

Wetland Soil Carbon in a Watershed Context for the Prairie Pothole Region

Rebecca L. Phillips,* Cari Ficken, Mikki Eken, John Hendrickson, and Ofer Beerli

Abstract

Wetland restoration in the Prairie Pothole Region (PPR) often involves soil removal to enhance water storage volume and/or remove seedbanks of invasive species. Consequences of soil removal could include loss of soil organic carbon (SOC), which is important to ecosystem functions such as water-holding capacity and nutrient retention needed for plant re-establishment. We used watershed position and surface flow pathways to classify wetlands into headwater or network systems to address two questions relevant to carbon (C) cycling and wetland restoration practices: (i) Do SOC stocks and C mineralization rates vary with landscape position in the watershed (headwater vs. network systems) and land use (restored vs. native prairie grasslands)? (ii) How might soil removal affect plant emergence? We addressed these questions using wetlands at three large (~200 ha) study areas in the central North Dakota PPR. We found the cumulative amount of C mineralization over 90 d was 100% greater for network than headwater systems, but SOC stocks were similar, suggesting greater C inputs beneath wetlands connected by higher-order drainage lines are balanced by greater rates of C turnover. Land use significantly affected SOC, with greater stocks beneath native prairie than restored grasslands for both watershed positions. Removal of mineral soil negatively affected plant emergence. This watershed-based framework can be applied to guide restoration designs by (i) weighting wetlands based on surface flow connectivity and contributing area and (ii) mapping the effects of soil removal on plant and soil properties for network and headwater wetland systems in the PPR.

Core Ideas

- Wetland soil carbon varies with upland land use but not landscape position.
- Carbon mineralization rates vary with landscape position.
- Soil removal for wetland restoration may affect plant re-establishment.

THE PRAIRIE POTHOLE REGION (PPR) is populated by a high density of shallow, glaciated wetlands (van der Valk, 1989) and represents one of the most important regions in North America for breeding, nesting, and migrating grassland birds and waterfowl (Igl and Johnson, 1997; Beyersbergen et al., 2004; Niemuth et al., 2006). Nearly 1 million ha of wetlands are found in the North Dakota PPR (Stewart and Kantrud, 1973; Tiner, 1999), where spatiotemporal variation in wetland hydroperiod (Beerli and Phillips, 2007) is prominent and critical to waterfowl habitat. Wetland hydroperiod varies with topographic position (Zhang et al., 2007) and drives soil carbon (C) dynamics by altering redox potential (Mitsch and Gosselink, 2007). Historical land use of the areas surrounding these wetlands is also known to influence soil C (Gleason et al., 2011). However, a lack of knowledge regarding surface and groundwater drainage networks for these depressional wetlands has hindered understanding of potential surface water connections among wetlands in a watershed (Winter, 2003) and how these might affect the C cycle. Understanding the role of landscape position with respect to surface water flows and soil C dynamics is needed to support managers and mitigation banking teams interested in maintaining C sequestration or minimizing C losses (Cahill et al., 2009).

The hydrology and biogeochemical cycling for PPR wetland networks is largely dependent on interactions among watershed position, climate, and surface and groundwater flows (Winter, 2003). Understanding surface water interactions among wetlands in the PPR is problematic, however, because the region is geologically young and lacks strong changes in elevation and deeply eroded drainage networks (Bluemle, 1981). Visual observations or coarse-resolution elevation data cannot discern watershed boundaries or multiple pathways for surface drainage networks among wetlands (USEPA, 2015). High-resolution digital elevation model (DEM) data (<1 m vertical resolution) have now been modeled to map drainage lines, catchment areas, and other watershed characteristics (McCauley and Anteau, 2014) at

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Abbreviations: AOI, area of interest; CRP, Conservation Reserve Program; DEM, digital elevation model; NWI, National Wetlands Inventory; PPR, Prairie Pothole Region; SOC, soil organic carbon; TauDEM, Terrain Analysis Using Digital Elevation Model.

scales relevant to the geomorphology of the PPR. For example, these data can now be applied to map headwater (Gomi et al., 2002), or geographically isolated (Tiner, 2003), wetland systems separately from wetlands connected by higher-order drainage lines at lower reaches of the watershed (Strahler, 1957; Gomi et al., 2002). Mapping and understanding potential wetland connectivity through surface flow networks will likely have important implications for wetland restoration, soil C dynamics, and processes influencing soil organic carbon (SOC) sequestration.

Hypoxic or anoxic wetland soil conditions generally slow SOC turnover rates and enhance SOC sequestration. However, mineralization of available SOC to CO₂ is stimulated when wetlands are drained and the C buried beneath them is exposed to oxygen (Mitsch and Gosselink, 2007). Release of SOC to CO₂ is also stimulated by disturbance, such as plowing native prairie grasslands during conversion to annual crop production (Reicosky et al., 1997; Paustian et al., 1997). Carbon mineralization rates have been measured across large landscapes and provide an indication of the potential effects of disturbance on SOC (Ahn et al., 2009). These incubation studies indicate that the effects of land use on C mineralization may persist long after the initial disturbance (Ahn et al., 2009; McLaughlan and Hobbie, 2004). Thus, an understanding of C losses through mineralization may be more informative than SOC inventory data alone. Overall, both land use and position in the landscape are expected to influence wetland C cycling in PPR landscapes but, to the best of our knowledge, have not been explicitly tested.

Soil removal in the PPR is commonly prescribed for wetland mitigation/restoration projects by state Interagency Review Teams in an effort to enhance the hydroperiod by increasing catchment volume (US Department of Defense and USEPA, 2008). Increasing catchment volume can provide benefits to water quality (Jordan et al., 2003) and waterfowl (Johnson et al., 2005), and there is a need to understand restoration effects and to measure restoration success (Fennessy and Craft, 2011). In the PPR, restoration typically involves removal of shallow marsh soils near wetland edges (Stewart and Kantrud, 1971), where hydric vegetation might trap eroded soil from upland crop fields (Luo et al., 1997). Soil removal is intended to expose previously buried seed banks and high-quality soil (Doran et al., 1998; Harris, 2003). However, removal of soil near the surface may actually stimulate C mineralization (Paustian et al., 1997; Reicosky et al., 1997) and reduce water holding capacity, root penetration, C stocks, nutrient availability, and the establishment of desired plant species (Bruland and Richardson, 2005; Bantilan-Smith et al., 2009; Ahn and Dee, 2011). It remains unclear if plant emergence in the shallow marsh zone will be affected by removal of organic and mineral soil horizons in the PPR.

We hypothesized that SOC stocks and cumulative C mineralized (conversion of C to CO₂) during laboratory incubations would be greater for wetland systems connected by multiple drainage lines in the lower reaches of the watershed (“network wetlands”) than for headwater wetland systems (Gomi et al., 2002). We also hypothesized that plant emergence would be compromised after removal of organic and/or mineral soil horizons. To address these hypotheses, we evaluated wetlands at three large (~200 ha) sites in central North Dakota, which we refer to as focus areas. Each focus area was comprised of more than 20 emergent wetlands surrounding by either re-established or native

prairie grasslands. We used field, greenhouse, and laboratory studies to evaluate SOC and plant emergence after soil removal (Marton et al., 2014; Fennessy and Craft, 2011). With this work, our goal was to better understand the importance of landscape position and land use with respect to soil C cycling in the context of wetland restoration and to examine potential impacts of soil removal on plant emergence and C sequestration.

Materials and Methods

Area of Interest

The total area of the PPR is 77.8 million ha, and 12.8 million ha of the PPR is located in North Dakota. Nested inside the PPR are the Missouri Coteau and Northern Glaciated Plains ecoregions (Omernik, 1987), where the density of water bodies is high and spatiotemporally variable (Beeri and Phillips, 2007). Physiography and land use for this region are described by Bluemle (1981), Strong et al. (2005), Beeri and Phillips (2007), and Phillips et al. (2015). We delineated a 1.2 million ha area of interest (AOI) with a center point near Max, ND (Fig. 1). Most wetlands listed for this region in the National Wetlands Inventory (NWI) are classified as palustrine, emergent seasonal or palustrine, emergent temporary (US Fish and Wildlife Service, 2015). These terms are designated for wetlands that remain dry most of the year and fill with water only after spring rains, substantive snowmelt, or groundwater discharge (Stewart and Kantrud, 1971). When precipitation is below average, most temporary wetlands will remain dry all year. Average (30-yr)

Focus Area Locations

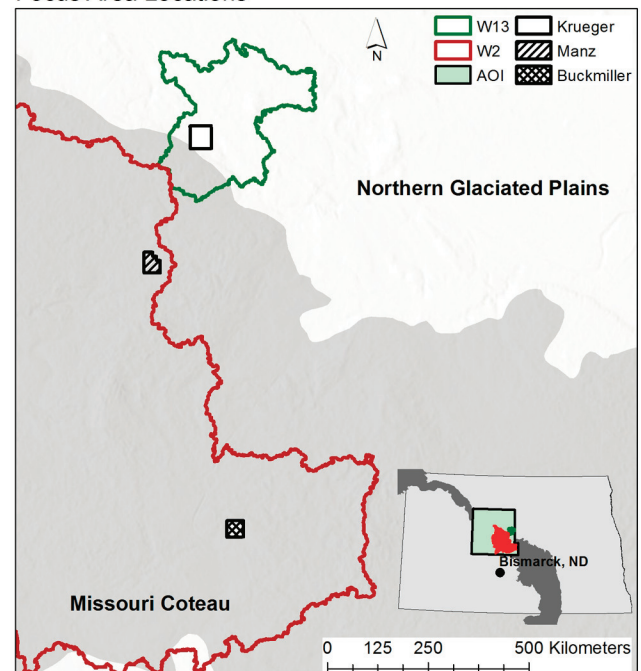


Fig. 1. Focus areas (Buckmiller, Krueger and Manz) were located within the Missouri Coteau and Northern Great Plains ecoregions. Denoted in the legend are watershed identification numbers that correspond with mapped watersheds outlined in red (W2) and green (W13). The intersection of W2 and W13 watersheds is the edge of the Missouri Coteau where elevation drops and slopes toward the Northern Glaciated Plains. The area of interest (AOI) depicted in the map inset represents the entire area where digital elevation model data were obtained on 20 Apr. 2007. The inset also shows the scale of the W2 and W13 watersheds relative to the AOI.

annual rainfall within our AOI is 450 mm, and average annual temperature is 6°C (Menne et al., 2015).

Since the 1980s, large tracts of land previously used for annual crop production were enrolled in the Conservation Reserve Program (CRP), although many of these lands have recently been converted back to crop production (USDA–FSA, 2012). Conservation Reserve Program enrollment requires “resting” lands for a period of time by seeding fields previously used for crop production to perennial grasses. In the central North Dakota PPR, these are typically mixtures of smooth brome [*Bromus inermis* (Leyss.)], crested wheatgrass [*Agropyron cristatum* (L.)], western wheatgrass [*Pascopyrum smithii* (Rybd.) Á. Löve], needle-and-thread [*Hesperostipa comata* (Trin. & Rupr.) Barkworth], and alfalfa (*Medicago*) species (USDA–FSA, 2012). We identified three privately owned, central North Dakota focus areas for this study (Fig. 1), where multiple wetlands were surrounded by either grasslands enrolled in the CRP for over 10 yr or native prairie. Two focus areas were located on the west side of the PPR in the Missouri Coteau ecoregion, and one focus area was located on the east side of the PPR in the Northern Glaciated Plains ecoregion (Fig. 1).

Digital Elevation Data

Evaluation of PPR wetlands in a watershed context required that we first acquire and model high-resolution DEM, similar to McCauley and Anteau (2014), for a landscape that extended well beyond sites where field data were collected. Spatially expansive data would ensure that there would be a high probability that all areas potentially contributing surface flows to specific depressions would be included. High-resolution DEMs were acquired over the AOI the week of 20 Apr. 2007 by Intermap Technology shortly after snow melt and before green-up (Fig. 1). The southeast corner of the data (47°14'48" N, 100°14'1" W) was near Wing, ND, and the northwest corner (48°15'9" N, 101°45'40" W) was near Fort Berthold, ND. Precipitation in 2006 through spring 2007 was 45% below the 30-yr average (Menne et al., 2015), so many seasonal and temporary wetlands did not contain water when the DEM data were collected, which is common during dry years (Beeri and Phillips, 2007). Data were acquired using an on-board Twin Otter aircraft equipped with an interferometric synthetic aperture radar sensor (Intermap, 2012). Data were geometrically corrected according to National Geodesic Survey benchmarks and geographic position system field points collected within 1 wk of the flyover. The bare earth model provided by Intermap Technologies was produced using algorithms to remove buildings, vegetation, roads, and other elevated features (Intermap, 2015). Data vertical accuracy is reportedly <1 m (Mooney et al., 2006), and this was validated using ground control point captured during image acquisition.

The data were first processed using the open source ArcGIS extension Terrain Analysis Using Digital Elevation Models (TauDEM) by Tarboton (2005). Eighteen major pour points, or outlets, were identified that drain into the major central North Dakota river systems (the Missouri, Souris, and Cheyenne Rivers). Watersheds were built around each of the 18 pour points using TauDEM analysis tools (Tarboton et al., 1991). Two of the three focus areas used in this study (named Manz and Buckmiller) were located in the W2 watershed, and one focus area (named Krueger) was located in the W13 watershed (Fig. 1). Drainage networks

were mapped in the Arc Hydro module of ArcGIS (version 9.2) using a minimum flow accumulation of 0.008 km, and streams were classified according to the Strahler stream order (Strahler, 1957). The water routing algorithm used in Arc Hydro is such that water is routed from one 5-m pixel into neighboring pixels of lower elevation. To identify potential surface water flows and catchment areas where water could pond, we filled all depressions within the DEM and subtracted the unfilled DEM from the filled DEM, which is referred to as a difference grid (McCauley and Anteau, 2014). This grid contains catchment area and depth information. We did not specify a minimum fill depth because this landscape is populated with thousands of shallow pothole wetlands (Beeri and Phillips, 2007). Only catchments >0.0025 ha (a single pixel) were retained in the map output. Culverts, bridges, and roads can affect water flows, and these obstructions were corrected by processing raw DEM to bare earth digital terrain model (Intermap, 2015). Modeled catchments are depressions in the landscape that could hold water, as compared with wetlands, which are delineated by the NWI (US Fish and Wildlife Service, 2015).

We classified each NWI wetland in our focus areas according to landscape position and drainage networks using the Strahler stream order (Strahler, 1957) as outlined by Gomi et al. (2002). Briefly, wetlands were classified as headwater systems when they did not intersect with streams, when they were intersected by stream orders <2, and when they were located at the upper reaches of the watershed, with no wetlands upstream potentially contributing flow (Gomi et al., 2002). Wetlands that were located in a catchment within 50 m of higher-order drainage lines (Strahler stream order >1) were classified as network systems (Gomi et al., 2002). We would expect greater surface flow accumulation and connectivity for those network systems transected by higher stream orders than headwater systems. Headwater systems, however, may be hydrologically connected when they rise and spill over beyond their catchment volume into neighboring wetlands or by way of groundwater flow systems (Winter, 2003).

Focus Area Description

The three focus areas were located within 40 km of each other in rural areas of Sheridan County, ND (Fig. 1). The site furthest to the south was Buckmiller (47°25'18" N, 100°28'12" W), followed by Manz (47°39'8" N, 100°34'41" W) directly north of Buckmiller and Krueger (47°45'35" N, 100°30'51" W) located east of Manz. Each focus area was comprised of >20 palustrine, emergent, NWI wetlands (US Fish and Wildlife Service, 2015). Wetlands in the PPR are characterized by concentric bands of vegetation zones, with plant communities that co-occur and vary predictably with distance from the lowest point in the wetland (Stewart and Kantrud, 1971). We focused on the shallow marsh vegetation zone, which is normally saturated from spring to early summer and is recognized by hydrophytic vegetation of intermediate height (<0.5 m), such as spike rush (*Eleocharis macrostachya* Britt.) and Baltic rush (*Juncus balticus* Willd.) species (Stewart and Kantrud, 1971). Surrounding these hydric vegetation zones at each of the focus areas were either grasslands managed under the CRP for over 10 yr or native prairie grasslands that were occasionally harvested for hay or lightly grazed by cattle (<0.2 AU ha⁻¹). Grasslands managed under the CRP were dominated by smooth brome, crested wheatgrass, and Kentucky bluegrass [*Poa pretensis* (L.)], whereas native prairie grasslands were

dominated by western wheatgrass, needle-and-thread grass, and Kentucky bluegrass. Soils at all three focus areas were dominated by fine, loamy, mixed superactive frigid Typic Argiustolls and Haplustolls (Soil Survey Staff, 2008). Soil particle size was predominantly sand (42–50%), with similar proportions of silt and clay (20–30%), and soil pH ranged from 6.2 to 7.5. All focus areas were managed by the same owner, with an emphasis on minimizing wildlife habitat disturbance. The emergent wetlands in the focus areas were small (average, <1 ha), with hydroperiods that vacillated seasonally and annually (Beeri and Phillips, 2007). Each NWI wetland was designated as either headwater or network systems based on catchment colocation and watershed position classification. Wetlands were also designated according to upland land use as either CRP or prairie grasslands.

Estimates for dry catchment depth, as determined from the modeled DEM, were compared with field estimates of depth at six catchments within each focus area. These catchments did not contain water during the DEM data acquisition, so the remote sensing-based elevation data were not obscured by standing water. Field estimates of depth were determined by first navigating to the lowest point around the perimeter of the catchment (known as the pour point). From this point, height data were collected within the length of each catchment every 5 m using a set of modified Robel poles (Robel et al., 1970) connected by a level line. Depth estimates in the field were matched to each 5 × 5 m pixel from the DEM across the catchment. Observed versus modeled depth was evaluated using the RMSE for the purpose of estimating potential error in modeled catchment depth.

Soil Carbon Experiment

We randomly selected two headwater and two network wetland systems within each focus area (Fig. 1) and land cover class (native prairie vs. CRP grassland) and then randomly selected four points around the perimeter of each wetland in the shallow marsh zone (Phillips et al., 2005). This zone is often excavated during restoration, and our aim was to evaluate the potential effects of soil removal on seedbank, plant emergence, and SOC. Because network wetlands are inundated longer each year than headwater wetlands, we expected more anoxic conditions would increase SOC burial. At each point, duplicate cores (5 × 10 cm depth) were collected within 1 m of each other in plastic sleeves on 12 Sept. 2012. For this initial study, we limited sampling to 10 cm because microbial activity and C inputs are greatest near the surface. Cores were gently saturated with deionized water in the field, allowed to freely drain, stored at 4°C, transported to the laboratory, and processed within 24 h of collection. One set of cores was composited by wetland and used for laboratory incubations, soil moisture determination, and analysis of C. These were well mixed and coarsely (4 mm) sieved (Franzluebbers, 1999). A subsample was removed for determination of gravimetric moisture content and oven-dried at 105°C for 48 h (Marton et al., 2014). Another subsample was dried at 35°C for 3 to 4 d, ground to pass a 0.106-mm sieve, and analyzed for total C by dry combustion (Nelson and Sommers, 1996) using a Carlo Erba NA 1500 Elemental Analyzer (CE Elantech). Using the same fine-ground soil from the C analyses, soil inorganic C was measured by quantifying the amount of CO₂ produced using a volumetric calcimeter after application of dilute HCl stabilized with FeCl₂ (Loeppert and Suarez, 1996). Because inorganic C was such a

minor fraction of total C, results are reported as SOC. We used these SOC data to estimate percentage of SOC pool mineralized over the course of 90-d incubations (Ahn et al., 2009). The second set of cores was used for bulk density, which was determined as the quotient of oven-dried mass divided by core volume (Marton et al., 2014). Concentration data for SOC (g kg⁻¹ dry soil) were multiplied by bulk density and sampling depth (soil layer thickness) to convert SOC to an area basis (Mg ha⁻¹) for the 0- to 10-cm soil depth.

The amount of C mineralized was determined in accordance with previous studies using laboratory incubations in the absence of new organic matter inputs and calculating cumulative CO₂ respired over a 90-d time course (Ahn et al., 2009; McLaughlan and Hobbie, 2004). A total of 12 vials (12-mL exetainer vial, Labco Unlimited) per wetland were prepared, and the equivalent of 3 g dry mass of soil was transferred into each of 10 vials. Two empty vials per wetland were used as the abiotic control. Vials were capped and vented and allowed to incubate in a 22°C water bath. The mass of water in each vial at the beginning and end of the incubation was recorded. Respiration of CO₂ was measured in the headspace of each vial on 11 occasions over the 90-d period. Beginning on Day 1, vials were evacuated and flushed with CO₂-free air for 5 min, and headspace was analyzed on a gas chromatograph (Model 3800 gas chromatograph and Combi-Pal auto-sampler, Agilent Technology). Vials were then transferred to a 22°C water bath, and headspace was analyzed again 24 h later. When vials were not being analyzed, they remained in the 22°C water bath. Gas chromatography details may be found in Phillips et al. (2009). The precision of the gas chromatography analysis, expressed as the coefficient of variation for 10 replicate standards (369, 1748, and 4986 μL L⁻¹ CO₂), was consistently <2%. This protocol was repeated on Days 3, 6, 10, 15, 22, 30, 38, 50, 71, and 90. Respiration rates were calculated using the difference in headspace CO₂ determined over each 24-h period and used to determine cumulative CO₂ respired over 90 d (McLaughlan and Hobbie, 2004).

Soil Removal Experiment

Wetlands selected for the soil removal experiment were those network systems targeted for restoration by the North Dakota Interagency Review Teams at the Krueger focus area. The goals of this restoration effort were to enhance water storage capacity and to remove seedbanks of invasive hydric species by removing 0.15 m of soil from the shallow marsh surrounding three wetlands at the Krueger focus area (personal communication, D. Dewald, North Dakota Interagency Review Team, May 2010). Soil cores were collected before commencement of restoration activities and placed in a greenhouse to determine the number of plants emerging from the existing seedbank after soil removal. The restoration plan was to remove sediment in the shallow marsh zone and did not include tillage.

We identified and geo-located three shallow marsh areas surrounding each wetland. At each point, four cores (10 cm diam. × 90 cm depth) were collected using a tractor press on 27 May 2010 and processed the following day. Each core was randomly assigned one of four treatments: O horizon removal, 1/2 of the A horizon plus O horizon removal, full A horizon removal, and control (no removal). The soil removed was reserved for seed bank evaluation. Average (SD) depth of the O horizon was

2.8 cm (0.6), and average depth of the A horizon was 21.6 cm (5.7). Cores were placed at random locations on stands in the greenhouse and regularly watered to maintain soil saturation. The number of plants that emerged was recorded every week for 8 wk. The soil removed for this experiment was evaluated to determine seedbanks for these soil layers (O layer, O plus 1/2A horizon, O plus full A horizon). Soils removed from the cores were mixed and spread into flat trays (30 × 30 × 4 cm). Flats were kept near the cores and under the same conditions. Species emerging from the flats were identified and recorded weekly for 12 wk (Bai et al., 2014; Galatowitsch and van der Valk, 1996). The five species most frequently observed for each layer removed were reported.

Data Analysis

We tested for significant differences in SOC stocks, cumulative C mineralization, and the percentage of the SOC pool mineralized with a mixed ANOVA (Littell et al., 1996). A nested hierarchical model was used with wetland nested inside wetland system class (headwater or network), land use, and focus area (Phillips et al., 2015). For cumulative C mineralization and percent SOC mineralized, we controlled for possible differences in water content by including water content in the model as a covariate. All interactions were tested and retained only if significant. For the greenhouse study, the effect of soil removal treatment on the number of plants that emerged was determined with a mixed ANOVA that included the random effects of sample collection site nested inside wetland. Data were transformed as needed to achieve normality before analysis.

Results

Wetland Mapping

Watersheds designated W2 and W13 (Fig. 1) were populated by a total of 40,235 and 2435 catchments, respectively, and the average number of catchments for both watersheds was 1.5 catchments ha⁻¹. The number of NWI wetlands within W2 and W13 was 37,734 and 1924, respectively, and the average number of wetlands for both watersheds was 1.4 wetlands ha⁻¹. Comparisons between benchmark data and bare earth elevation data for the full AOI (Fig. 1) yielded a RMSE of 0.7 m (Intermap Technologies, unpublished data). The deepest point for those catchments surveyed manually ranged from 0.4 to 1.8 m, with an average of 1.2 m. Root mean square error for manual field estimates of catchment depth, as compared with modeled depth, was 0.4 m.

Figure 2 represents the Krueger focus area and illustrates catchment and NWI classification with drainage lines. The Manz and Buckmiller focus area maps may be found in Supplemental Fig. S1 and S2. At all three focus areas, we mapped a total of 98 NWI wetlands and 221 catchments (Eken and Phillips, 2015). The 123 catchments that were not wetlands were small (0.05–0.1 ha) and shallow (<0.5 m depth). These were below the minimum area criterion for NWI. All NWI wetlands were collocated within catchments (Fig. 2; Supplemental Fig. S1 and S2). Average modeled catchment area and depth for our three focus areas ranged from 0.8 to 5.4 ha and from 0.6 to 3.3 m, respectively. Figure 2 also depicts two drainage lines transected by the road near the north and south edges of the focus area. These lines are connected across the road, indicating the road obstruction

was successfully removed by the bare earth model (Intermap, 2015), so modeled flows were not impeded. Headwater wetland systems were noticeably smaller than network systems. At the Krueger focus area, 40 of the 67 wetlands were classified as network and 27 were classified as headwater systems (Fig. 2). At the Manz focus area, 39 of the 83 wetlands were classified as network and 44 were classified as headwater systems (Supplemental Fig. S1). At the Buckmiller focus area, 32 of the 47 wetlands were classified as network and 15 were classified as headwater systems (Supplemental Fig. S2).

Soil Carbon

Average (\pm SE) SOC stocks for wetlands surrounded by CRP grasslands for network and headwater systems were similar, with 37.8 (3.5) Mg C ha⁻¹ for headwater and 37.4 (2.0) Mg C ha⁻¹ for network systems at the 0- to 10-cm soil depth increment. Average SOC stocks for wetlands surrounded by prairie grasslands were also similar for both systems, with 64.0 (7.8) Mg C ha⁻¹ for headwater and 77.7 (8.3) Mg C ha⁻¹ for network systems. However, SOC stocks varied significantly with surrounding land use ($p < 0.01$). Shallow marsh soils surrounded by CRP grasslands were 46% lower, on average, than SOC stocks for shallow marsh soil surrounded by native prairie. Cumulative C respired over 3 mo, on the other hand, varied with wetland system ($p < 0.01$) but not land use. We observed greater cumulative C respired for network systems connected by higher-order drainage lines at lower positions in the watershed (Fig. 3) than for headwater systems ($p < 0.05$). Whereas the average percentage of bulk SOC pool mineralized was 2% for headwater systems, the average percentage of bulk SOC pool mineralized was 4% for the network system. None of the interactions tested was significant.

Soil Removal

Soil removal significantly influenced plant emergence ($p < 0.05$) (Supplemental Fig. S3). The average (\pm SE) number of plants that emerged 4 wk after removal of O, 1/2 A, and A horizons was 6 (3.3), 0.5 (0.4), and 0.1 (0.1), respectively. The number of plants that emerged from control cores was 15 (4.9). A list of species that emerged for each soil removal treatment may be found in Supplemental Table S4. For the seedbank study, using the soil removed from these cores, we found similar species in O horizon, 1/2A + O horizon, and O + A horizon layers (Supplemental Table S5). Four species were dominant in all seedbank layers. These included *Potentilla norvegica* (L.), *Eleocharis compressa* (Sull.), *Juncus bufonius* (L.), and *Triglochin palustris* (L.). None of these species was listed as invasive (USDA, 2014), but all are common to wetland and/or wet grassland environments in the PPR.

Discussion

Strong differences in SOC stocks between land uses affirm the importance of wetlands surrounded by native prairie with respect to C sequestration in the PPR (Gleason et al., 2011). Soil organic C stocks for wetland soils surrounded by CRP grasslands were 46% greater than wetland soils surrounded by native prairie grasslands, which are similar to SOC differences between natural and restored wetlands reported by Marton et al. (2014) and Fennessy and Craft (2011). Stocks of SOC reported here are in

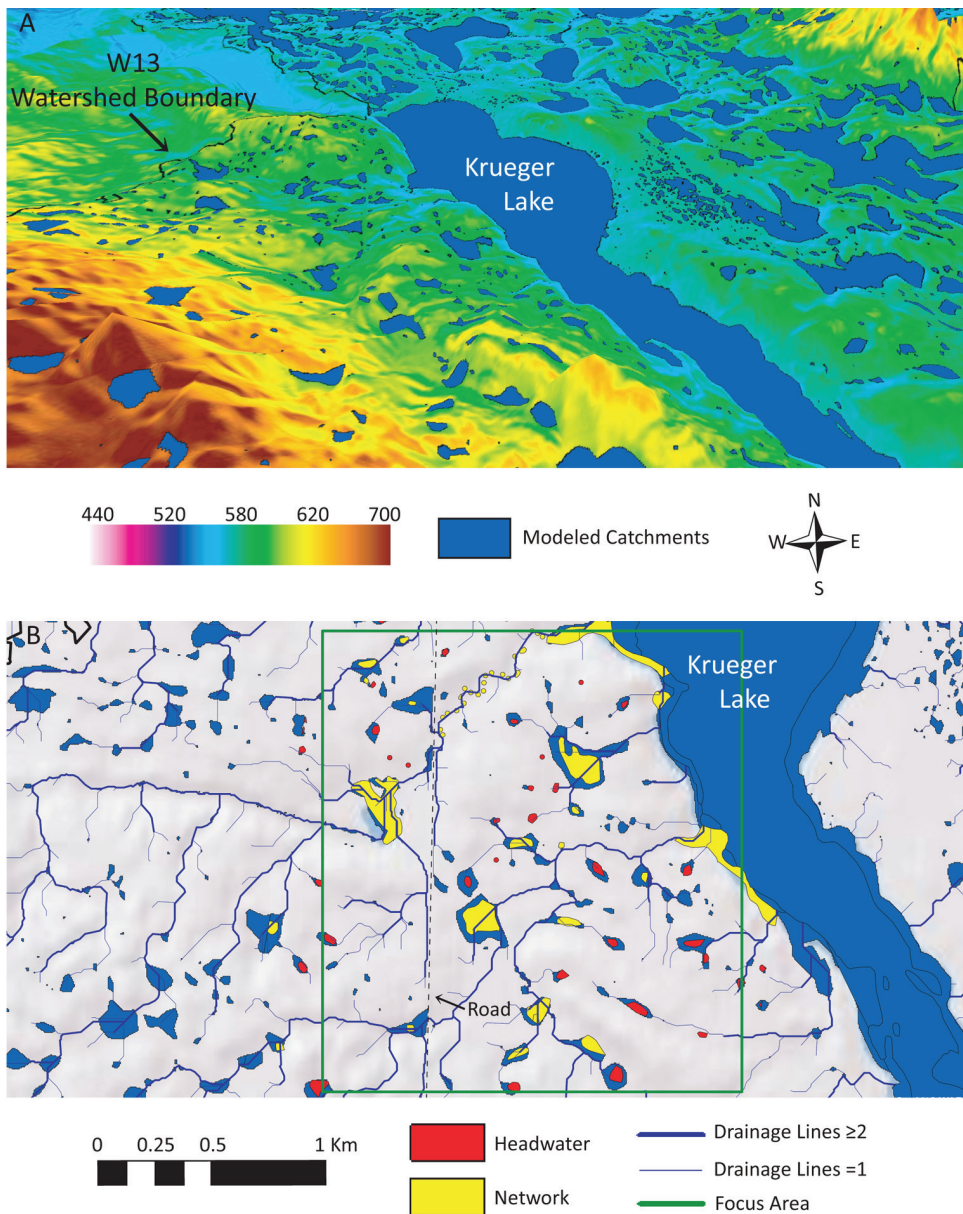


Fig. 2. Krueger focus area model output and classification (A) three dimensional view of topography with respect to modeled catchments and (B) classification of National Wetlands Inventory wetlands into network (yellow) and headwater (red) systems depicted within modeled catchments (blue). Catchments shown in blue only in (B) were not collocated with wetlands.

the range of other wetland SOC reports in the PPR (Phillips and Beeri, 2008; Gleason et al., 2011). Differences in SOC stocks were found despite over 10 yr of conservation grassland management, suggesting that the impacts of agricultural cropping disturbance on SOC stocks may be evident at decadal time scales (Ballantine and Schneider, 2009; Gleason et al., 2011; Marton et al., 2014). Management data before conversion to CRP were not available; however, we suspect tillage of shallow marsh soils in dry years before CRP contributed to differences in SOC.

Soil organic C stocks beneath network systems tend to receive greater inputs of plant organic matter, dissolved organic C, and erosional C than headwater systems (Mitsch and Gosselink, 2007), yet we found SOC stocks to be similar. Carbon mineralization rates, on the other hand, were widely different (Fig. 3). Cumulative C mineralized over 90-d incubation for network systems were twice as high as headwater systems, and this result may help explain why SOC stocks for both wetland systems were similar. Evidence of higher mineralization rates but similar SOC for wetlands connected by higher-order drainage lines suggests greater organic matter inputs lower in the watershed were

balanced by higher rates of C turnover (Bedard-Haughn et al., 2006). This would mean that both headwater and network systems might be valued similarly with respect to C sequestration (Brinson, 1993). We found wetlands surrounded by re-established grasslands mineralized a greater fraction of the SOC pool than wetlands surrounded by native grasslands (Ahn et al., 2009). This has important implications for grassland re-establishment and the potential to restore wetland SOC stocks. Because C mineralization rates were similar for wetlands surrounded by both native and re-established grasslands, greater and/or more recalcitrant organic matter inputs would be required to completely restore SOC to native grassland levels. Additional investigations are needed to test this hypothesis. Overall, our results suggest potential controls on PPR wetland C cycling in surface soils may be associated with not only land use but also with position in the watershed and proximity to surface flow networks, defined here as headwater and network systems.

We evaluated plant emergence in the absence of sowing and found soil removal may reduce the number of emergent plants in the short term (Supplemental Fig. S3). Other researchers found

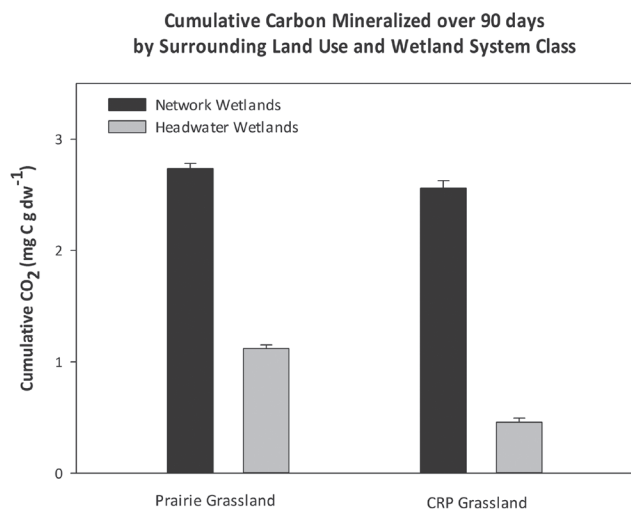


Fig. 3. Average (\pm SE) cumulative carbon mineralized over 90 d by land use and wetland system class. CRP, Conservation Reserve Program.

soil removal enhanced emergence of desirable hydric species as seedbanks of invasive species were removed (Dalrymple et al., 2003; Hausman et al., 2007; Beas et al., 2013). Here, the seedbank was dominated by native instead of invasive species, with similar species for all three depth layers (Supplemental Table S5). This result suggests removal of soil does not necessarily result in removal of invasive species from the seedbank. This short-term study should be followed up with additional work to determine if soil removal effects are detrimental or beneficial to PPR wetland ecosystems at longer time scales in the field, as suggested by Seabloom and van der Valk (2003).

Watershed characteristics such as catchment areas, drainage lines, and wetland position in the landscape indicate potential surface water connectivity and water retention (Gomi et al., 2002), with implications for water quality and flood control (National Research Council, 1995). Those wetlands with potential connectivity through higher-order drainage networks can easily be delineated from geographically isolated headwater wetlands (Tiner, 2003). Connectivity among network wetlands in the PPR is often intermittent and may only occur during high-rainfall years. However, network systems may be weighted more heavily than headwater systems in restoration projects because these are less limited by contributing area in the watershed. These types of maps (Fig. 2; Supplemental Fig. S1 and S2) can guide practitioners in a manner similar to aerial photographs by supporting more explicit evaluation of potential surface water connectivity and restoration potential in the context of both wetland surface flows and catchment areas. These maps can also be made more available to practitioners and producers using online resources (Eken and Phillips, 2015) to further benefit a wider audience.

This study aimed to broadly and simply address issues salient to practitioners currently involved in restoration projects in the PPR, with a particular emphasis on evaluating wetlands and wetland SOC in a watershed context (National Research Council, 1995). Removal of soil (and SOC) from these geologically young glacial wetlands in the PPR may have a greater impact on soil quality and subsequent plant re-establishment than removal of well-developed, deep soils heavily affected by agricultural tillage (Ahn and Dee, 2011). We did not find evidence that native seedbanks were dominated by weedy species or buried by redistribution of

upland sediment into these wetlands. Instead, similar seedbanks were observed in organic and mineral soil horizons. Removal of SOC stocks will affect water holding capacity and nutrient retention (Doran et al., 1998), with unforeseen consequences on additional ecosystem functions. Other factors alter SOC stocks in the PPR that were not addressed here (Johnson et al., 2005; Johnston, 2014). Headwater wetlands were small and often geographically isolated (Tiner, 2003), so excavation could damage ecosystems critical for safeguarding rare and threatened species (Richardson et al., 2015). Results of this study point to the importance of evaluating PPR wetland SOC, SOC turnover, and restoration in a watershed context.

Conclusions

Catchment areas and potential surface flow connections among wetlands within a watershed cannot be reliably discerned at large spatial scales with field observations alone, yet these data are important to understanding the wetland ecosystem C cycle. Therefore, we suggest a framework for evaluating wetlands in a watershed context for large landscapes in the PPR. Maps can be applied to target wetlands with the highest probability of hydrologic restoration within the local watershed using modeled drainage network and catchment information. Data may also be used to weigh potential implications of soil removal during restoration on SOC and plant emergence. Depending on restoration goals, evaluation of seedbanks and watershed tools may improve restoration design to enhance wetland ecosystem services.

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