incubation study (Note: the diagram is not to scale).

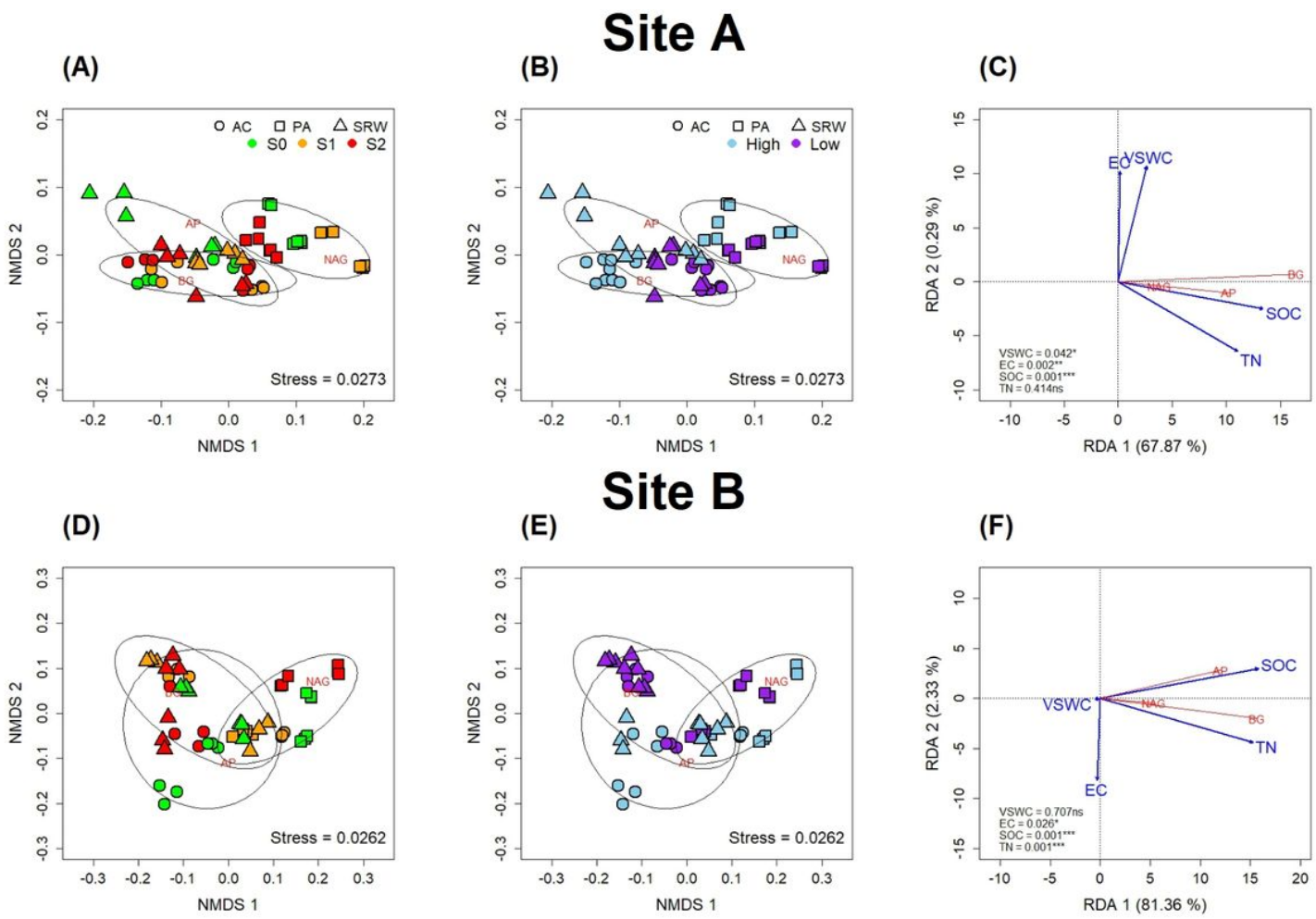

Figure 2

Non-metric multidimensional scaling (NMDS) and redundancy analysis (RDA) of soil extracellular enzyme activities (e.g., β-glucosidase = BG, N-acetyl glucosaminidase = NAG, alkaline phosphatase = AP) visualized with land-use practices (e.g., annual crop = AC, pasture = PA, short rotation willow = SRW), groundwater salinity treatments (e.g., S0 = control, S1 = 6 mS cm-1, S2 = 12 mS cm-1), and groundwater table depth treatments from site A (panels A, B, and C) and site B (D, E, and F). Blue vectors (r > x) indicate linear correlations between the ordination with soil electrical conductivity (EC), soil organic carbon (SOC), volumetric soil water content (VSWC), and total nitrogen (TN). Directions and lengths of the vectors indicate the strength of correlations between variables. The angles between vectors reflect their correlations (i.e., a vector pair with an angle of 20° have strong positive correlation as cos(20) = 0.94, and with an angle of 90° are uncorrelated as cos(90) = 0). *, **, *** Indicate there is a statistically significant difference at $p \leq 0.05$, $p \leq 0.01$ and $p \leq 0.001$, respectively; ns, is not significantly different ($p > 0.05$).

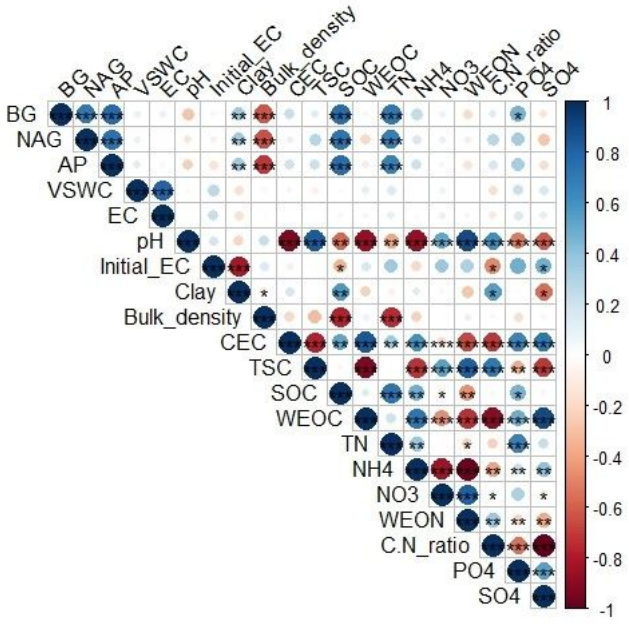

Figure 3

Spearman rank-order correlations among β-glucosidase (BG), N-acetyl glucosaminidase (NAG), alkaline phosphatase (AP) activities with initial soil physiochemical properties, namely volumetric soil water content (VSWC), electrical conductivity (EC), pH, clay, bulk density, cation exchange capacity (CEC), total soil carbon (TSC), soil organic carbon (SOC), water extractable organic carbon (WEOC), total nitrogen (TN), NH4+-N, NO3–N, water extractable organic nitrogen (WEON), carbon and nitrogen (C/N) ratio, PO43–P, SO42–S. Negative correlations are depicted in red and positive correlations in blue. Increasing correlation strength is indicated by increasing circle diameter and deeper color. *, **, *** indicate there is a statistically significant relationship at $p \leq 0.05$, $p \leq 0.01$, and $p \leq 0.001$ level of significance, respectively, and remaining are not significant ($p > 0.05$).

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- Supplementarymaterialsrevised.docx
- GraphicalAbstract.png