Soil Enzyme Activity as Affected by Land-Use, Salinity, and Groundwater Fluctuations in Wetland Soils of the Prairie Pothole Region

Shayeb Shahariar1 • Bobbi Helgason1 • Raju Soolanayakanahally2 • Angela Bedard-Haughn1

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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.

Keywords Extracellular enzyme activities (EEAs) • Land-use practice • Shallow groundwater table fluctuations • Salinity • Wetland soils • Prairie pothole region (PPR)

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; Lu 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 semiarid 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; McAuley 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 draw-down 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.

**Materials and Methods**

### 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.

### 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).

### 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.

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Groundwater salinity levels for the treatments of S1 and S2 were attained by mixing Na₂SO₄: KCl: CaCl₂: MgSO₄ 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 of 44%, respectively.

Collection of Soils for Enzyme Activity

Soils for EEA analyses 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).

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 MUF (4-methylumbelliferone) based high-throughput fluorometric microplate assay (Bell et al. 2013; Hargreaves and Hofmockel 2015). EEA 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-glycopyranoside for BG, 4-Methylumbelliferyl N-acetyl-β-D-glucosaminide for NAG, and 4-Methylumbelliferyl phosphate for AP). Substrate amended soils were incubated for 3 h at 24 °C at 140 rpm on a mechanical shaker. All the samples were centrifuged for 5 min 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 to 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.

**Analyses of Soil Physiochemical Properties**

Each of the additional soil core collected for soil physiochemical properties were divided into three sub-samples according to analysis requirements. The first sub-sample 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 h (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 determination 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. 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 permutational 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, 

**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), “corplot” (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, 

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and VPA analyses were carried out using “vegan” package. All statistical tests were statistically significant at p-values ≤0.05.

**Results**

**Soil EEAs**

**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).

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).

**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).

**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 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 (nmol activity g⁻¹ Ch⁻¹) | NAG (nmol activity g⁻¹ Ch⁻¹) | AP (nmol activity g⁻¹ Ch⁻¹) | VSWC (%) | EC (mS cm⁻¹) | BG (nmol activity g⁻¹ Ch⁻¹) | NAG (nmol activity g⁻¹ Ch⁻¹) | AP (nmol activity g⁻¹ Ch⁻¹) | VSWC (%) | EC (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     |

*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 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).

### 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, $\text{SO}_4^{2-}$ 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 $\text{SO}_4^{2-}$ 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 $\text{SO}_4^{2-}$ contents were SRW > PA = AC in site A, and SRW = AC > PA in site B, suggesting no observed consistent land-use patterns between sites.

### 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, $\text{NH}_4^+$, $\text{NO}_3^-$, C/N ratio, and $\text{PO}_4^{3-}$, whereas negatively correlated with pH, background EC, WEOC, WEON, and $\text{SO}_4^{2-}$, however, not significantly ($p > 0.05$) (Fig. 3).

### 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

| Sources of variation | Site A | Site B |
|----------------------|--------|--------|
|                      | 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.
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.

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...
Discussion

Land-Use, Groundwater Salinity, and Water Table Effects on Soil EEA

Land-Use

In this experiment, the highest soil EEA 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 PO₄-P contents, and reflected the highest soil EEA 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, PO₄-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 hydrolizing 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 range-land, 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 arylsulphatase activities under general crop rotation and conservation tillage compared to a single crop and conventional tillage. Hence, it suggested that the production of EEAs 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).

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.
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 high 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).

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 NH4-N and PO4-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.

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.

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Data Availability All relevant data and materials from this experiment are included in the supplementary materials.

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Declarations

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

Consent to Participate Not applicable.

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