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Ecosystem Recovery Across a Chronosequence of Restored Wetlands in the Platte River Valley

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Abstract

Wet meadows in the Platte River valley (PRV) consist of linear wetlands in mesic prairie matrix systems that have been degraded and diminished for agriculture. Restoration in this region is a widespread practice that involves land contouring and seeding native species, however ecosystem recovery following restoration has never been examined. We quantified recovery trajectories and rates of above- and belowground plant biomass, soil physical and chemical properties, and C and N pools in a chronosequence of six restored wet meadows in relation to three natural wetlands. Within each site, we sampled sloughs (deeper habitats) and adjacent margins (slightly higher elevation) for three consecutive years. Varying hydrologic regimes between habitats resulted in differential patterns in ecosystem measurements (bulk density, C mineralization) in both natural and restored wetlands. Total aboveground biomass (TAB), root biomass, root C and N storage, total soil C and N, microbial N, and extractable N increased with years restored in both margins and sloughs. The model predicted rates of increase did not differ between habitats, but elevations of linear regressions were higher in sloughs than margins for root N, total soil C, total soil N, MBN, and extractable total N ($P < 0.05$). Our results suggest that bulk density and soil organic matter (SOM) represent two useful, easily measured indices of ecosystem recovery, because they were correlated with many pools and fluxes of C and N. Furthermore, we conclude that most change in ecosystem structure and function during the first decade following restoration occurs in shallow soil depths, and ecosystem recovery varies with subtle differences in elevation and associated plant community structure.

Key words: aboveground biomass; belowground; carbon; function; restoration; mineralization; nitrogen; root biomass; wet meadow.

Introduction

Wetlands represent some of the most productive systems that play an important role in the global cycling and storage of carbon (for example, Euliss and others 2006) and mitigation of excess nutrients (Schlesinger 1997; Cirmo 1998; Hamersley and Howes 2002). Despite these valuable functions, over half of the wetlands that once existed in the conterminous United States have been degraded through land development and conversion to agriculture (Vileisis 1997).

In the Great Plains of the United States, wetlands have been drained and leveled for crop production. In one major watershed of this region, the central

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Platte River Valley (PRV) of Nebraska, it is estimated that 74–80% of wet meadow systems have been drained for agriculture (Sidle and others 1989) and now comprise less than 5% of land area in the PRV (Sidle and others 1989; U.S. Fish and Wildlife Service 1997). The extensive degradation of wetlands in this region is of particular concern because the PRV is used extensively by migratory birds on the central flyway (including the federally endangered Interior Least Tern, *Sterna antillarum* and Whooping Crane, *Grus americana*).

Changes in ecosystem structure and function following conversion into row-crop agriculture have been well-documented (Haas and others 1957; Anderson and Coleman 1985; Mann 1986). Cultivation degrades soil physical structure by disrupting aggregates (Harris and others 1966; Low 1972), increasing erosion, and enhancing decomposition, which result in decreased storage of carbon (C) and nitrogen (N) in soil (Tiessen and others 1982; Mann 1986; Davidson and Ackerman 1993; Davis and others 2004). Some recovery occurs through natural succession following cessation of cropping, but this may require considerable time (Dormaar and Smoliak 1985; Burke and others 1995; Ihori and others 1995). Active restoration is increasingly used to assist recovery of degraded systems and generally involves removal of abiotic and/or biotic filters and re-introduction of vegetation or other structure to hasten recovery (Hobbs and Norton 1996). Recovery of aboveground vegetation has often been the focus of wetland restoration (for example, Reinartz and Warne 1993; Galatowitsch and van der Valk 1996a), and few studies have focused on changes belowground following restoration (Bishel-Machung and others 1996; Holt and others 2000). Belowground studies suggest that there may be constraints to aboveground restoration success such as hydrology (Shaffer and Ernst 1999) and biogeochemical cycling (Mitsch and Gosselink 2000).

Wetland restoration and creation is increasingly common in the PRV and typically involves land contouring followed by introduction of native vegetation. Land contouring is performed to replace topographic variability that is altered during agricultural production. Linear depressions are created, which hold water during wet periods. Despite substantial resources and effort that have gone into wetland restoration in the PRV, ecosystem recovery patterns of these restored wetlands are virtually unknown. Therefore, we measured a suite of above- and belowground properties and processes in natural wetlands and across a chronosequence of restored wetlands. We also compared means of the three most recently restored wetlands with means of natural wetlands. By comparing these measurements, we could document the degree of degradation from cultivation and quantify recovery of plant productivity and root biomass and recovery of belowground pools and transformations of C and N. Additionally, to identify relationships between aspects of recovery, we tested for correlations between measurements. We examined recovery of ecosystem properties and processes in the two major habitats in these systems, sloughs and margins, because of subtle differences in hydrology and plant communities (Whiles and Goldowitz 2001; Henszey and others 2004; Meyer 2007). We predicted that degradation of belowground stores of C and N in the soil would be severe (relative to widely reported rates in mesic non-wetland systems), due to the highly organic and labile stores of C and N in these wetland soils. We hypothesized that plant productivity and root biomass would recover relatively rapidly following restoration, whereas increases in soil C and N pools would be limited. Lastly, we predicted faster recovery rates of C and N pools and fluxes in sloughs than margin habitats due to presumably higher productivity and limited decomposition in the more inundated habitats.

Methods

We sampled three natural and six restored wetlands located along an approximately, 90-km stretch of the PRV in central Nebraska (from 40 N 48′ 27.94′, 98 W 23′0.56′ to 40 N 40′6.16′, 99 W 20′9.63′). These systems are palustrine, emergent wetlands with non-persistent hydroperiods (Cowardin and others 1979). The study sites exist as components of a complex of wet meadows that include mesic prairies with dendritic linear slough complexes in low-lying areas. Water levels in the sloughs are regulated by groundwater connections to the river channels, precipitation, and evapotranspiration (Wesche and others 1994; Whiles and Goldowitz 1998). Soil in natural wetlands is generally poorly drained, gently sloping (0–2%) silty clay loam alluvium over sandy and gravelly alluvium. Mean average air temperature in this area ranges from 24°C in July to −7°C in January. Mean annual precipitation is 630 mm year^{-1}, of which approximately 31% falls in May and June.

All sites shared similar topographical characteristics, and all were intermittent. Natural sites were chosen to represent a hydrologic gradient based on Whiles and Goldowitz (2001) to account for natural hydrologic variation among wetlands. Prior to restoration, restored sites were cultivated to corn and soybeans for more than 40 years. Restoration sites were contoured and then sown with seeds or planted with seedlings of native species collected from local natural wetlands. Restored sites ranged from 1 to 7 years since seeding (Table 1). Within each of the nine sites, three 30-m transects were established, one along the deepest part of the linear wetland (slough) and one along the contour of each lateral edge (margin).

We quantified total aboveground net primary productivity (ANPP) at each site at peak biomass in late September for 3 years (2002–2004) by clipping all vegetation at ground level within a 0.1-m^2 sampling frame (Briggs and Knapp 1995). Samples were collected at six random points along the slough transect and three along each margin transect at each site. We discarded previous year's growth based on color and texture characteristics, and then current year's growth was dried (50°C) and weighed. As some ANPP samples included woody vegetation that was more than 1 year old, we refer to any samples including woody plants as total aboveground biomass (TAB).

Root biomass was measured in September for three years (2002–2004). In each site, we removed 12 soil cores (5 cm diameter x 20 cm deep), six along the slough transect and three in each margin. Cores were placed in polyethylene bags and stored at 4°C. In the laboratory, we crumbled soil by hand through a 4-mm diameter sieve, removed large roots, and then washed roots and soil over a 250-μm sieve to collect fine roots. Roots were dried for 1 week at 50°C and weighed, ground, and redried. Root tissue percent C and N was determined by dry combustion coupled with gas chromatography on a Thermo CN autoanalyzer (Milan, Italy).

We collected soil in 2004 and 2005 to quantify multiple pools and fluxes of C and N. In each site, we removed 12 cores (2 cm diameter) from each slough transect and 6 from each margin transect and separated the core into two depth fractions (0–10 cm and 10–20 cm) with a spatula. We composited soil cores by habitat and depth for each site. Bulk density was sampled to convert analyte concentrations to volumetric amounts (that is, g m^{-2}).

In the laboratory, soil was homogenized through a 4-mm sieve. Gravimetric soil moisture was determined from an approximately 100-g subsample dried at 105°C. In 2004 and 2005, total C and N was determined from an approximately 50-g subsample of dried (65°C) and ground soil through dry combustion on a Thermo CN analyzer. We sent subsamples of soil collected in 2005 to the Kansas State University Soil Testing Laboratory to quantify cation exchange capacity (CEC), Mehlich-3 phosphorus (P), potassium (K), pH, and textural characteristics (% sand, % silt, and % clay). In 2005, we also used a 25-g subsample to quantify soil organic matter (SOM) by drying soil for 1 week at 105°C, followed by combustion at 450°C for 4 h to determine ash free dry mass of soil.

In 2005, we determined extractable inorganic N from two replicate subsamples of soil from each depth within each habitat in each site. Approximately 10 g of soil was extracted with 2 mol l^{-1} KCl on an orbital shaker (New Brunswick Scientific, Edison, New Jersey) for 1 h at 200 rpm (rotation frequency 3.33 Hz). Solutions were filtered through 0.4-μm polycarbonate membranes and frozen until analysis. We determined concentrations of NH_4–N and NO_3–N on a Flow IV segmented flow autoanalyzer (OI Analytical, College Station, Texas) using the phenol blue method for NH_4^+ and cadmium reductions of NO_3^- to NO_2^- followed by sulfanilamide diazotization (Keeney and Nelson 1982).

We obtained an in situ index of relative inorganic N availability among sites in 2005 using ion exchange resins (Binkley and Matson 1983). We filled nylon bags with 10 g each of strongly acidic cation (Dowex 50 WX2) and strongly basic anion (Dowex 1X8–50) exchange resins (Sigma Chemical, St. Louis, Missouri) preloaded with H^+ and Cl^-. Resin bags were buried in the surface 10 cm of soil at each site (three in each margin, six in each slough) in July and collected in October. In the laboratory, we rinsed bags with deionized water and then extracted and analyzed for inorganic N using the same methods as extractable N.

In 2005, we determined microbial biomass and mineralization of C and N using soil adjusted to 50% water holding capacity (WHC). We determined microbial biomass C (MBC) and N (MBN) using the fumigation-incubation procedure (Jenkinson and Powlson 1976). We pre-incubated 6-g subsamples of soil in 160-ml serum bottles for 5 days at 23°C. We then fumigated half of the subsamples with ethanol-free chloroform ($CHCl_3$) for about 24 h. Chloroform was then removed by repeated evacuation of the desiccator. Serum bottles were sealed and incubated for 10 days at 23°C. Following incubation, we removed a subsample (0.5 ml) of headspace gas and analyzed it for CO_2–C concentration on a gas chromatograph equipped with a thermal conductivity detector and a 2-m Porpak column (Shimadzu, Tokyo, Japan). Following headspace gas sampling, we extracted, filtered, and analyzed soil for inorganic N using the same methods described for extractable inorganic N. We calculated MBC and MBN from the differ-

Table 1. Hydrologic, Soil Textural, and Plant Community Characteristics of Margin and Slough Habitats of Natural and Restored Wetland Study Sites in the Platte River Valley

Site name	Year of restoration	Figure symbol[1]	Age[2]	Hydroperiod[3]			Maximum depth (cm)			Habitat	Texture (%)			Dominant plants[4]
				2003	2004	2005	2003	2004	2005		Sand	Silt	Clay	
Mormon East	Natural	●	NA	3–6	3, 11–12	1–6	32	20	32	Margins	71	22	7	*Carex emoryi*, *Phalaris arundinacea*, *Phyla lanceolata*
										Sloughs	79	17	4	*Phyla lanceolata*, *Phalaris arundinacea*, *Carex emoryi*
Mormon Middle	Natural	●	NA	3–6	3	2–3, 5–6	39	43	26	Margins	90	6	4	*Polygonum* spp., *Phyla lanceolata*, *Typha* spp.
										Sloughs	77	17	6	*Polygonum* spp., *Typha* spp., *Eleocharis* spp.
Mormon West	Natural	●	NA	0	3	6	0	32	10	Margins	45	33	22	*Carex emoryi*, *Helianthus maximiliani*, *Spartina pectinata*
										Sloughs	71	7	22	*Carex emoryi*, *Spartina pectinata*, *Iva annua*
Uridil	1995	▲	7	0	0	5–6	0	0	36	Margins	89	7	4	*Spartina pectinata*, *Hordeum jubatum*, *Helianthus maximiliani*
										Sloughs	89	9	2	*Spartina pectinata*, *Schoenoplectus pungens*, *Salix exigua*
Studnicka	1996	■	6	4–6	3	5–6	42	34	36	Margins	54	35	11	*Spartina pectinata*, *Iva annua*, *Symphyotrichum lanceolatum*
										Sloughs	83	8	9	*Iva annua*, *Salix exigua*, *Typha* spp.
Johns	1998	●	4	5–6	3	4–6	20	9	55	Margins	86	11	3	*Helianthus maximiliani*, *Salix exigua*, *Typha* spp.
										Sloughs	95	0	5	*Typha* spp., *Salix exigua*, *Lobelia* spp.
Derr	2000	▼	2	0	0	6	0	0	20	Margins	70	23	8	*Desmanthus illinoensis*, *Conyza canadensis*, *Elymus canadensis*
										Sloughs	86	9	5	*Spartina pectinata*, *Amaranthus* spp., *Conyza canadensis*
Speidell 2000	2000	◆	2	0	0	0	0	0	0	Margins	87	11	2	*Populus deltoides*, *Spartina pectinata*, *Desmanthus illinoensis*
										Sloughs	69	23	8	*Spartina pectinata*, *Eleocharis* spp., *Schoenoplectus pungens*
Speidell 2001	2001	⬣	1	0	0	0	0	0	0	Margins	73	23	4	*Andropogon gerardii*, *Populus deltoides*, *Sporobolus cryptandrus*
										Sloughs	99	0	1	*Agalinis aspera*, *Calamagrostis stricta*, *Populus deltoides*

[1] *Natural site data were presented as means of all natural sites, so individual sites do not have unique symbols.*
[2] *Age = age in years of the restored wetlands when the study began (2002). NA = not applicable; used to indicate natural sites that have no restoration year, and age is not known.*
[3] *Hydroperiod = months with standing water (1 = Jan, 2 = Feb, and so on). No hydrology measurements were taken during 2002. Measurements were only taken through July 2005.*
[4] *Dominant plants were taken from data in Meyer 2007.*

ence between fumigated and unfumigated CO_2-C and inorganic N, respectively, then divided by a correction factor of 0.4 for MBC and 0.6 for MBN (Voroney and Paul 1984).

Potential net N mineralization rates were determined using a 15-d aerobic incubation. We pre-incubated subsamples of soil (6 g) for 5 days at 23°C. Following the pre-incubation, we extracted half the samples for ''initial'' inorganic N concentrations and extracted the remaining half following the incubation period for ''final'' inorganic N concentrations using the same methods as for extractable N. We estimated daily net ammonification, nitrification, and N mineralization rates as the difference between ''final'' and ''initial'' measurements of NH_4–N, NO_3–N, and NH_4–N + NO_3–N, respectively divided by the incubation period (Robertson and others 1999).

We measured potential C mineralization (soil respiration) rates from approximately 20-g subsamples of soil contained within a 125-ml flask sealed in a 940-ml glass mason jar containing approximately 5 ml water to maintain humidity. Prior to the onset of a 30-d incubation period, we pre-incubated samples for 1 week at 23°C, then aerated jars and removed any emerged seedlings. During the incubation, we sampled headspace gas every 3 days and analyzed gas samples for CO_2–C using the same gas chromatography methods described for MBC.

Statistical Analyses

All statistical analyses were performed separately in each habitat. Subsamples within each site were averaged by depth. To quantify the degree of degradation in soil total C, soil total N, and organic matter associated with cultivation, we compared means of the three most recently restored sites with means of the natural sites using *t*-tests appropriate for homogeneity or heterogeneity of variances. Recovery patterns of TAB and belowground parameters across the chronosequence were analyzed using simple linear regression procedures. If there was no detectable change with time since restoration, we compared the means of restored wetlands and natural sites using *t*-tests. If significant linear changes over time were detected in both habitats, we compared slopes and elevations of regressions with analysis of covariance (ANCOVA). We calculated Pearson's correlation coefficients to test for relationships among variables and identify potential useful belowground indicators of recovery. All analyses were performed using SAS statistical software (SAS 2003) ($\alpha = 0.05$, *P*-values < 0.10 reported).

Results

Total aboveground biomass in the restored wetlands increased with years since restoration in both habitats and became representative of the natural systems within 10 years. Within natural wetland margins TAB averaged 724 ± 90 g m^{-2} and was highly variable between years, for example it almost doubled from 2002 to 2003 (Figure 1). Within sloughs of natural wetlands, TAB averaged 634 ± 100 g m^{-2} and fluctuated from about 475 to about 830 g m^{-2} throughout the study (Figure 1).

Root biomass in the most recently restored margins and sloughs was 87 and 50% lower than natural margins and sloughs, where biomass was 2055 ± 1134 and 518 ± 337 g m^{-2}, respectively. Root biomass and C and N storage in roots increased linearly with years restored in both margins and sloughs (Figure 1). Percent C and N in root tissue was similar across the restored chronosequence resulting in no change in root quality (as indicated by C:N) with years restored.

Most differences in soil physical and chemical characteristics across the chronosequence were limited to the surface 10 cm in both habitats. In margins, bulk density was similar among restored sites and averaged over all sites was higher in restored (1.53 ± 0.06 g cm^{-3}) than in natural (0.91 ± 0.06 g cm^{-3}) wetlands in the surface 10 cm ($P < 0.001$) (Figure 2). Bulk density also remained slightly higher in restored (1.62 ± 0.04 g cm^{-3}) than natural (1.40 ± 0.19 g cm^{-3}) wetlands in the 10–20 cm depth ($P = 0.097$) (Figure 2). In sloughs, bulk density in the surface 10 cm decreased with years restored (Figure 2) but remained 33% higher than the natural sloughs (0.80 ± 0.12 g cm^{-3}) following 10 years of restoration. In the 10–20 cm depth of sloughs, average bulk density across all restored sites was 27% higher than natural wetlands (1.29 ± 0.27) ($P = 0.067$) (Figure 2).

Few directional changes in soil chemical properties with years restored occurred in either habitat, but natural sites differed from restored wetlands in some cases. No directional changes in CEC, pH, soil P, or soil K occurred in the surface 20 cm of either habitat, although differences between natural and restored wetlands (averaged over all sites) were evident in both habitats (Table 2). In margins, mean CEC and mean K were similar between natural and restored sites in both depths (Table 2). Although CEC did not differ between natural and restored sites in the surface 10 cm in sloughs, natural sites had higher mean CEC than restored sites in the 10–20 cm depth (Table 2). Mean pH was

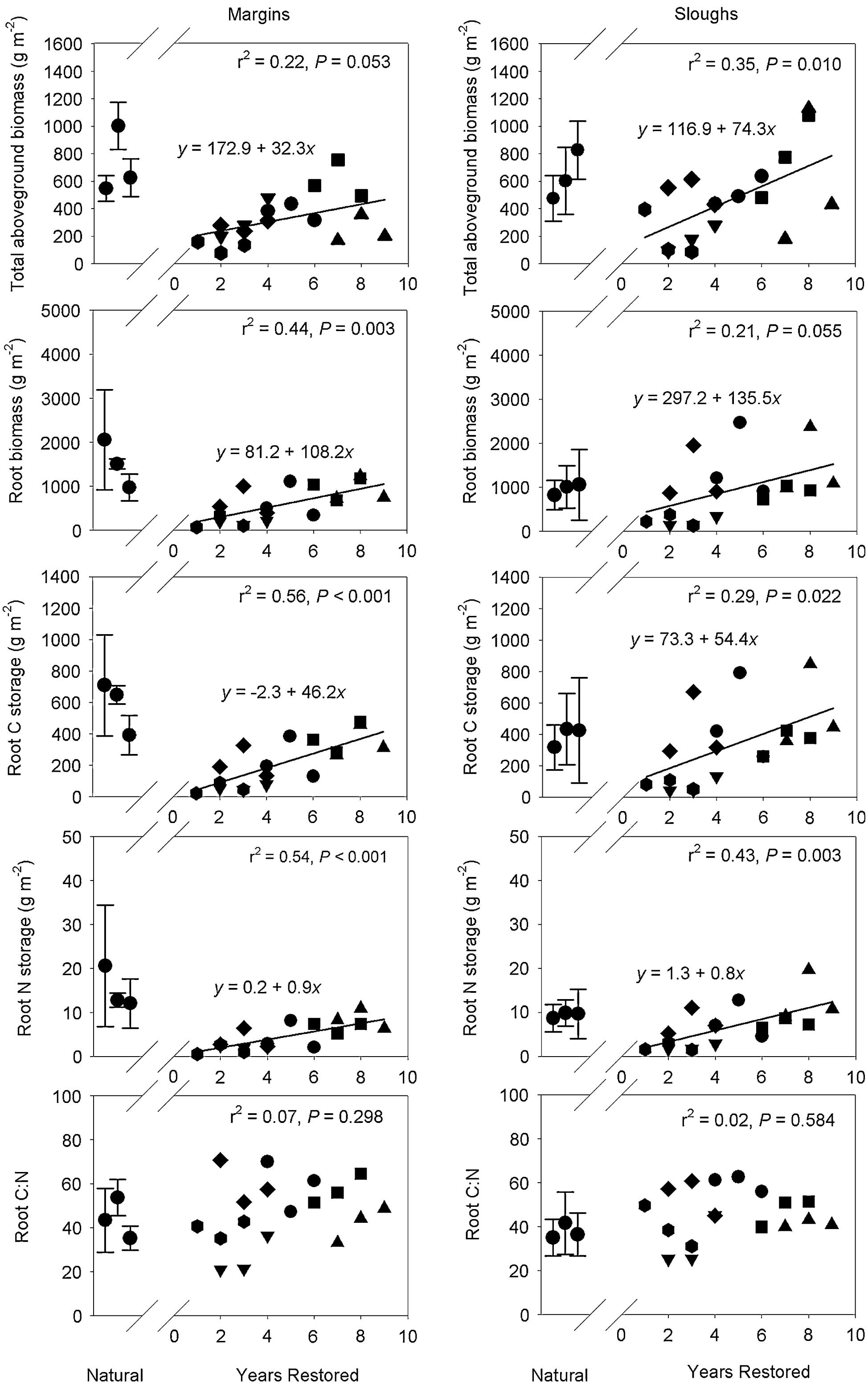

Figure 1. Temporal changes in total aboveground biomass (TAB), root biomass, root storage of C, root storage of N, and root C:N ratios in margins and sloughs of natural wetlands (means ± standard error) and restored wetlands (symbols according to Table 1). Regression lines indicate significant changes with years restored.

significantly higher in restored margins and sloughs than natural margins and sloughs in both depths (Table 2). Also, Mehlich-3 P was lower in restored margins and sloughs than in natural margins and sloughs in the surface 10 cm only (Table 2).

Soil organic matter was substantially reduced following cultivation. In the surface 10 cm, SOM was 79% lower in restored margins (1672 ± 752 g m^{-2}) and 82% lower in sloughs of three most recently restored sites (1592 ± 768 g m^{-2}) compared to nat-

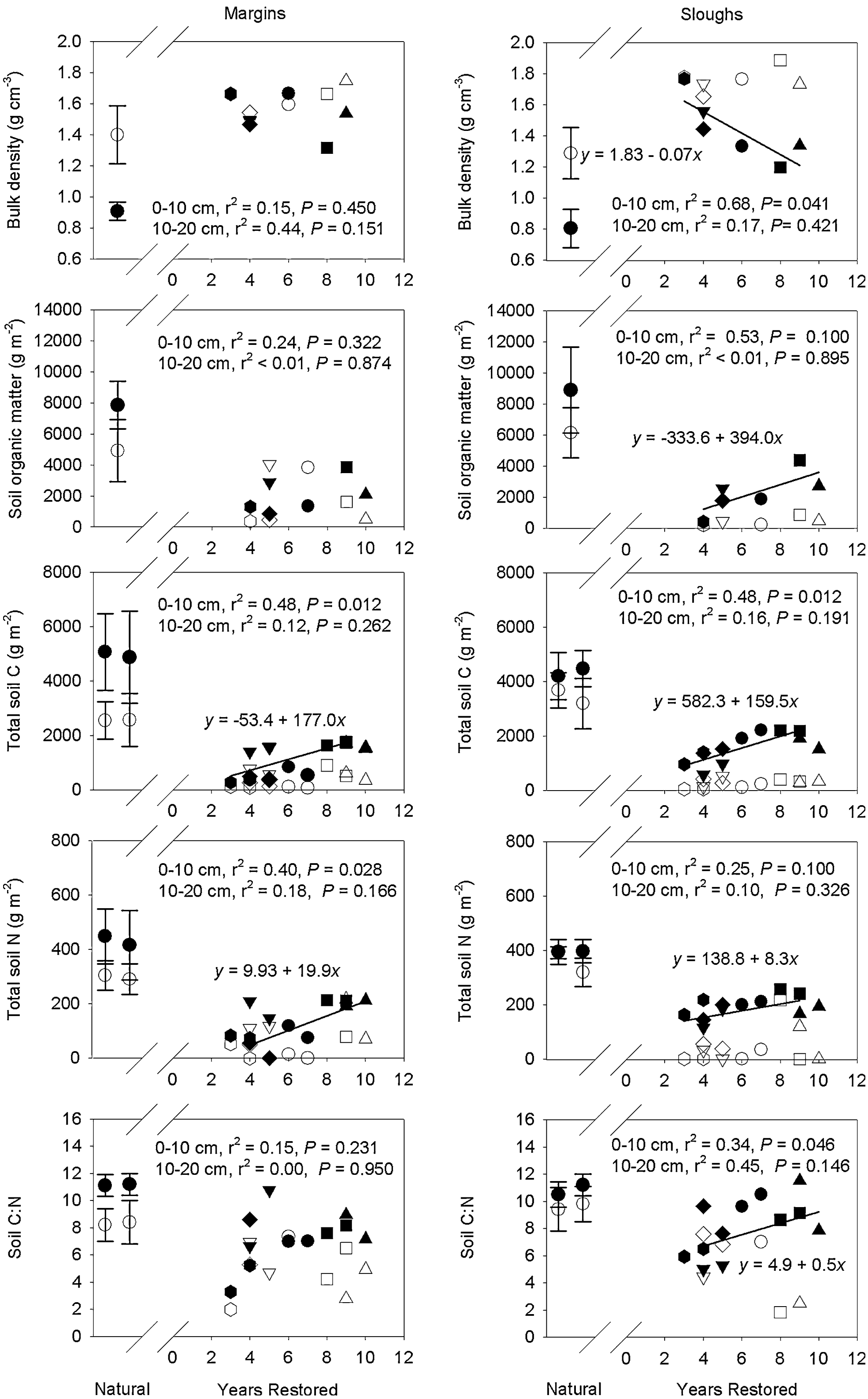

Figure 2. Physical and chemical characteristics of soil in margins and sloughs of natural wetlands (means ± standard error) and restored wetlands in the 0–10 cm (*closed symbols*) or 10–20 cm depth (*open symbols*) (symbols according to Table 1). Regression lines indicate significant changes with years restored (0–10 cm, *dark lines*, 10–20 cm, *dotted lines*).

ural wetlands (margins: 8907 ± 2781, sloughs: 7846 ± 1526 g m^{-2}). In margins, SOM did not change with years restored, and mean SOM in the natural wetlands was 74 and 63% higher than the restored sites in the surface 10 cm ($P < 0.001$) and 10–20 cm depth ($P = 0.074$), respectively (Figure 2). In sloughs, SOM increased linearly from 4 to 10 years of restoration in the upper 10 cm (Fig-

Table 2. Chemical Characteristics in Margins and Sloughs of the Natural and Restored Platte River Wetlands in the 0–10 and 10–20 cm Depths

Wetland type		Habitat	Depth	pH (g m^{-2})	P (g m^{-2})	K (g m^{-2})	CEC[1] (mol_c m^{-2})
Natural mean		Margin	0–10	5.71	2.65	20.87	18.89
		Margin	10–20	5.70	4.64	26.64	14.93
		Slough	0–10	5.73	4.71	24.68	17.46
		Slough	10–20	5.81	4.05	27.47	27.38
Restored mean		Margin	0–10	7.73	1.09	20.81	18.16
		Margin	10–20	7.40	1.01	13.64	21.51
		Slough	0–10	7.55	1.12	14.58	16.64
		Slough	10–20	7.44	1.04	11.57	7.03
t-test							
	P values	Margin	0–10	0.002	0.032	0.493	0.879
		Margin	10–20	0.009	0.317	0.139	0.440
		Slough	0–10	0.002	0.001	0.233	0.875
		Slough	10–20	0.004	0.308	0.054	0.008

P-values represent results of t-tests between natural and restored sites by location and depth.
[1]CEC = cation exchange capacity, presented as moles of charge (mol_c) per square meter.

ure 2). No recovery of SOM with time since restoration occurred in the 10–20 cm depth, and mean SOM was approximately 10 times greater in natural wetlands than restored sites ($P = 0.050$) (Figure 2).

Cultivation substantially reduced both total soil C and N. Average total soil C in the 0–10 cm fraction for the three youngest restored margins (714 ± 420 g m^{-2}) and sloughs (971 ± 285 g m^{-2}) was 86 and 77% lower than natural sloughs and margins, where total C was 5093 ± 1415 and 4202 ± 874 g m^{-2}, respectively. Average total N was 74 and 65% lower in the surface 10 cm of the three youngest restored margins (116 ± 58 g m^{-2}) and sloughs (140 ± 16 g m^{-2}) than natural sites, where total N in margins and sloughs was 448 ± 101 and 394 ± 46 g m^{-2}, respectively. Total soil C increased linearly across the chronosequence in the surface 10 cm of margins and sloughs (Figure 2). In the 10–20 cm depth, there was no change in soil C over time in either habitat and soil C was an average of 86 and 93% lower in margins and sloughs of restored systems, respectively ($P < 0.005$) (Figure 2). Total soil N also increased linearly in the surface 10 cm of restored margins and sloughs (Figure 2) but remained 74 and 88% lower in restored margins and sloughs compared to natural margins in the 10–20 cm depth ($P < 0.001$) (Figure 2). Soil C:N ratios increased linearly in the surface 10 cm of sloughs, but did not show discernable patterns with years restored in the deeper fraction of sloughs or within the surface 20 cm of margins (Figure 2).

Changes in active and labile soil C pools with years restored varied with depth and habitat in the restored wetlands. MBC did not change across the chronosequence in either depth of margins or sloughs (Figure 3). Within margins, mean MBC in restored sites was 10 and 1% of mean MBC in natural sites in the 0–10 cm and 10–20 cm depths, respectively (Figure 3). Likewise in sloughs, mean MBC was far lower in restored than natural sites in both depths (Figure 3). We surmised that the fumigation-incubation procedure may have inadequately estimated MBC in these restored wetlands containing predominantly sandy soil, as soil respiration rates indicated an active microbial community.

Potential C mineralization rates in the 0–10 cm depths of margins and sloughs of the three youngest sites were 77 and 34% of those in natural wetlands. In natural wetlands, potential C mineralization rates were 2.10 ± 0.8 and 2.18 ± 1.0 g C m^{-2} d^{-1} in margins and sloughs, respectively. Potential C mineralization rates increased linearly with time since restoration within the surface 10 cm of the restored margin habitat, but no change was observed over the chronosequence in deeper soil (Figure 3). Potential C mineralization rates of restored sloughs were also within the range of natural systems (Figure 3) and increased across the chronosequence within the 10–20 cm depth (Figure 3).

Recovery of active and labile N pools was limited to shallow soil depths in restored wetlands. MBN increased with time since restoration in the surface 10 cm within margins and in both depths within sloughs (Figure 4). Potential net N mineralization

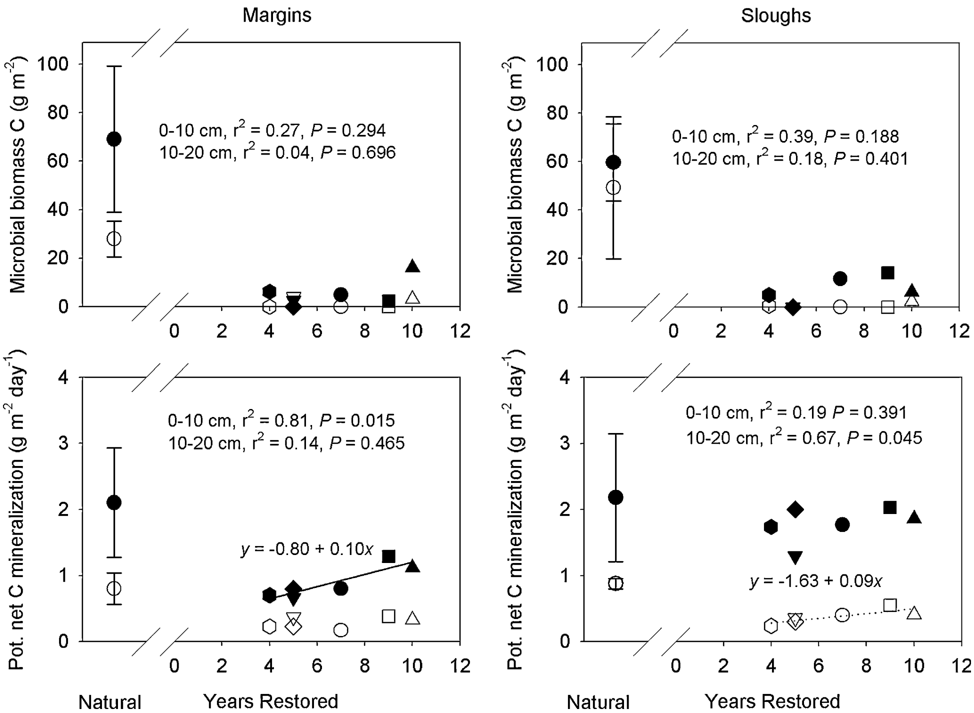

Figure 3. Microbial biomass C and potential C mineralization rates in margins and sloughs of natural wetlands (means ± standard error) and restored wetlands in the 0–10 cm depth (*closed symbols*) or 10–20 cm depth (*open symbols*) (symbols according to Table 1). Regression lines indicate significant changes with years restored (0–10 cm, *dark lines*, 10–20 cm, *dotted lines*).

rates did not change with years restored in the surface 20 cm of either habitat (Figure 4), but net rates were similar and low in both habitats across chronosequence. Potential net N mineralization in natural sites exceeded that of restored sites only in the 10–20 cm depth in sloughs ($P = 0.004$) (Figure 4). Net N mineralization rates largely reflected that of net nitrification rates in both margins and sloughs. Net ammonification rates in both habitats and depths were near zero or negative, indicating that mineralized NH_4^+ was rapidly nitrified during the aerobic incubation.

Changes in inorganic N availability with years restored were evident in both habitats of restored wetlands. Within margins, total extractable inorganic N (TIN) in the surface 10 cm increased during restoration, which was driven by an increase in NO_3–N across the chronosequence (data not presented). TIN increased linearly with years restored in both depths of restored sloughs (Figure 4). Despite increases in TIN, there were no changes in resin-collected N over the chronosequence in either habitat of restored sites, and resin-collected N in natural sites exceeded that of restored wetlands by more than 80% (margins, $P = 0.086$, sloughs, $P = 0.067$) (Figure 4).

Comparison of Recovery Rates Between Habitats

Differential patterns in ecosystem recovery were observed between the two habitats. Changes in bulk density (decreasing over time) and SOM (increasing over time) were only observed in slough habitats (Figure 2). Furthermore, increasing C mineralization rates across the restoration chronosequence were only observed in the margin habitat because recovery had occurred in the slough habitat (Figure 3). TAB (Figure 1), root biomass, root storage of C, root storage of N (Figure 1), total soil C, total soil N (Figure 2), MBN (Figure 4), and extractable total N (Figure 4) all showed linear changes with years restored in both margins and sloughs but the slopes did not differ between regression equations in margins and sloughs for any parameter. However, elevations of linear regressions for these parameters were higher in sloughs than margins for changes in root N storage ($F = 4.91$, $P = 0.034$), total soil C ($F = 9.34$, $P = 0.006$), total soil N ($F = 7.70$, $P = 0.011$), MBN ($F = 12.49$, $P = 0.006$), and extractable total N ($F = 13.75$, $P = 0.005$) over time. There was a weak difference in elevations for root biomass ($F = 2.84$, $P = 0.101$) and root C storage ($F = 2.79$, $P = 0.104$).

Correlations Among Ecosystem Components and Processes

Many pools and fluxes of nutrients and soil properties tend to be correlated. We chose to examine relationships of two variables (bulk density and SOM) that represent relatively easily quantified ecosystem components with all other pools and

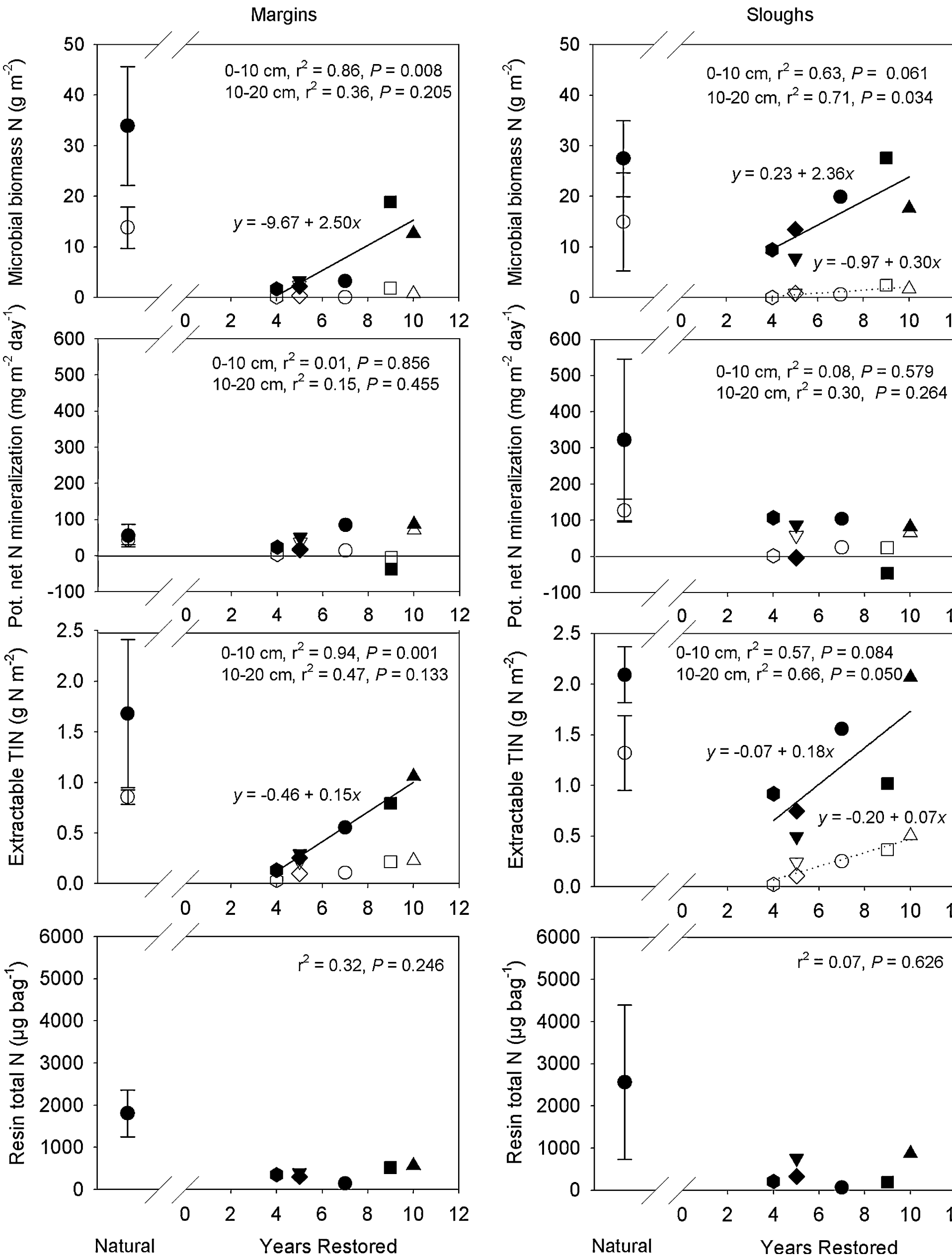

Figure 4. Microbial biomass N, extractable inorganic N, and laboratory-based N transformation rates in margins and sloughs of natural wetlands (means ± standard error) and restored wetlands in the 0–10 cm depth (*closed symbols*) or 10–20 cm depth (*open symbols*) (symbols according to Table 1). Regression lines indicate significant changes with years restored (0–10 cm, *dark lines*, 10–20 cm, *dotted lines*).

fluxes of C and N to elucidate practical potential indices of ecosystem recovery. In the surface 10 cm, bulk density was inversely correlated with most pools and fluxes of C and N examined (Table 3). In the surface 10 cm, SOM was positively correlated with root biomass and soil C and N pools and fluxes (Table 3).

Discussion

Aboveground Recovery Following Restoration

Estimates of TAB, which includes ANPP of herbaceous plants, in natural wetlands fell within the low range of other similar freshwater systems (for example, Auclair and others 1976; Hoagland and others 2001). Changes in TAB across the restoration chronosequence indicated that this functional attribute recovers rapidly in both margins and sloughs. Craft and others (1999) also found a rapid recovery (5–10 years) of productivity parameters such as ANPP in North Carolina *Spartina* marshes. A similar and rapid recovery pattern of ANPP has also been shown in restored grasslands in this region (Baer and others 2002). Hence, our study and others add to growing evidence that function (for example, productivity) recovers more rapidly than community structure in restored systems, as indi-

Table 3 Relationships Between Bulk Density and Soil Organic Matter and Other Ecosystem Variables in the Surface 10 cm of Margins and Sloughs of Platte River Wetlands

	Bulk density		SOM	
	r^2	*P*-value	r^2	*P*-value
Margins, 0–10 cm				
Root biomass	−0.71	0.033	0.75	0.020
SOM[1]	−0.95	<0.001	–	–
Soil total C	−0.89	0.001	0.93	<0.001
Soil total N	−0.85	0.003	0.92	<0.001
Soil C:N ratio	−0.98	<0.001	0.96	<0.001
Microbial biomass C	−0.83	0.006	0.93	<0.001
C mineralization	−0.75	0.020	0.75	0.020
Microbial biomass N	−0.89	0.001	0.96	<0.001
Extractable TIN[2]	−0.76	0.016	0.82	0.007
Resin extractable N	−0.81	0.009	0.68	0.040
Sloughs, 0–10 cm				
Root biomass	−0.56	0.116	0.53	0.142
SOM	−0.81	0.008	–	–
Soil total C	−0.95	<0.001	0.81	0.008
Soil total N	−0.91	<0.001	0.74	0.023
Soil C:N ratio	−0.88	0.002	0.75	0.020
Microbial biomass C	−0.89	0.001	0.92	<0.001
C mineralization	−0.33	0.387	−0.22	0.569
Microbial biomass N	−0.61	0.080	0.67	0.048
Extractable TIN	−0.74	0.023	0.46	0.217
Resin extractable N	−0.65	0.058	0.84	0.005

[1]*SOM = soil organic matter.*
[2]*TIN = total extractable inorganic nitrogen.*

cated by persistent differences in plant and macroinvertebrate community structure within these sites (see Meyer 2007). This pattern also has been observed at higher trophic levels (for example, Wallace and others 1986; Whiles and others 1993; Whiles and Wallace 1995). Consequently, productivity may not be a reliable indicator of recovery or restoration success, depending on restoration objectives.

Temporal variability in ANPP, and factors governing it, further complicate the use of productivity as a recovery metric. For example, Whigham and others (2002) found that ANPP in restored Maryland wetlands was highly variable and more closely linked with precipitation than with time since restoration. Similarly, wetlands in our study showed an increase in TAB and ANPP in margins from 2002 to 2003 and a subsequent decrease from 2003 to 2004, and it is likely that this was linked to precipitation patterns. Although snow and rainfall in both years were well below average for the region, precipitation in 2003 was more than 10 cm higher than 2002, and most occurred during the growing season, which likely caused the increase in biomass (for example, Gross and others 1990; Dunton and others 2001). Total precipitation in 2004 was approximately 10 cm higher than in 2003, but more rain fell early in the growing season (April–July) during 2003 when most plant growth occurs.

Root Establishment Across the Restoration Chronosequence

Although much less studied (Bradbury and Grace 1983), belowground biomass typically exceeds aboveground biomass in freshwater wetlands (Mitsch and Gosselink 2000). Estimates of root biomass in our study were similar to other wetlands (for example, Hoagland and others 2001) and the change in root biomass following restoration approached the natural systems within a decade. Similarly, Craft and others (1999) reported that soil macro-organic matter (including live roots, dead roots, and rhizomes) increased quickly in restored North Carolina *Spartina* marshes and was similar to corresponding values in natural marshes within 5–10 years. Shafer and Streever (2000) also found that belowground biomass in dredged marshes in Texas increased with age and was similar to that of natural marshes in about 10 years. This recovery pattern is also consistent with agricultural systems in south central Nebraska, where Baer and others (2002) documented a linear increase and recovery of root biomass in a chronosequence of restored grasslands.

Soil Physical, Chemical, and Biological Changes Following Restoration

Recovery of soil physical, chemical, and biological properties can lay the foundation for return of ecosystem function (Shaffer and Ernst 1999). Soil texture neither changed with time since restoration nor differed between natural and restored sites. This was likely due to homogeneity of sand-dominated substrates throughout the PRV (Currier 1997). The consistently higher soil pH in restored sites may be related to lower organic matter of restored wetlands, as low pH in some wetlands is caused by organic acids produced during decomposition (Nair and others 2001). Lower amounts of P (surface 10 cm) and K (10–20 cm of sloughs) in restored wetlands were likely related to changes in nutrient retention caused by cultivation-induced decreases in SOM.

Bulk density is useful as an index of soil function (Parr and others 1992; Karlen and others 1997) because it is associated with SOM, root penetration, hydraulic conductance, aeration, infiltration, and biological activity (Low 1972; Coote and Ramsey 1983). Bulk density decreased in the upper soil surface of sloughs due to recovery of roots and increases in SOM, as indicated by negative correlations in both habitats. Concurrent decreases in bulk density and increases in SOM frequently occur following wetland restoration (Craft 2000; Bruland and Richardson 2005). The relationship between bulk density and many soil parameters that are indicative of increasing soil function support the use of bulk density as an easily measured indicator of recovery in restored systems.

If patterns of increasing SOM in restored wetlands that we observed remain linear, it would take just over 20 years of restoration for SOM in the surface 10 cm of sloughs to match levels found in natural systems. As no change in SOM with time occurred in the 10–20 cm depth in sloughs, or in the surface 20 cm of margins, no predictions can be made regarding recovery of SOM at lower depths or higher topographic positions within restored wetlands. The lack of SOM in younger sites in our study may be related to lack of hydrologic recovery. Drier sites have been shown to accumulate less organic matter than wetter sites (for example, Paul and Clark 1989). There is potentially feedback between SOM accrual and hydrology as development of SOM will increase WHC of predominantly sandy soils and further limit decomposition. Restoration practices that aim to restore hydrology may be key in sequestering C.

Large organic matter pools are found in wetlands due to high productivity and decreased decomposition in inundated environments (Schlesinger 1997; Mitsch and Gosselink 2000). As restored or created wetlands often have less organic matter than comparable natural wetlands (Confer and Niering 1992; Bishel-Machung and others 1996; Galatowitsch and van der Valk 1996b; Whittecar and Daniels 1999; Campbell and others 2002), and because SOM often increases with time since restoration (Craft and others 1999; Craft 2000; Edwards and Proffitt 2003), SOM may also represent an informative index of wetland recovery (for example, Bruland and Richardson 2006). SOM is a key element of soil quality as it impacts root development, soil porosity, water infiltration rates, and cation adsorption capacity, which can affect aspects of ecosystem structure and function. Stauffer and Brooks (1997) reported that increased organic matter in central Pennsylvania marshes resulted in positive changes in plant species richness, vegetative cover, and plant survivorship, as well as increases in total N levels. Also, organic matter provides the substrate and energy source for many microbial processes (Zak and others 1990; Haynes 2000; Hofman and others 2003). Groffman and others (1996) found that microbial biomass in fens of New York was strongly regulated by organic matter and N status. Similarly, Bruland and Richardson (2004) found that SOM in Virginia coastal plain wetlands was correlated with bulk density, soil moisture, MBC, among other properties. These relationships underscore the importance of SOM recovery in wetland restored wetlands, because increases in organic matter are related to positive changes in ecosystem function.

Euliss and others (2006) suggested that freshwater wetlands are important sinks of C, and that restoration of all cropland wetlands in the prairie pothole region of North America could potentially result in the sequestration of 2327 g of C m^{-2} within a period of 10 years. Euliss and others (2006) also reported that the organic C content of prairie potholes was comparable to native grasslands (Blank and Fosberg 1989), but that carbon sequestration rates were five times higher in restored wetlands than in restored grasslands (Follett and others 2001). We compared storage and accrual rates of C (0–10 cm) in our study with a chronosequence of restored grasslands in southeast

Nebraska enrolled in the Conservation Reserve Program (Baer and others 2002) and found that total C in native grasslands (~3000–4000 g C m^{-2}; Baer and others 2002) was lower than in natural wetlands (~3400–5600 g C m^{-2} in sloughs and ~2600–7400 g C m^{-2} in margins). Furthermore, the accrual rate of total C in restored grasslands (30 g C m^{-2} $year^{-1}$; Baer and others 2002) was five to six times lower than the accrual rate in restored wetlands in our study (margins, 177 g C m^{-2} $year^{-1}$; sloughs, 160 g C m^{-2} $year^{-1}$). If increases remain linear within these wetland systems, total C would reach levels found in natural sites in both margins (4980 ± 885 g C m^{-2} $year^{1}$) and sloughs (4338 ± 445 g C m^{-2} $year^{-1}$) in just over 25 years following restoration. Therefore, our results support Euliss and others (2006) and the restored wetlands in the PRV represent important sinks for atmospheric C and can contribute to C sequestration for decades following restoration.

Cultivation of soil decreases total N due to increased mineralization rates, removal of N in harvested plant material, and leaching or volatilization of inorganic N (Low 1972; Tivy 1987). Rates of N increase (8–20 g N m^{-2} $year^{-1}$) in restored wetlands were similar to those measured in a set of restored (1–25 years) North Carolina salt marshes (7–11 g N m^{-2} $year^{-1}$; Craft 2000). These increases showed the potential of these restored wetlands as N sinks. According to Tisdale and others (1985), soil C:N ratios above 20 indicate N immobilization by microbes, whereas soils with C:N ratios below 20 may provide sufficient N for plant uptake. Soil C:N ratios in natural sites ranged from 8–12, indicating ample N for plant uptake, and values were within the range of other reported freshwater wetland values. For example, soil C:N ratios ranged from 2–10 in Chinese riparian wetlands (Bai and others 2005), from 7–8 in Iranian calcareous wetlands (Raiesi 2006), and from 13–20 in marsh meadows in Slovenia (Hacin and others 2001). Nair and others (2001) reported that the C:N values in natural wetlands in central and north Florida ranged from 15–25 and decreased with time in restored wetlands. In contrast, we found that soil C:N ratios increased only in restored sloughs with time and became more similar to natural wetlands. Low values (3–6) in newly restored systems occurred because %C in the soil was also low (for example, ~0.1%). Nair and others (2001) cautioned that C:N ratios may be less meaningful in wetlands with low values of C and N, such as those that were found in our restored wetlands.

Changes in total C and N occur slowly and can be difficult to detect because of large background levels of C and N in the soil (Karlen and others 1999). Thus, recovery patterns of other pools (for example, active and labile) following restoration can be more apparent (for example, Baer and others 2002). Microbial biomass can indicate a system‘s ability to support nutrient cycling and other ecosystem functions (Smith and Paul 1990; Duncan and Groffman 1994), and C mineralization rates can be used as a measure of overall soil biological activity (Paul and Clark 1989). Constructed wetlands often have lower levels of microbial activity than natural systems (Lindau and Hossner 1981; Craft and others 1988; Langis and others 1991). We found no change in MBC in either habitat, which could impact functional recovery in restored systems, as soil microbes play key roles in energy flows and nutrient transformation in the ecosystem (Tate 2000). However, significant positive changes in C mineralization and MBN in both habitats suggest that microbial activity was increasing with years restored. Discrepancies between measurements may be related to fumigation-incubation methods we used to estimate MBC in the restored wetlands. The effectiveness of the fumigation was apparent from the differences in inorganic N between fumigated and unfumigated soil and subsequent patterns in MBN. Less discrepancy in soil CO_2 efflux could result from slow recovery of the microflora and insufficient incubation period (see Paul and others 1999).

One of the most important ecosystem services provided by wetlands is retention and or removal of excess available N, particularly in predominantly agricultural landscapes. Nitrogen can be retained within organisms, sediments, and pore water, or permanently removed via denitrification. Patterns of increasing total extractable N with time were probably related to increases in SOM, and this was supported by positive correlations between SOM and extractable TIN. Despite increases in extractable N, patterns of N mineralization did not show discernable changes with years restored other than much lower net N mineralization relative to natural wetlands. These potentials were measured under aerobic conditions that may have increased nitrification, as extractable and resin-collected inorganic N did not exhibit consistently higher concentrations of NO_3^- in the field. In situ measurements of N mineralization are needed to more adequately describe dynamics of N mineralization and retention following restoration in these hydrologically variable systems.

Implications for Ecosystem Assessment

This study represents the first assessment of functional recovery in restored wetlands of the PRV. Our results showed promising recovery of some key ecosystem properties such as ANPP or TAB, root biomass, and root storage of C and N, which increased rapidly in restored wetlands and were similar to natural systems after about 10 years. Increases in total C and N in soil add to a growing body of evidence that substantiates the importance of prairie wetlands as sinks for C and N. Despite evidence of recovery, some ecosystem properties and corresponding functions were lacking in restored wetlands. One of the most striking was the lack of recovery of bulk density or SOM in margin habitats, both of which differed greatly from natural systems. Based on close associations with other belowground properties, recovery of some ecosystem processes and functions (for example, microbial biomass and mineralization rates of C and N) may depend on the accrual of organic matter and concurrent decrease in bulk density. Thus, without significant changes in organic matter, recovery in margins may not proceed. Furthermore, if newly restored sites do not develop moist soil conditions, long-term recovery may not proceed toward older restored wetlands and ultimately natural systems.

Our study elucidated metrics that may have utility as indicators of recovery following restoration; in particular, bulk density and SOM, the two properties that were most correlated with other measures of soil physical and biological processes. Additionally, measures of total soil C and N increased linearly in both habitats, suggesting predictable trajectories with time since restoration. However, measures of total C and N are more difficult to attain than SOM and bulk density. Most changes occurred only within the surface 10 cm across the 10-year chronosequence. Lastly, assessments of recovery should account for differences in elevation and communities influenced by subtle changes in topography.

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