Functional Differences between Natural and Restored Wetlands in the Glaciated Interior Plains

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We measured soil properties, carbon and nutrient (nitrogen, phosphorus) pools, ambient and potential denitrification, and phosphorus sorption index (PSI) in natural depressional wetlands and depressional wetlands restored through the U.S. Department of Agriculture (USDA) Wetland Reserve Program. We measured the same suite of variables in natural and USDA Conservation Reserve Program–restored riparian buffers and in agricultural fields adjacent to both systems to determine the degree to which ecosystem services are being provided through restoration in different hydrogeomorphic settings. Organic carbon and nutrient pools, PSI, and denitrification were greater in natural than in 5- to 10-yr-old restored depressional wetlands. In riparian soils, carbon and nutrient pools, PSI, and denitrification were comparable between restored and natural systems, suggesting that these services develop quickly after restoration. Restored depressional wetlands had lower soil organic C, N, and P relative to agricultural soils, whereas the opposite trend was observed in restored riparian soils. Four-year-old restored riparian buffers achieved equivalence to natural riparian buffers within 4 yr, whereas restored depressional wetlands took longer to provide these ecosystem services (i.e., PSI, denitrification, C storage) at levels comparable to natural wetlands. Restored depressional wetlands and riparian buffers provide ecosystem services lost through previous conversion to agriculture throughout the Midwest; however, the development of these services depends on hydrodynamics (pulsed versus nonpulsed), parent material, soil texture (sand, clay), and disturbance regime (prescribed fire) of the site. As restoration continues throughout the region, C sequestration and nutrient removal in these systems is expected to increase water quality at the local and regional levels.

Wetlands and riparian buffers provide ecosystem services such as water storage and flood protection, biodiversity support, carbon (C) storage and sequestration, and water quality improvement benefits (Mitsch et al., 2001; Zedler, 2003; Fennessy and Craft, 2011). However, more than half of the wetland area in the United States at the time of European settlement (~90 million ha) has been cleared for agriculture and urban development (Dahl, 2000). Between the 1950s and 1970s, nearly 200,000 ha of wetlands were lost annually. Annual losses slowed between the mid-1980s and mid-1990s to around 24,000 ha each year, primarily due to wetland protection measures such as decreased incentives for wetland drainage and increased wetland restoration and creation (Dahl, 2006). The most recent inventory indicated an overall loss of over 25,000 ha between 2004 and 2009 (Dahl, 2011).

Historically, the agricultural Midwest experienced drastic wetland drainage for conversion to agriculture, with statewide wetland losses of up to 90% between 1780 and 1890 (Dahl, 1990). High agricultural density and loss of wetland ecosystem services in this region has led to increased nutrient and sediment delivery to the Mississippi River, contributing to water quality degradation of downstream water and to hypoxia in the Gulf of Mexico (Goolsby et al., 1999; Rabalais et al., 2002; Zedler, 2003; Fennessy and Craft, 2011). Reintroduction of nutrient and sediment removal, through practices such as changing inflow rates and water retention times (Jordan et al., 2003) or wetland restoration, can provide long-term benefits to local and regional water quality.

The Glaciated Interior Plains (GIP) of the midwestern United States, also known as the Corn Belt, has >1 million wetland conservation projects totaling ~110,000 ha, including wetland restoration, creation, and enhancement through conservation programs initiated under the Farm Bill and programs such as the Wetland Reserve Program (WRP) and Conservation Reserve Program (CRP) through the USDA Natural Resources Conservation Service. These programs are used to restore wetlands and riparian buffers in the agricultural landscape of the GIP and elsewhere (Fennessy and Craft, 2011).

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Abbreviations: CRP, Conservation Reserve Program; OM, organic matter; PSI, phosphorus sorption index; SOM, soil organic matter; TNC, The Nature Conservancy; WRP, Wetland Reserve Program.

Restoring depressional wetland and riparian buffers, both of which were historically abundant in the agriculturally modified landscape of the Midwest, is intended to reintroduce specific ecosystem services (e.g., C sequestration, nutrient removal) to the landscape. Wetlands in particular can be significant sinks for atmospheric CO_2, thereby influencing global C cycling, through peat formation, sediment accumulation, and plant biomass, and these processes are often much greater than in terrestrial habitats and agricultural fields (Bridgham et al., 2006; Euliss et al., 2006). However, not all systems provide comparable services, and not all services develop at similar rates (Brinson, 1993). For example, depressional wetlands are more isolated and less likely to intercept surface and ground water and therefore have a minimal effect on local water quality, but they are more likely to serve as C sinks (Brinson, 1993). Conversely, riparian buffers are able to intercept and transform nutrients, particularly NO_3–N and PO_4–P, thereby ameliorating water quality degradation (Brinson, 1993; Racchetti et al., 2011; Marton et al., 2013).

The ability of wetlands to store C, N, and P is a function of age and hydrologic and disturbance regimes (Craft et al., 1999; Craft and Casey, 2000; Bruland et al., 2003; Neff et al., 2005; Ballantine and Schneider, 2009). In depressional wetlands receiving little input of energy and nutrients from the surrounding landscape, autochthonous inputs from above- and belowground biomass are more important to soil development (Ballantine and Schneider, 2009). Conversely, greater allochthonous inputs in riverine, riparian, and tidal wetlands lead to greater rates of sediment and organic C, N, and P accumulation (Craft and Casey, 2000). Thus, wetland and riparian restoration cannot only provide water quality benefits through nutrient and sediment removal but also can increase C sequestration on the landscape.

Soil organic C and nitrate (NO_3–N) concentrations, temperature, and soil moisture affect denitrification, which contributes to water quality improvement. These factors are influenced by landscape position, soil properties, and hydrologic and disturbance regimes (Groffman and Tiedje, 1989; Bruland et al., 2006; Ullah and Faulkner, 2006; Orr et al., 2007). There is conflicting evidence on the N-removal efficiency through denitrification in restored depressional wetlands and riparian buffers compared with their natural counterparts. For example, Bruland et al. (2006) found that three out of four natural wetlands had greater denitrification relative to their paired created/restored wetlands receiving topsoil additions and the reintroduction of flooding. Marton et al. (2013) measured greater denitrification potentials in depressional wetlands and riparian buffers restored under the WRP and CRP programs relative to adjacent agricultural fields, whereas Orr et al. (2007) reported no increase in denitrification from a midwestern floodplain 2 yr after reintroduction of flooding.

Wetlands and riparian buffers also intercept and remove P from surface water and have been restored to improve water quality in agricultural landscapes (Woltemade, 2000; Kovacic et al., 2006). Fertilizer use is responsible for 31% of the P inputs to the Gulf of Mexico, and it is predominantly associated with sediment and soil erosion (Goolsby et al., 1999). Phosphorus is stored by sorption onto soil particles and deposition and by plant uptake and incorporation into soil organic matter (SOM) (Reddy et al., 1998). Phosphorus sorption represents a short-term sink and varies depending on soil texture (i.e., clay content); pH; and the amount of Al, Fe, and SOM in the soil (Richardson, 1985; Bridgham et al., 2001; Bruland and Richardson, 2004b). Accumulation of P in SOM is a long-term storage process and is slow in restored wetlands relative to organic C and N (Craft et al., 1999; Ballantine and Schneider, 2009).

Through the USDA, depressional wetlands and riparian buffers are being conserved and restored in agricultural landscapes such as the Piedmont-Coastal Plain (De Steven and Lowrance, 2011), the California Central Valley (Duffy and Kahara, 2011), the Mississippi Alluvial Valley (Faulkner et al., 2011), the Prairie Pothole Region (Gleason et al., 2011), the GIP (Fennessy and Craft, 2011), and elsewhere. The primary goal of these restoration and conservation practices is to restore ecosystem services such as water storage, wildlife habitat, and water quality improvement benefits (Fennessy and Craft, 2011). Approximately 5700 ha of restored wetland and 580 ha of restored riparian buffers were established in Indiana between 2001 and 2007; however, the effectiveness of these programs has not been documented in many regions, particularly in the GIP, which has experienced drastic wetland loss (~18.6 million ha) and is a large source of N to downstream waters (Mitsch et al., 2001).

To address this knowledge gap, we measured water quality improvement functions (i.e., denitrification and P sorption) and C stocks and sequestration in natural and restored depressional wetlands and riparian buffers in the agricultural landscape of the GIP and compared them with adjacent agricultural fields. Our primary goal was not to compare two different systems but rather to determine if restored depressional wetlands and restored riparian buffers provide water quality improvement benefits comparable to natural systems and if restoration increased the delivery of these services relative to the agricultural fields from which they were restored. We predicted that water quality improvement functions (i.e., denitrification and phosphorus sorption) and C storage would be greater in natural systems relative to restored systems in depressional wetlands and in riparian buffers.

Materials and Methods

Site Description

We sampled 10 restored and five natural depressional wetlands in northern Indiana and four restored and four natural riparian buffers in central Indiana (Table 1). We also sampled five agricultural fields adjacent to the restored wetlands and two agricultural fields adjacent to the restored riparian buffers to characterize changes in ecosystem services after restoration. Restored wetlands were located at Kankakee Sands Preserve, owned by The Nature Conservancy (TNC), and were between 0.5 and 3 ha in size with water depth ranging from 1 to 40 cm. These wetlands were restored under the WRP by filling in surrounding drainage ditches with soil excavated from on-site between 1999 and 2005 (C. O'Leary, personal communication). At the time of sampling, these systems were between 5 and 10 yr post-restoration. The WRP-restored wetlands are depressional, precipitation-fed systems, and the soils are mapped as Granby loamy fine sand (sandy, mixed, mesic Typic Endoaquolls). The wetlands are surrounded by restored mesic prairie. Fire has been used as a management tool in the mesic prairie since 2002 by the TNC, with fires occurring every 2 to 3 yr in the spring or fall (T. Anchor, personal communication). Other surrounding land consists of row-crop agriculture on a rotation of 3 yr of corn (*Zea mays* L.) and 1 yr of soybean [*Glycine max* (L.) Merr.]. Dominant vegetation of the depressional wetlands consisted of *Schoenoplectus pungens* (Vahl) Palla, *Polygonum pensylvanicum* L., *Eleocharis erythropoda* Steud., *Juncus brachycephalus* (Engelm.) Buchenau, *Scirpus cyperinus* (L.) Kunth, *Leersia oryzoides* (L.) Sw., *Phalaris arundinacea* L., and *Solidago altissima* L.

Natural wetlands consisted of five depressional wetlands located at the Willow Slough Fish and Wildlife Area owned and managed by the Indiana Department of Natural Resources. Natural depressional wetlands had a comparable hydrogeomorphic setting and water depths. These sites were selected as reference systems due to their similar hydrogeomorphic setting and accessibility. Because there are a limited number of natural depressional wetlands in the agricultural landscape of northwestern Indiana, these sites represent the best natural analog of undisturbed, reference depressional wetlands. Soils were mapped as Adrian drained muck (sandy, mixed, euic, mesic Terric Haplosaprists) or undrained Newton loamy fine sand (sandy, mixed, mesic Typic Humaquepts). Natural depressional wetlands contained herbaceous vegetation and were dominated by *Calamagrostis canadensis* (Michx.) P. Beauv., *Thelypteris palustris* Schott, *Boehmeria cylindrica* (L.) Sw., *Polygonum* sp., and *Scirpus cyperinus* (L.) Kunth.

Table 1. Locations of all study sites.

Hydrogeomorphic setting	Site type	Site number	Latitude	Longitude
Depressional	restored	1	41.050408	−87.452633
		2	41.044350	−87.453556
		3	41.040797	−87.443183
		4	41.040194	−87.438392
		5	41.032250	−87.462150
		6	41.033703	−87.460667
		7	41.038250	−87.465317
		8	41.037422	−87.464853
		9	41.043150	−87.465353
		10	41.041706	−87.465139
	natural	1	40.964308	−87.516053
		2	40.965781	−87.514414
		3	40.975108	−87.477789
		4	40.976153	−87.476947
		5	40.999161	−87.512308
	agricultural	1	41.055994	−87.483644
		2	41.057811	−87.471325
		3	41.056883	−87.471147
		4	41.057797	−87.460561
		5	41.056900	−87.461203
Riparian	restored	1	40.132267	−85.958375
		2	40.132233	−85.959783
		3	40.131192	−85.960797
		4	40.129931	−85.961278
	natural	1	40.133400	−85.959911
		2	40.131781	−85.960925
		3	40.130078	−85.961769
		4	40.128839	−85.962942
	agricultural	1	40.129447	−85.959639
		2	40.126800	−85.960261

The natural and restored riparian buffers were located in the Strawtown Koteewi Park in Hamilton County, Indiana along the west fork of the White River. The restored riparian buffers were approximately 20 to 30 m in width and were restored in 2006 by ceasing row-crop agriculture and planting trees [*Betula nigra* L., *Taxodium distichum* (L.) Rich.]. Restored riparian buffers were 4 yr old at the time of sampling. Soils in the natural and restored riparian buffers were mapped as Genesee silt loam (fine-loamy, mixed, superactive, mesic Fluventic Eutrudepts). The land adjacent to the restored riparian buffers is cultivated for corn during the growing season and left fallow during winter. Natural riparian buffers range from 30 to 40 m in width, and the dominant trees are *Celtis occidentalis* L., *Populus deltoides* Bartram ex Marsh., *Fraxinus pennsylvanica* Marsh., *Acer saccharinum* L., and *Platanus occidentalis* L. The understory is dominated by *Urtica dioica* L.

Agricultural fields adjacent to the restored wetlands ($n = 5$) were within 100 m from the restored depressional wetlands and were mapped as Granby loamy fine sand (sandy, mixed, mesic Typic Endoaquolls). The fields had been previously planted with corn but were fallow at the time of sampling. Agricultural fields adjacent to riparian buffers ($n = 2$) were within 50 m from the restored riparian buffers and were mapped as Genesee silt loam (fine-loamy, mixed, superactive, mesic Fluventic Eutrudepts) and were fallow at the time of sampling but had been previously cultivated the previous year with corn.

Soil Sampling and Analysis

Four 5-cm-deep soil cores (8.5 cm in diameter) were collected from each site in November 2009 and placed in resealable plastic bags. Soils were placed on ice and transported back to the laboratory for analysis. Soils were stored at 4°C, and analyses were started within 1 wk after collection. Each core was processed separately as subsamples and then averaged by site for statistical analysis. We selected the top 5 cm for analysis based on the use of fire as a management tool by TNC, which would have been most susceptible to fire and therefore most likely to represent the combined effects of restoration and fire.

Field-moist soils were homogenized and analyzed for pH, extractable N (NO_3–N, NH_4–N) and P (PO_4–P), phosphorus sorption index (PSI), and soil moisture content. Extractable N was extracted using 2 mol L^{-1} KCl (Mulvaney, 1996), and extracts were analyzed (Quickchem 8500, Lachat Instruments). Extractable P was extracted using 0.5 mol L^{-1} $NaHCO_3$ and analyzed using the ascorbic-acid method (Kuo, 1996). Standard curves for extractable N and P were prepared before each analysis, and all curves had r^2 values of ≥0.99 (data not shown). Soil pH was measured in a 1:1 soil:water ratio (Thomas, 1996) using a pH probe (Thermo Fisher Scientific). Phosphorus sorption index was determined by adding 25 mL of 130 mg P L^{-1} to 5 g of field-moist soil and shaking for 24 h at 120 rpm, and the supernatant was analyzed for P using the ascorbic-acid method (Bruland and Richardson, 2004b). The index is calculated by $X(\log C)^{-1}$, where X is the amount of P sorbed over 24 h and C is the inorganic P concentration in solution at the end of the 24-h incubation, corrected for the volume of the supernatant. Standard curves were prepared by serial dilution of the 130 mg P L^{-1} solution. All standard curves had r^2 values of ≥0.99 (data not shown). Soil moisture content was determined by measuring the change in mass of a 5-g sample after drying at 105°C to a constant weight.

After completing the field-moist analyses, the remaining soils were dried, ground, and passed through a 2-mm mesh sieve. Organic C and total N were determined using a 2400 CHN Analyzer (PerkinElmer). An in-house soil standard was analyzed after every 10 samples and resulted in mean (±SD) organic C and total N concentrations of 5.9 ± 0.62% C and 0.35 ± 0.02% N as compared with long-term multiyear means of 6.1% C and 0.37% N. Carbonates were removed by placing subsamples in a desiccator with a Petri dish of concentrated HCl for 24 h (Hedges and Stern, 1984). Total P was determined using the ascorbic-acid method after a nitric-perchloric digestion (Sommers and Nelson, 1972). Standards were digested and analyzed concurrently with all samples (National Institute of Standards and Technology, Estuarine Sediment, 1646a) with a mean recovery of 86%. Concentrations were determined using standard curves generated from a serial dilution of a KH_2PO_4 solution and were analyzed before and after sample analysis. All total P standard curves had r^2 values of ≥0.99. Bulk density was determined by dividing the total dry weight of each soil sample by the volume of the core (Craft et al., 2007). All results were expressed on a dry gram basis. Soil organic C and total N and P pools were determined using the concentration, depth, and bulk density measurements. Particle size was determined for all soils using the hydrometer method (Gee and Bauder, 1986).

Denitrification

We collected additional soils twice from wetlands and riparian buffers to characterize ambient and potential denitrification. We did not measure denitrification from agricultural soils, assuming that the rates on these aerobic soils are negligible. Wetlands were sampled in June and August of 2010, and riparian buffers were sampled in November 2010 and May 2011. We collected four soil cores (8.5 cm diameter by 5 cm deep) from each site. Soils were placed into resealable plastic bags and transported on ice to the laboratory. Soil moisture, organic matter, and extractable N (NO_3–N, NH_4–N) and P (PO_4–P) were analyzed as previously described. Water was collected from each site for use in the denitrification assays.

Ambient and potential denitrification was measured using the acetylene-inhibition method (Orr et al., 2007). Twenty-five grams of field-moist soil were added to 125-mL Wheaton bottles with screw caps equipped with gray-butyl septa. Fifty milliliters of site water were added to each bottle. For ambient denitrification, water was amended with chloramphenicol (0.21 mmol L^{-1}) to inhibit microbial growth. For potential denitrification assays, site water was amended with chloramphenicol (0.21 mmol L^{-1}), and glucose (20 mmol L^{-1}) and potassium nitrate (18 mmol L^{-1}) were added to remove potential C and N limitations. Bottles were flushed with ultrahigh-purity N_2 gas for 5 min, and 10% of the N_2 headspace was replaced with acetylene to block the reduction of N_2O to N_2. Incubations were conducted at 25°C for 4 h with 5-mL headspace samples collected after 15, 30, 60, 120, and 240 min and stored in 2-mL evacuated Wheaton vials equipped with aluminum crimp tops and gray-butyl septa. Bottles were shaken vigorously by hand for 30 s before collecting gas samples to equilibrate N_2O between the soil slurry and headspace. Samples were analyzed for N_2O using an SRI Greenhouse Gas 8610C gas chromatograph (SRI Instruments) equipped with an electron capture detector, and concentrations were corrected for dilution through multiple sample collections. Standard N_2O curves were made using standard concentration gases (Air Liquide) and had r^2 values of ≥0.95. Denitrification rates were determined by regression of N_2O accumulation against time. A 5-g field-moist sample was weighed into an aluminum weigh boat and dried to a constant weight to determine the soil moisture content. All denitrification rates were expressed on a dry weight basis.

Statistical Analysis

Differences in soil properties (pH; bulk density; extractable N and P; PSI; soil organic C; total N and P, C, N, and P pools; % OM, % sand, % silt, and % clay) were tested using a one-way ANOVA with site type (agriculture, restored, natural) as the main effect (SPSS, 2010). Tukey's honestly significant difference test was used to test for differences between main effects. Separate ANOVAs were conducted for depressional wetlands and riparian buffers. Data were first tested for normality using the Kolmogorov-Smirnov test ($\alpha = 0.05$). All data, except bulk density, were natural-log transformed to meet the assumptions of the ANOVA. Correlation analysis was used to determine associations between PSI and soil organic C; total N; total P; extractable N (NO_3–N, NH_4–N); soil moisture content; and % sand, silt, clay, and organic matter.

Ambient and potential denitrification data were natural-log transformed and tested using a two-way ANOVA based on site type (natural, restored) and season. Separate ANOVAs were performed for wetlands and riparian buffers. Correlation analyses were performed between denitrification rates and soil properties on nontransformed data. All analyses were conducted at $\alpha = 0.05$.

Results

Depressional Wetlands

Soils in natural and restored wetlands and adjacent agricultural fields were dominated by sand (79–91%). Natural and restored depressional wetlands had significantly greater sand, silt, and clay relative to adjacent agricultural fields ($p < 0.001$) (Table 2). Conversely, natural wetlands had greater percent soil organic matter, organic C, total N, and total P concentrations and lower bulk density and pH ($p < 0.001$) than the restored wetlands and agricultural fields (Tables 2 and 3). Natural wetland soils had gravimetric water content that was 2 to 3 times higher than restored wetland and agricultural soils ($p < 0.001$) (Table 3). In contrast, extractable PO_4–P was 10 times greater in agricultural soils than in natural and restored wetland soils ($p < 0.001$) and NO_3–N was greater in agricultural and natural wetland soils than in restored wetlands ($p < 0.001$). There was no difference in NH_4–N between natural and restored wetlands and adjacent agricultural fields (Table 3).

On an area basis, natural depressional wetlands had significantly greater mean soil organic C (1478 g m^{-2}) and N pools (156 g m^{-2}) than restored depressional wetlands (1021 g organic C m^{-2}; 83 g N m^{-2}) (Fig. 1), whereas agricultural soils had intermediate organic C and total N pools. Conversely, mean soil P pools were significantly greater in agricultural soils (15 g P m^{-2}) than in restored depressional wetland soils (11 g P m^{-2}), whereas natural depressional wetlands had an intermediate value (13 g P m^{-2}).

Table 2. Bulk soil properties in agricultural, restored, and natural depressional wetlands and riparian buffers (0–5 cm).†

System‡	Sand	Silt	Clay	Bulk density	Organic matter	Organic C	Total N	Total P
	%			g cm^3	%			µg g^{-1}
				Wetland				
Agriculture	91 ± 0.4b§	2.2 ± 0.2c	7.0 ± 0.5b	1.13 ± 0.04a	4.8 ± 0.20b	2.4 ± 0.10b	0.22 ± 0.01b	270 ± 11b
Restored	95 ± 0.2a	4.4 ± 0.2b	0.7 ± 0.1a	1.05 ± 0.04a	4.4 ± 0.50b	2.2 ± 0.26b	0.18 ± 0.02b	230 ± 17^b
Natural	94 ± 1.2a	6.0 ± 1.2a	0.5 ± 0.3a	0.49 ± 0.05b	15 ± 1.1b	9.2 ± 1.0a	0.78 ± 0.08a	620 ± 66a
				Riparian				
Agriculture	84 ± 0.7a	2.6 ± 0.3ab	14 ± 0.8a	1.0 ± 0.05b	4.4 ± 0.29b	2.2 ± 0.15b	0.23 ± 0.01b	1050 ± 51a
Restored	80 ± 0.8b	3.5 ± 0.3a	16 ± 0.6a	1.3 ± 0.04a	9.7 ± 0.13a	4.5 ± 0.13a	0.27 ± 0.01ab	1010 ± 29a
Natural	87 ± 0.7a	2.2 ± 0.4b	11 ± 0.7a	1.0 ± 0.07b	10 ± 0.47a	4.8 ± 0.28a	0.30 ± 0.01a	1010 ± 29a

† Sample sizes: restored wetlands, $n = 10$; natural wetlands, $n = 5$; natural and restored riparian buffers, $n = 4$; agricultural fields adjacent to wetlands, $n = 5$; agricultural fields adjacent to riparian buffers, $n = 2$.

‡ Separate analyses were conducted for each system (depressional wetland, riparian).

§ Values (means ± 1 SE) with different letters represent significant differences between agriculture, restored, and natural sites (Tukey's honestly significant difference test; $\alpha = 0.05$).

Water quality improvement functions of natural wetlands also were greater than in restored wetlands. Mean P sorption was approximately two to three times greater ($p < 0.001$) in natural depressional wetlands (297 mg P kg soil^{-1}) than in restored wetlands and agricultural fields (114 and 86 mg P kg soil^{-1}, respectively), which did not significantly differ (Fig. 2). Natural depressional wetlands also had rates of ambient (88.8 ng N g soil^{-1} h^{-1}) and potential (329.3 ng N g soil^{-1} h^{-1}) denitrification that were three times greater than in restored wetlands (32.4 and 106.7 ng N g soil^{-1} h^{-1}, respectively) (Fig. 3). There was no difference in ambient denitrification among sampling dates, although potential denitrification was greater in August than in June ($p = 0.008$).

Riparian Buffers

Soil organic C, N (total and extractable NO_3–N, NH_4–N), and P (total and extractable PO_4–P) did not differ between natural and restored riparian buffers ($p > 0.05$) (Tables 2 and 3). Natural riparian buffers had significantly lower mean pH, bulk density, and silt and had significantly greater mean soil moisture and sand than restored riparian buffers (Tables 2 and 3). Natural and restored riparian soils contained 2 times more organic matter ($p < 0.001$) and organic C ($p < 0.001$), approximately 30 times more extractable NO_3–N, and twice as much PO_4–P than adjacent agricultural soils (Table 2). Organic C and N pools were significantly greater ($p < 0.005$) in natural (2464 g C m^{-2} and 156 g N m^{-2}) and restored riparian soils (2868 g C m^{-2} and 173 g N m^{-2}) relative to adjacent agricultural soils (1100 g C m^{-2} and 113 g N m^{-2}) (Fig. 1). Conversely, mean total P pools were significantly lowest in agricultural soils (52 g m^{-2}) and greatest in restored riparian soils (64 g m^{-2}) ($p = 0.015$).

In contrast to wetlands where P sorption was greatest in natural soils, PSI did not differ among riparian buffers and agricultural soils (Fig. 2). Ambient and potential denitrification also did not differ between natural and restored riparian soils ($p \geq 0.12$) (Fig. 3), although ambient denitrification was greater in spring (May 2011) (188 ng N dry g soil^{-1} h^{-1}) than in fall (Nov. 2010) (122 ng N dry g soil^{-1} h^{-1}). Potential denitrification was three to four times greater than ambient denitrification and did not differ between the two sampling periods ($p = 0.26$).

Discussion

Wetlands

Overall, surface soils from 5- to 10-yr-old restored wetlands provided lower levels of water quality improvement potential (i.e., N removal via denitrification and P removal via sorption), C sequestration, and N and P storage than their natural counterparts. There were no functional differences between the restored depressional wetlands based on time since restoration. In fact, despite being restored for up to 10 yr, surface soils from restored wetlands did not differ with respect to PSI (Fig. 2) and

Table 3. Field-moist soil properties of agricultural, restored, and natural depressional wetlands and riparian buffers (0–5 cm).

System‡	pH	Soil moisture	NH_4–N	NO_3–N	PO_4–P
		%	µg g^{-1}		
			Wetland		
Agriculture	7.0 ± 0.1a§	19 ± 1.1c	1.8 ± 0.34a	2.8 ± 0.86a	5.7 ± 0.8a
Restored	6.8 ± 0.1a	36 ± 1.8b	2.4 ± 0.78a	0.80 ± 0.13b	0.42 ± 0.05b
Natural	5.2 ± 0.1b	60 ± 2.9a	2.7 ± 0.69a	15 ± 5.8a	0.15 ± 0.02c
			Riparian		
Agriculture	7.3 ± 0.02c	26 ± 0.8ab	1 ± 0.1a	1 ± 0.2b	4 ± 2b
Restored	7.7 ± 0.05a	23 ± 1.0b	1 ± 0.1a	26 ± 2a	8 ± 1a
Natural	7.5 ± 0.04b	34 ± 3.0a	2 ± 0.3a	30 ± 4a	11 ± 1a

† Sample sizes: restored wetlands, $n = 10$; natural wetlands, $n = 5$; natural and restored riparian buffers, $n = 4$; agricultural fields adjacent to wetlands, $n = 5$; agricultural fields adjacent to riparian buffers, $n = 2$.

‡ Separate analyses were conducted for each system (depressional wetland, riparian).

§ Values (mean ± 1 SE) with different letters represent significant differences between agriculture, restored, and natural sites (Tukey's honestly significant difference test; $\alpha = 0.05$).

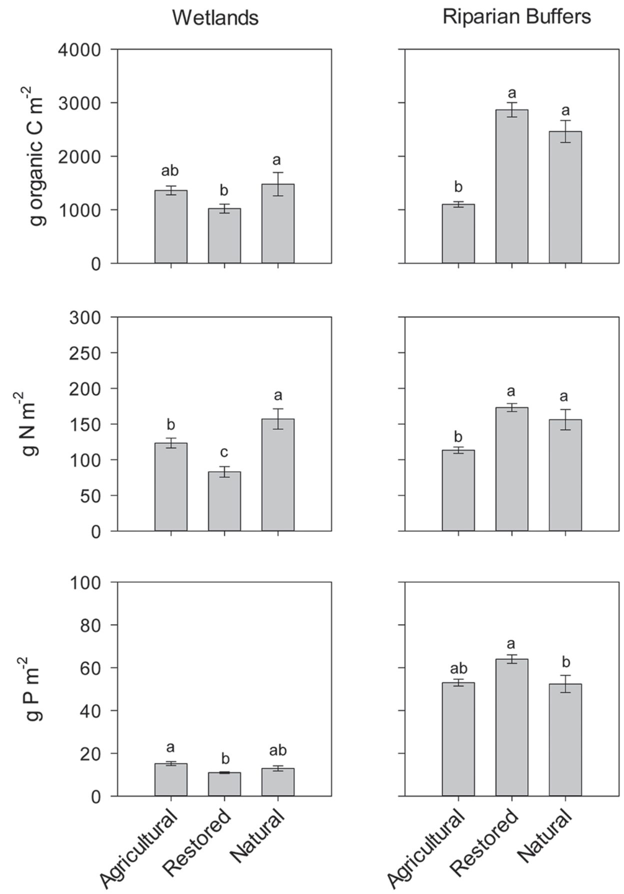

Fig. 1. Mean (±1 SE) C, N, and P pools in the top 5 cm of soil in agricultural, restored, and natural wetlands and riparian buffers. Different lowercase letters indicate significant differences between agricultural, restored, and natural soils within wetlands and riparian buffers separately based on Tukey's honestly significant difference (α = 0.05).

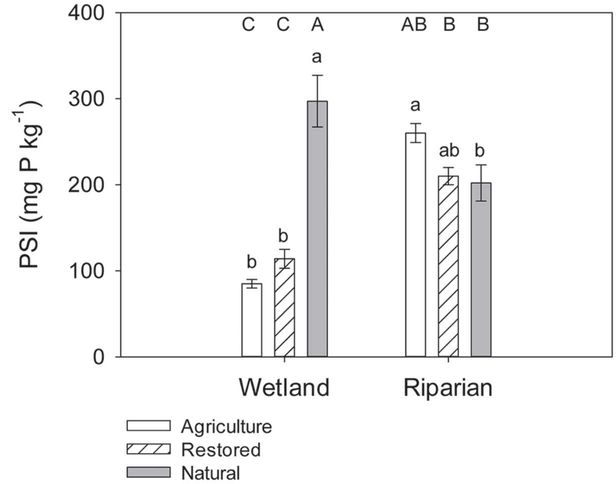

Fig. 2. Mean (±1 SE) P sorption index (PSI) from soils of agricultural, restored, and natural depressional wetlands and riparian buffers. Different uppercase letters indicate significant differences between each of the six groups based on Tukey's honestly significant difference (α = 0.05). Different lowercase letters indicate significant differences between agricultural, restored, and natural soils within wetlands and riparian buffers separately.

stored less N than those of agricultural land (Fig. 1). It also is likely that differences between natural and restored depressional wetlands would be even greater in deeper soils, which can recover more slowly than surface soils (Hossler and Bouchard, 2010).

Other studies of freshwater wetland soils have reported smaller stocks of organic C in restored wetlands than in natural wetlands. Fennessy et al. (2008) measured soil organic C pools (0–10 cm) of approximately 8000 g m^{-2} in natural depressional wetlands in Ohio, whereas restored wetlands averaged 4790 g m^{-2}. Ballantine and Schneider (2009) found soil organic matter pools ranging from 3300 g m^{-2} (1650 g organic C m^{-2}) in depressional wetlands 3 to 5 yr after reintroduction of impounded water to 5530 g m^{-2} (2765 g organic C m^{-2}) in natural wetlands. They suggest that the lower soil organic matter pools in the restored wetlands were the result of lower aboveground primary production and less time to accumulate SOM pools relative to natural wetlands.

Restored depressional wetlands contained less organic C, N, and P than agricultural soils, which may be due to periodic disturbance from prescribed fires. The restored wetlands exist within a mosaic of restored prairie and oak–savanna habitats that is burned every 1 to 2 yr (C. O'Leary, personal communication). Fires occur in late summer to early fall during dry-down periods, which allows the fires to burn through the wetlands, thereby limiting the amount of organic inputs in the upper layers of the soil profile. For example, fire can reduce organic C and total N concentrations in surface and subsurface peat layers (Smith et al., 2001). Similarly, Neff et al. (2005) found that fire reduced soil organic C by 37% and total N stocks by 33% in the top 8 cm of forest soils, whereas the lower mineral horizons remained unaffected. Conversely, Smith et al. (2001) reported an increase in total P concentrations after burns, which they attributed to conservation of P in the system coinciding with soil loss and consolidation of remaining soil mineral material.

Similar to organic C and total N, we measured lower total P concentrations in the restored depressional wetlands relative to the nearby agricultural fields. Agricultural fields and natural depressional wetlands do not receive prescribed burns, but they did have similar hydrogeomorphic settings. Even though the restored wetland and agricultural soils were mapped as the same series (Granby loamy fine sand), we cannot rule out initial differences in soil properties among them because the most underperforming agricultural land (e.g., sandy or wet) is often taken out of cultivation and enrolled in WRP (or CRP) programs. For example, our restored depressional wetlands had greater sand and less clay and organic matter than the adjacent agricultural soils (Table 2). Low SOM and clay content in the restored wetlands can limit the delivery of other ecosystem services, such as C accumulation by slowed decomposition in anaerobic soils, N removal via denitrification, and P removal via sorption (Groffman and Tiedje, 1989; Mitsch et al., 2001; Bruland and Richardson, 2004a,b; Bruland et al., 2009). Therefore, it is possible that the differences in soil C, N, and P between restored wetlands and agricultural lands were the result of different preexisting conditions or the effects of fire, which would tend to decrease C and N but increase P.

Another possible explanation for the similarities between restored depressional wetlands and agricultural soils is the legacy effect of agriculture. For example, Graham et al. (2005) found peatlands restored by ceasing agriculture and then reflooding in Oregon's Upper Klamath basin had significantly greater bulk density, and therefore greater pools of organic C, total N, and

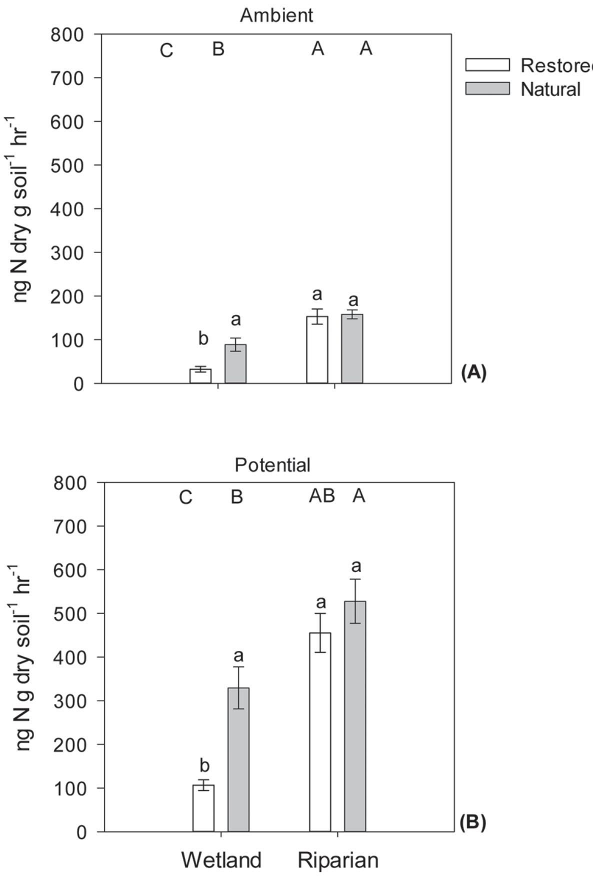

Fig. 3. (a) Ambient and (b) potential denitrification in restored and natural depressional wetlands and riparian buffers. Different uppercase letters indicate significant differences between each of the four groups based on Tukey's honestly significant difference (α = 0.05). Different lowercase letters indicate significant differences between restored and natural soils within wetlands and riparian buffers separately. Differences were tested by comparing log-transformed data.

total P, than nearby natural peatlands. The restored peatlands in Oregon had experienced compaction and P enrichment after drainage and conversion to agriculture and did not sequester comparable amounts of C, N, and P as natural wetlands did within 8 yr after restoration.

In addition to greater C stocks and nutrient (N, P) pools, P sorption was greater in natural wetlands than in restored wetlands and agricultural fields and was positively correlated across all sites with percent organic C ($r^2 \geq 0.67$; $p < 0.01$) and negatively correlated to sand content ($r^2 = 0.19$; $p < 0.01$). Similarly, Bruland and Richardson (2004a) found that PSI in created wetlands amended with topsoil in Virginia was positively correlated with soil OM. In their study, sites that had received topsoil amendments had an average PSI of 259 mg P kg^{-1}, whereas unamended soils sorbed 191 mg P kg^{-1}. In their study, amended and unamended soils had PSI values comparable to what we measured in restored and natural depressional wetlands (114 and 297 mg P kg^{-1}, respectively). In addition to OM, iron, aluminum, and calcium can increase P sorption (Hogan et al., 2004), although these are often associated with clay content (Richardson, 1985; Reddy et al., 1999). The low clay content of our wetland soils (0.5–7.0%) suggests that organic matter was responsible for P sorption.

Similar to the patterns for PSI, denitrification was greater in natural wetlands than in restored wetlands. Across all sites, potential denitrification was significantly greater than ambient denitrification, suggesting that these systems were limited by C and/or N. We measured much lower rates of ambient denitrification in our restored wetlands (65 ng N g soil^{-1} h^{-1}) than in the natural wetlands (198 ng N g soil^{-1} h^{-1}), with corresponding soil moisture contents of 32 and 63%. Denitrification has been found to be lower in other restored freshwater wetlands relative to natural wetlands, along with lower microbial community diversity and lower soil moisture (Peralta et al., 2010). Bruland et al. (2006) measured lower potential denitrification in created and restored wetlands than in natural wetlands in riverine and nonriverine systems in North Carolina. Hunter and Faulkner (2001) also measured lower potential denitrification in restored bottomland forested wetlands than in natural forested wetlands. In our natural and restored wetlands, ambient denitrification was positively correlated with soil NO_3–N ($r^2 = 0.07$), soil moisture ($r^2 = 0.18$), and OM ($r^2 = 0.21$).

Riparian Buffers

In contrast to wetlands, where soil organic C pools were lower in restored than in natural wetlands, soil organic C pools did not differ between restored and natural (3040–3810 g m^{-2}) riparian surface soils but were two times greater than in agricultural (1510 g m^{-2}) soils (Fig. 1). Soil N pools were also greater in restored and natural riparian soils than in agricultural soils, whereas soil P pools were comparable between all three systems (Fig. 1). However, had we measured subsurface soils we likely would have found differences in P pools because deeper soils recover more slowly than surface soils (Hossler and Bouchard, 2010). These findings highlight the ability of riparian buffers to sequester C and N in surface soils relatively quickly after cessation of row crop agriculture. In contrast to our findings, Young-Mathews et al. (2010) reported lower soil C and N concentrations in natural riparian buffers relative to adjacent agricultural fields in the Sacramento Valley, California. They suggested that the lower C and N concentrations resulted from deposition of mineral sediment low in organic matter and erosion of surface soils during flooding events. Despite lower soil C and N concentrations, Young-Mathews et al. (2010) reported greater overall ecosystems services (e.g., nutrient retention, biodiversity, and woody C storage) in riparian buffers compared with agricultural fields from which they were restored.

Phosphorus sorption index also did not differ between restored and natural riparian soils. Phosphorus sorption measured by Bruland and Richardson (2004b) in two natural riparian wetlands in North Carolina (858–1664 mg P kg^{-1}) was four to eight times greater than we measured in any of our riparian (202–260 mg P kg^{-1}) or wetland soils (86–297 mg P kg^{-1}). They also found that P sorption was positively correlated to soil organic matter, clay content, and aluminum. Our PSI values correlated with organic C ($r^2 = 0.13$; $p < 0.05$) although not with clay content, and we did not measure extractable aluminum. We found comparable short-term P removal via sorption between agricultural and restored and natural riparian buffers in surface (0–5 cm) soils (Fig. 2).

Denitrification did not differ between natural and restored riparian buffers, which could be attributed to their similar soil properties (e.g., NO_3–N, soil moisture, texture, and organic C) (Tables 2 and 3). Across all sites, ambient denitrification was positively correlated to soil NH_4–N ($r^2 = 0.21$) and soil moisture ($r^2 = 0.19$). There was no correlation between denitrification and extractable NO_3–N, organic matter, or soil texture. Hanson et al. (1994) found that denitrification in natural riparian wetlands was strongly influenced by soil moisture and extractable NO_3–N but not by NH_4–N.

Restoring Ecosystem Services: Landscape Considerations

Not all wetlands provide the same ecosystem services, and there can often be a trade-off in which services are restored, and different rates of restoration may be implemented for different functions (Zedler and Kercher, 2005; Orr et al., 2007). For example, Aronson and Galatowitsch (2008) found lower wetland plant diversity in restored wetlands of the prairie pothole region relative to natural wetlands, although biodiversity was increased relative to the agricultural fields they replaced. On the other hand, Rewa (2007) reported comparable diversity of amphibians, birds, and invertebrates between restored and natural depressional wetlands.

We measured lower water quality improvement functions and C pools in restored wetlands than in natural wetlands. Furthermore, we measured lower C, N, and P storage in restored wetlands than in agricultural fields, indicating that the WRP-restored wetlands failed to improve the delivery of these ecosystem services in surface soils within 5 to 10 yr. However, it is possible that, given enough time, these services would reach levels comparable to natural depressional wetlands (Hossler and Bouchard, 2010; Orr et al., 2007). At the same sites, Hopple and Craft (2012) measured comparable plant species richness in restored and natural wetlands that they attributed to management activities such as prescribed burns, active seeding, and invasive species removal used by The Nature Conservancy at the site. These findings suggest that management activities (e.g., fire) that are used to optimize one ecosystem service (plant biodiversity) may reduce the ability to deliver other services (C sequestration).

Our measurements of water quality improvement potential and C sequestration among restored wetland and riparian buffers can help improve policies pertaining to ecosystems in agricultural landscapes by providing greater insight into the relative provisioning of ecosystem services through different conservation practices. However, the applicability of our results will be contingent on several factors, such as soil type, hydrogeomorphic setting, method of restoration, fire occurrence and frequency, and other management practices. As outlined by Zedler (2003) and Fennessy and Craft (2011), restoring wetlands, particularly in agricultural landscapes, reintroduces ecosystem services such as water quality improvement functions, flood abatement, C sequestration, and biodiversity support. Furthermore, Mitsch et al. (2001) suggested that between 21,000 and 52,000 km^2 of wetlands and riparian buffers, respectively, must be restored in the Mississippi River watershed to make a significant reduction in N and P loading to the Gulf of Mexico, although only approximately 800 km^2 of wetlands and riparian buffers have been restored in the GIP since 2000 (Fennessy and Craft, 2011). With continued wetland and riparian buffer restoration in the GIP and other portions of the Mississippi River watershed, N and P loadings to the Gulf could decrease, resulting in improved water quality while simultaneously sequestering C. In particular, wetlands and riparian buffers with a higher degree of hydrologic connectivity will provide a greater level of ecosystem services relative to more hydrologically isolated systems.

Riparian buffers provided greater nutrient removal and C sequestration than agricultural fields and depressional wetlands. Furthermore, after only 4 to 5 yr after restoration, restored and natural riparian buffers performed equally well, suggesting that reintroduction of water quality improvement functions and C sequestration occurs more rapidly in riparian buffers than in wetlands, consistent with greater hydrologic connectivity allowing for more rapid nutrient processing; greater C, N, P, and sediment (e.g., clay) accumulation; and priming of soil denitrifiers. However, recovery may have been slower at deeper depths in the soil profile. Conversely, even after 5 to 10 yr following restoration, restored wetlands sequestered less C and removed less N and P than adjacent agricultural lands, likely due to prescribed fire, although restored wetlands had greater plant biodiversity (Hopple and Craft, 2012), highlighting the tradeoff in services obtained with restoring different systems (e.g., wetland vs. riparian). Future restoration in agricultural landscapes should focus on areas with higher hydrologic connectivity, finer-textured soils, and limited anthropogenic disturbances. Despite their differences, enrolling agricultural land into wetland and riparian conservation practices will increase ecosystem service delivery, although strategic placement will depend on specific goals. Riparian buffers can provide greater nutrient removal and C sequestration than depressional wetlands, although in hydrologically isolated agricultural landscapes, depressional wetlands over time can increase ecosystem services relative to adjacent agricultural lands.

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