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Plant Community Recovery following Restoration in Temporally Variable Riparian Wetlands

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Abstract

Wetlands historically provided many ecosystem services but most have been lost or degraded through land conversion. Recent appreciation for wetland values and increasing ecotourism in the Central Platte River Valley (U.S.A.) has promoted restoration of wet meadow systems, although recovery patterns are not well known. We quantified plant community structure in sloughs (deeper habitats) and adjacent margins (slightly higher elevation) of six wetland sites, restored for 1–7 years at the onset of a 3-year study, and three natural wetlands to assess recovery dynamics. Plant community metrics recovered differentially between habitats. Within restored margins, richness and diversity showed a weak quadratic response with time since restoration, indicating that both indexes overshoot natural levels shortly following restoration. Within sloughs, richness and diversity showed no change with time, suggesting that recovery occurs more quickly in these deeper, moister habitats. Percent similarity of plant communities in restorations and natural wetlands increased linearly over time. However, ordinations of plant community composition showed that recovery was strongly influenced by site-specific hydrology and that recovery may not be a linear trajectory toward natural systems. The analysis and interpretation of plant community dynamics revealed several challenges to restoration assessment, including the role of interannual variability in precipitation, limitations to hydrologic recovery, and temporal variability in plant community structure in natural systems that resulted in "moving targets" for recovery comparisons. Temporal variability in climate must be considered when assessing restoration success in systems where plant community structure is responsive to variable moisture regimes.

Key words: **assessment, Platte River, slough, temporal variability, vegetation, wet meadow.**

Introduction

Worldwide, 53% of wetlands have been lost (Mitsch & Gosselink 2000). Similarly, over half of the original wetland area that once existed within the conterminous United States has been lost (Vileisis 1997). In the U.S. Great Plains, most wetlands have been drained for crop production and other developments. Along the Platte River, a major river system of the Great Plains, it is estimated that over 70% of natural wet meadow habitat has been lost, and this habitat now comprises less than 5% of the land area in the Platte River valley (PRV) (Sidle et al. 1989; U.S. Fish and Wildlife Service 1997). The severe degradation of wetlands in the PRV is of particular concern because this region is extensively used by migratory birds on the central flyway to acquire energy and nutrients essential for migration and reproduction (U.S. Fish and Wildlife Service 1997). Seven to nine million individuals of 300 bird species, including the federally endangered Interior Least Tern (*Sterna antillarum*) and Whooping Crane (*Grus americana*), migrate annually along this route (Krapu et al. 1984; Currier et al. 1985; Austin & Richert 2001).

Heightened awareness of the wetland services and the extent of loss and degradation of wetland habitats has resulted in increased efforts to protect remaining systems and spawned widespread restoration efforts. Following the removal of anthropogenic disturbance (e.g., ceasing crop production), recovery of some ecosystem aspects occurs through natural succession (Dormaar & Smoliak 1985; Burke et al. 1995; Ihori et al. 1995). However, natural recovery often requires extensive time. Therefore, restoration aims to catalyze natural recovery processes through habitat manipulations (e.g., returning hydrology) (Wilcox et al. 2006), reintroduction of historic plant species (e.g., seeding) (Reinartz & Warne 1993), and/or management (e.g., prescribed fire) (Clark & Wilson 2001). Plants are often the focus of wetland restorations (e.g., Willard et al. 1990; Reinartz & Warne 1993; Galatowitsch & van der Valk 1996*a*) because vegetation is tightly coupled to wetland function (Mitsch & Gosselink 2000). Although restoration is a labor-intensive process in the PRV, evaluations of these restorations have been limited in frequency, duration, and scope (but see Currier 1994; Whitney 1997; Currier 1998).

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Restoration assessment typically incorporates comparisons of restored sites with reference information (e.g., nondegraded natural sites) to evaluate recovery. White and Walker (1997) outlined the difficulties of selecting and using reference information, chiefly that natural systems are temporally and spatially variable. Similarly, Hobbs and Harris (2001) noted that because natural systems are dynamic, restoration goals should not be based on static attributes. Hence, seasonal, interannual, and disturbance-induced variability of natural systems need to be considered when using natural systems as "targets" for comparisons with restored sites.

Assessing recovery is important because documented limitations in recovery may lead to improvements in restoration techniques in these and similar systems. Alternatively, documented successes can be used to justify further restoration efforts. Consequently, our overall objective was to evaluate wetland restorations in the central PRV by (1) comparing plant community structure in nearby restorations (1–7 years old at beginning of study) and natural wetlands and (2) following temporal recovery trajectories. We predicted that measures of community structure (richness, diversity) would increase with time since restoration and would be highest in natural wetlands. We also predicted that plant communities in restorations would become more similar to natural communities over time.

Methods

Study Region

We measured plant community structure and function in three natural and six restored wetlands along an approximately 90-km stretch of the central PRV in south-central Nebraska (from 40°48′27.94″N, 98°23′0.56″W to 40°40′6.16″N, 99°20′9.63″W). This region consists of the braided shallow channels of the Platte River and associated wet meadows. Wet meadows are large areas of mesic prairie, dominated by grasses and sedges. In low-lying areas within these wet meadows are meandering linear wetland sloughs. These wetland sloughs range from ephemeral to perennial, with water levels regulated by precipitation and river discharge through groundwater connection (Whiles & Goldowitz 1998). Vegetation in the natural wetlands is dominated by sedges and rushes (e.g., Emory's sedge [*Carex emoryi* Dewey], Softstem bulrush [*Schoenoplectus tabernaemontani* (K.C. Gmel.) Palla], *Eleocharis* spp. R. Br. [spikerush]), grasses (e.g., Prairie cordgrass [*Spartina pectinata* Bosc ex Link], Switchgrass [*Panicum virgatum* L.], Foxtail barley [*Hordeum jubatum* L.]), and forbs (e.g., Lanceleaf fogfruit [*Phyla lanceolata* (Michx.) Greene], Water smartweed [*Polygonum amphibium* L.], Swamp verbena [*Verbena hastata* L.]). Soil in natural wetlands is primarily gently sloping (0–2), poorly drained, and consists of silty clay loam alluvium over sandy and gravelly alluvium. Climate is temperate with warm summers (July mean temperature = 24°C) and cold winters (January mean temperature = −7°C). Mean annual precipitation is 630 mm/yr, most of which falls in May and June. Growing season precipitation (April through September) was approximately 280 mm in 2002, approximately 420 mm in 2003, approximately 380 mm in 2004, and approximately 460 mm in 2005 (National Weather Service 2006).

We selected nine sites, including three natural and six restored wetlands ranging in age from 1 to 7 years at the initiation of the 3-year assessment (Table 1). Sites had similar geomorphology, and all were intermittent, with dry periods occurring in late summer. To account for natural hydrologic variability, we chose natural sites along a gradient of hydrology based on data from Whiles and Goldowitz (2001). All restored sites were previously crop fields that were contoured and planted with native seeds or seedlings collected from nearby natural wetlands. Restored sites were all planted with high diversity mixes of locally collected native seed (Table 1), and the

Table 1. Platte River wetland study site characteristics including age class, year of restoration, age of restored site at the onset of the study, seeding effort, and hydroperiods throughout the study.

						Hydroperiod[c]		
Site Name	*Age Class*	*Year of Restoration*	*Age*[a]	*Figure Symbol*	*Seeding Effort*[b]	*2003*	*2004*	*2005*
Mormon East	Natural	Native	—	○	—	3–6	3, 11–12	1–6
Mormon Middle	Natural	Native	—	□	—	3–6	3	2–3, 5–6
Mormon West	Natural	Native	—	△	—	0	3	6
Uridil	Restored	1995	7	▲	~150	0	0	5–6
Studnicka	Restored	1996	6	■	~150	4–6	3	5–6
Johns	Restored	1998	4	●	~200	5–6	3	4–6
Dahms/Derr	Restored	2000	2	▼	~200	0	0	6
Speidell 2000	Restored	2000	2	◆	~200	0	0	0
Speidell 2001	Restored	2001	1	⯃	~200	0	0	0

[a] Age in years of the restored wetlands when the study began (2002).

[b] Number of species seeded into wet meadow restorations, from C. Helzer 2008, The Nature Conservancy, Aurora, Nebraska; and B. Whitney 2008, Prairie Plains Resource Institute, Aurora, Nebraska, personal communication.

[c] Months with standing water (1 = Jan, 2 = Feb, etc.). No hydrology measurements were taken during 2002. Measurements were only taken through July 2005.

restoration of only one site (Johns) included transplants of three species (*C. emoryi*, Sensitive fern [*Onoclea sensibilis* L.], and Eastern marsh fern [*Thelypteris palustris* Schott] (K. Pfeiffer 2008, Platte River Whooping Crane Maintenance Trust, personal communication). Cattle grazing was used as an ongoing management tool on all natural sites (rest/rotation schedule), one of the older restorations (Uridil) (K. Pfeiffer, personal communication), and at one newly restored site (Dahms/Derr) (C. Helzer, The Nature Conservancy, personal communication). Short-term intensive grazing was used for 2 years on the Studnicka site, but ceased prior to the onset of the study (C. Helzer, personal communication). Cattle exclosures were built around study areas in sites that received cattle grazing. Dormant season (early spring) prescribed fire was also part of the management regime in all but two restored sites (Johns, Speidell 2001).

At each site, we conducted all sampling within a 30-m length (reach) along a linear section of wetland slough. Each reach was established adjacent to one of the deepest areas along the slough at each site and included three transects, one along the central deepest part of the wetland (slough) and two along the contour of each edge of the wetland (margin). Transects were located in slough and margin habitats based on observed differences in microhabitat and plant communities resulting from slight variation in topography between habitats (Meyer & Whiles 2002, SIUC, personal observation). We installed staff gauges at the deepest point of each slough to measure depth of standing water. Measurements of hydrology were based on the presence of standing water during monthly site visits.

Plant Community Composition and Metrics

We used plant community sampling approaches commonly used in grasslands, as these wet meadow systems were dominated by herbaceous vegetation, with many mesic prairie species. We established six 0.5 × 0.5–m quadrats spaced at 5-m intervals along each transect in each site. We visually estimated percent cover of all species in each quadrat in spring (approximately second week of June) and summer (approximately first week of August) for three consecutive years (2003–2005). We used the maximum cover value of each species in community analyses. Nomenclature followed USDA, NRCS (2006).

In each quadrat, we quantified richness (number of species) and Shannon–Wiener index of diversity (Shannon 1948). We calculated percent similarity (PS) of plant communities using relative cover in each restored site compared to the average relative cover of natural sites in each habitat according to Renkonen (1938). We assigned wetland indicator status (WIS) values to each species (USDA, NRCS 2006) to calculate the mean WIS for each site according to Wentworth et al. (1988). When plants could only be identified to genus, we estimated WIS values and life history based on common species within that genus.

Data Analyses

We analyzed changes in plant community metrics in the restorations over time in each habitat using linear and nonlinear regression procedures in Systat (2002). When no significant change in a parameter occurred over time, we compared means of natural and restored wetlands using t tests appropriate for homogeneity or heterogeneity of variances in SAS (SAS 2002). We log transformed data if necessary to satisfy regression assumptions of normality and constant variance of residuals. We chose an $\alpha = 0.05$, but because of high variability inherent in any field study, we present all relationships in which $p < 0.1$.

We also examined plant community composition using nonmetric multidimensional scaling (NMDS) (Minchin 1987). NMDS creates an ordination of composition data quadrats in various dimensions and adjusts the position of quadrats to minimize stress, which uses badness of fit of rank order regressions of ordination distances on dissimilarities (McCune & Grace 2002). We standardized the output to unit maxima. We calculated dissimilarities using the Bray–Curtis index (Bray & Curtis 1957), which has been shown to be one of the most effective techniques for ordination of community data (Faith et al. 1987). We performed the analysis in one to six dimensions and used 100 random starting configurations.

We performed vector fitting (Dargie 1984; Faith & Norris 1989; Kantvilas & Minchin 1989) to examine correlations between plant composition and potential explanatory variables (hydrology, site type, and restoration age). Hydrology was the number of months in each site in each year during which standing water was present, based on monthly visits to each site. Site type was a comparison of restored with natural sites. The restoration age variable was the age since restoration for each restored site. Vector fitting uses multiple linear correlation to find the direction across ordination space that has the highest correlation between sample coordinates and a particular variable. To test the statistical significance of the correlation, we randomly permutated values of the variable among quadrats, simulating the null hypothesis of no trend. We performed all ordination and vector fitting procedures using DECODA software (Minchin 1989).

Results

Plant Cover and Community Composition

We identified 109 taxa from Platte River wetlands (Table 2). There were no directional recovery patterns in total plant cover over time in either habitat (Fig. 1). In wetland margins, mean total percent cover was 44% higher in natural wetlands (107 ± 6) (mean ± SE) than in restored sites (63 ± 7) ($p = 0.0006$). In sloughs, total percent cover was highly variable in natural sites and average total cover was 45% higher (100 ± 14) than in restored sites (54 ± 6) ($p = 0.001$) (Fig. 1).

Table 2. Relative cover and characteristics of plant species collected in natural (N) and restored (R) Platte River wetlands, listed by group.[a]

				Margins		*Sloughs*	
Plant Taxon	*Family*	*Life History*[b]	*WIS*[c]	*N*	*R*	*N*	*R*
Grasses							
Agropyron cristatum (L.) Gaertn.	Poaceae	P	fac?	0.000	0.003	0.000	0.007
Andropogon gerardii Vitman	Poaceae	P	fac	0.000	0.051	0.000	0.013
Bromus inermis Leyss.	Poaceae	P	fac?	<0.001	<0.001	0.000	0.000
Bromus tectorum L.	Poaceae	A	fac?	<0.001	0.000	0.000	0.000
Calamagrostis stricta (Timm) Koel.	Poaceae	P	facw	0.009	0.025	0.000	0.042
Dicanthelium oligosanthes (Schult.) Gould	Poaceae	P	facu	0.000	0.000	0.000	<0.001
Digitaria spp. Haller	Poaceae	A	facu?	0.000	0.000	0.000	0.004
Distichlis spicata (L.) Greene	Poaceae	P	facw	0.000	0.003	0.000	0.001
Elymus canadensis L.	Poaceae	P	facu	0.000	0.016	0.000	0.004
Hordeum jubatum L.	Poaceae	P	facw	0.020	0.014	0.001	0.009
Leersia oryzoides (L.) Sw.	Poaceae	P	obl	0.000	0.000	0.000	<0.001
Panicum capillare L.	Poaceae	A	fac	0.000	<0.001	0.000	0.000
Panicum virgatum L.	Poaceae	P	fac	0.002	0.030	0.001	0.011
Phalaris arundinacea L.	Poaceae	P	facw	0.061	0.000	0.097	0.000
Poa pratensis L.	Poaceae	P	facu	0.007	0.000	0.001	0.000
Schizachyrium scoparium (Michx.) Nash	Poaceae	P	facu	0.000	0.003	0.000	<0.001
Setaria spp. Beauv.	Poaceae	A	upl?	0.000	0.012	0.005	0.015
Sorghastrum nutans (L.) Nash	Poaceae	P	facu	0.000	0.001	0.000	0.000
Spartina pectinata Bosc ex Link	Poaceae	P	facw	0.118	0.139	0.087	0.117
Sporobolus compositus (Poir.) Merr.	Poaceae	P	facu	0.016	0.012	0.002	0.013
Sporobolus cryptandrus (Torr.) Gray	Poaceae	P	facu	0.001	0.012	0.000	0.012
Forbs							
Alisma subcordatum Raf.	Alismataceae	P	obl	<0.001	0.002	0.002	<0.001
Amaranthus spp. L	Amaranthaceae		facu?	0.000	0.001	0.002	0.002
Cicuta maculata L.	Apiaceae	B/P	obl	0.014	0.002	0.001	0.001
Apocynum cannabinum L.	Apocynaceae	P	fac	0.014	0.002	0.015	0.022
Asclepias incarnata L.	Asclepiadaceae	P	obl	0.001	<0.001	0.000	0.000
Asclepias speciosa Torr.	Asclepiadaceae	P	fac	0.000	0.000	0.000	0.001
Asclepias syriaca L.	Asteracea	P	fac?	0.001	0.000	0.000	0.000
Achillea millefolium L.	Asteracea	P	facu	0.000	0.000	0.000	<0.001
Ambrosia spp. L.	Asteracea	A	facu	0.051	0.007	0.031	0.024
Ambrosia trifida L.	Asteracea	A	facw	0.001	0.003	0.000	0.000
Bidens cernua L.	Asteracea	A	obl	0.003	0.000	0.019	0.000
Bidens frondosa L.	Asteracea	A	facw	0.003	0.000	0.005	0.002
Cirsium altissimum (L.) Hill	Asteracea	B	facu?	0.000	0.002	0.000	<0.001
Conyza Canadensis (L.) Cronq.	Asteracea	A/B	facu	0.001	0.036	0.002	0.038
Coreopsis tinctoria Nutt.	Asteracea	A/P	fac	0.002	0.007	0.000	0.017
Erigeron philadelphicus L.	Asteracea	A	fac	0.000	0.004	0.000	0.008
Eupatorium altissimum L.	Asteracea	P	facu	0.000	0.000	0.000	<0.001
Euthamia graminifolia (L.) Nutt.	Asteracea	P	facw	0.001	0.001	0.008	0.000
Grindelia squarrosa (Pursh) Dunal	Asteracea	A/B	facu	0.000	<0.001	0.000	0.000
Helenium autumnale L.	Asteracea	P	obl	0.000	0.003	0.000	0.001
Helianthus annuus L.	Asteracea	A	facu	0.000	0.010	0.000	0.003
Helianthus grosseserratus Martens	Asteracea	P	facw	0.014	0.009	0.000	0.001
Helianthus maximiliani Schrad.	Asteracea	P	upl	0.068	0.070	0.037	0.012
Helianthus pauciflorus Nutt.	Asteracea	P	fac ?	0.000	0.001	0.000	0.000
Iva annua L.	Asteracea	A	fac	0.046	0.030	0.042	0.040
Lactuca serriola L.	Asteracea	A	fac	0.001	0.001	0.000	0.003
Liatris spp. Gaertn. ex Schreb.	Asteracea	P	facu ?	0.000	0.000	0.000	<0.001
Oligoneuron rigidum (L.) Small	Asteracea	P	facu	0.000	0.002	0.000	0.000
Packera plattensis (Nutt.) Weber & Löve	Asteracea	B/P	facu	0.000	0.000	0.001	0.000
Solidago spp. L.	Asteracea	P	facu ?	0.060	0.015	0.005	0.008
Symphyotrichum ericoides (L.) Nesom	Asteracea	P	fac	0.012	0.021	0.000	0.014
Symphyotrichum lanceolatum (Willd.) Nesom	Asteracea	P	facw ?	0.014	0.022	0.002	0.011
Taraxacum officinale G.H. Weber ex Wiggers	Asteracea	P	facu	0.000	0.002	0.000	0.001

Table 2. Continued

				Margins		Sloughs	
Plant Taxon	*Family*	*Life History*[b]	*WIS*[c]	*N*	*R*	*N*	*R*
Xanthium strumarium L.	Asteracea	A	fac	0.013	0.001	0.004	0.000
Lepidium densiflorum Schrad.	Brassicacea	A/B	fac	0.000	0.001	0.000	0.001
Lobelia spp. L.	Campanulaceae	P	obl	0.001	0.009	0.000	0.030
Chenopodium album L.	Chenopodiaceae	A	fac	0.000	0.006	0.000	0.003
Equisetum spp. L.	Equisetaceae	P	facw?	0.002	0.005	<0.001	0.002
Lotus corniculatus L.	Fabaceae	P	facu	<0.001	0.000	0.000	0.000
Dalea purpurea Vent.	Fabaceae	P	fac?	0.000	0.004	0.000	0.000
Desmanthus illinoensis (Michx.) MacM. ex Robins. & Fern.	Fabaceae	P	facu	0.000	0.092	0.002	0.016
Glycyrrhiza lepidota Pursh	Fabaceae	P	facu	0.000	<0.001	0.000	0.001
Medicago lupilina L.	Fabaceae	A/P	fac	0.000	<0.001	0.000	0.004
Melilotus officinalis (L.) Lam.	Fabaceae	B/P	facu	0.000	0.009	0.000	<0.001
Eustoma exaltatum (L.) Salisb. ex G. Don	Gentianaceae	P	facw	0.000	0.003	0.000	0.000
Myriophyllum spp. L.	Haloragaceae	P	obl?	0.000	0.000	0.000	0.005
Sisyrinchium spp. L.	Iridaceae	P	fac?	0.000	<0.001	0.000	0.000
Triglochin palustris L.	Junginacea	P	obl	0.000	0.004	0.000	0.001
Lycopus spp. L.	Lamiaceae	P	obl	0.020	0.003	0.013	0.012
Mentha arvensis L.	Lamiaceae	P	facw	0.009	<0.001	<0.001	0.000
Lythrum alatum Pursh	Lythraceae	P	obl	0.000	0.000	0.000	0.001
Lythrum salicaria L.	Lythraceae	P	obl	0.000	<0.001	0.000	0.005
Oenothera rhombipetala Nutt. ex Torr. & Gray	Onagraceae	A/B	facu	0.000	0.013	0.000	0.008
Polygonum amphibium L.	Polygonaceae	P	obl	0.008	0.000	0.018	0.000
Polygonum spp. L.	Polygonaceae	P	obl ?	0.076	0.003	0.131	0.005
Rumex crispus L.	Polygonaceae	P	facw	0.002	0.003	<0.001	0.003
Ranunculus cymbalaria Pursh	Ranunculaceae	P	obl	0.000	0.000	0.002	0.000
Galium spp. L.	Rubiaceae	P	facu?	0.005	0.000	0.000	0.000
Agalinis aspera (Dougl. ex Benth.) Britt.	Scrophulariaceae	A	facu	0.000	0.010	0.000	0.052
Agalinis tenuifolia (Vahl) Raf.	Scrophulariaceae	A	facw	0.000	0.001	0.000	0.000
Verbascum thapsus L.	Scrophulariaceae	B	fac?	0.000	0.000	0.000	0.002
Sparganium eurycarpum Engelm. ex Gray	Sparganiaceae	P	obl	<0.001	0.000	0.004	0.000
Phyla lanceolata (Michx.) Greene	Verbenaceae	P	obl	0.081	0.010	0.179	0.019
Verbena hastata L.	Verbenaceae	B/P	facw	0.001	0.002	0.000	0.015
Verbena stricta Vent.	Verbenaceae	P	fac?	0.000	0.003	0.000	0.001
Sedges and rushes							
Carex aurea Nutt.	Cyperaceae	P	facw	0.000	0.000	0.000	0.002
Carex brevior (Dewey) Mackenzie	Cyperaceae	P	fac	0.001	<0.001	0.000	<0.001
Carex crawei Dewey	Cyperaceae	P	facw	0.000	0.000	0.000	<0.001
Carex emoryi Dewey	Cyperaceae	P	obl	0.151	0.010	0.106	0.009
Carex gravida Bailey	Cyperaceae	P	fac?	0.000	0.000	0.000	<0.001
Carex molesta Mackenzie ex Bright	Cyperaceae	P	fac	<0.001	<0.001	0.000	<0.001
Carex pellita Muhl. ex Willd.	Cyperaceae	P	obl	<0.001	0.002	<0.001	0.000
Carex praegracilis W. Boott	Cyperaceae	P	facw	0.000	0.001	0.000	0.000
Cyperus acuminatus Torr. & Hook. ex Torr.	Cyperaceae	A/P	obl	0.000	0.001	0.000	0.000
Cyperus spp. L.	Cyperaceae	P	facw	0.003	0.002	0.001	0.000
Eleocharis spp. R. Br.	Cyperaceae	P	facw?	0.039	0.022	0.068	0.059
Fimbristylis puberula (Michx.) Vahl	Cyperaceae	P	obl	0.000	0.008	0.000	0.001
Schoenoplectus atrovirens Willd.	Cyperaceae	P	obl	0.000	0.003	0.003	0.001
Schoenoplectus maritimus (L.) Lye	Cyperaceae	P	obl?	0.000	0.001	0.000	<0.001
Schoenoplectus pungens (Vahl) Palla	Cyperaceae	P	obl	0.006	0.015	0.013	0.051
Schoenoplectus tabernaemontani (K.C. Gmel.) Palla	Cyperaceae	P	obl	0.000	0.002	0.000	0.016
Scirpus spp. L.	Cyperaceae	P	obl?	0.000	0.000	0.000	<0.001
Juncus dudleyi Wieg.	Juncaceae	P	facw	0.000	0.022	0.000	0.008
Juncus torreyi Coville	Juncaceae	P	facw	0.000	0.019	0.000	0.007
Typha							
Typha spp. L.	Typhaceae	P	obl	0.040	0.018	0.088	0.102

Table 2. Continued

Plant Taxon	Family	Life History[b]	WIS[c]	Margins		Sloughs	
				N	R	N	R
Woody							
Populus deltoides Bartr. ex Marsh.	Salicaceae	P	fac	0.000	0.077	0.000	0.027
Salix amygdaloides Anderss.	Salicaceae	P	facw	0.000	0.009	0.000	0.004
Salix exigua Nutt.	Salicaceae	P	facw	0.000	0.035	0.000	0.072
Unknown taxa				0.008	0.012	0.006	0.009

[a] Data are averaged by habitat (margins and sloughs) over 3 years (2003–2005).
[b] P, perennial; B, biennial; A, annual.
[c] According to USDA, NRCS (2006). Those with question marks could not be determined; WIS values from common genera were used.

Margin habitats of natural wetlands comprised, on average, 23 ± 6% grasses, 53 ± 7% forbs, 20 ± 4% sedges, and 4 ± 2% *Typha*. Collectively, the restored margins had an average of 32 ± 5% grass cover and 43 ± 5% forbs, and there was no change with time since restoration in either of these groups (Fig. 1). Mean relative sedge and rush cover in margins of restorations increased with years since restoration and became representative of natural wetlands (Fig. 1). *Typha* was only found in restored sites over 4 years old and was only found in one of the natural site margins (Fig. 1). Mean relative cover of woody vegetation in margins of restorations decreased with years since restoration, becoming more similar to natural margins that did not contain woody vegetation (Fig. 1).

Within sloughs of natural wetlands, average relative cover comprised 19 ± 7% grass, 52 ± 10% forb, 20 ± 4% sedges and rushes, and 9 ± 3% *Typha*. Mean relative grass cover in sloughs decreased with time since restoration (Fig. 1). Mean relative cover of forbs was 13 ± 7% less than in natural wetland sloughs and represented the range of cover observed in natural sloughs in all but one recently restored site (Fig. 1). The range of mean relative sedge and rush cover within restored wetland sloughs was also similar to the range that occurred in natural sites (Fig. 1). *Typha* was absent from the most recently restored wetland sloughs but was present in older restorations resulting in an increase in the cover of this species with time since restoration (Fig. 1). Presence of *Typha* was also inconsistent among the natural sloughs, occurring in only one of the three sites. Woody vegetation was not present in natural slough habitats but exhibited a slight increase across the restoration chronosequence (Fig. 1).

Average WIS values were low in both habitats in natural wetlands (Fig. 2). In margins the average WIS of natural sites was 2.15 ± 0.22 (Fig. 2), and values in restorations decreased with time across the chronosequence (Fig. 2). A similar pattern occurred in sloughs, where natural wetlands had an average WIS value of 1.6 ± 0.19 and values in restorations decreased with time since restoration (Fig. 2).

Species richness and diversity changed over the restoration chronosequence in the margins but not in sloughs. In margins of natural wetlands, both richness and diversity in sampling plots were fairly consistent among sites with averages of 8 ± 0.2 and 1.4 ± 0.1, respectively (Fig. 3). Within margins, richness showed a quadratic response with years since restoration and diversity showed a similar, but weaker, response over time (Fig. 3). When data from one older restored site (Uridil) were removed, there were strong, positive relationships between both indexes with time since restoration, with richness and diversity exceeding that of margins of natural sites. Within sloughs of natural wetlands, richness ranged from an average of 3 to 8 taxa per quadrat, and diversity ranged from 0.5 to 1.7 (Fig. 3). In contrast to margins, there were no directional changes in richness or diversity with years since restoration in sloughs (Fig. 3), and ranges of both indexes overlapped with those observed in the natural sloughs.

PS of plant communities in each site and habitat were compared to the average community composition across the natural sites over all years. In both margins and sloughs, PS of plant communities in restorations to those in natural wetlands was low, ranging from less than 10 to 46% (Fig. 4). However, there was an increase in PS to natural systems with time since restoration in both habitats (Fig. 4).

For both margins and sloughs, two-dimensional NMDS ordinations (stress: margins = 0.16, sloughs = 0.18) achieved from all 100 random starts were used because they had relatively low stress compared to one-dimensional solutions (stress: margins = 0.28, sloughs = 0.30). The addition of a three-dimensional solution did not appreciably decrease stress (stress: margins = 0.10, sloughs = 0.12) but would have decreased ecological interpretability.

For margins, fitted vectors of maximum correlation were highly significant for hydrology ($r = 0.65, p = 0.001$), site type ($r = 0.82, p < 0.0001$), and restoration age ($r = 0.72, p < 0.005$) (Fig. 5). The hydrology and site type vectors showed only marginal separation (7.1°) (Fig. 5), indicating similar shifts in plant taxa with increasing age and increasing hydroperiods. Composition shifts occurring along vectors were similar; for example, species most abundant in the driest sites (Stiff goldenrod [*Oligoneuron rigidum* (L.) Small], Purple prairie clover [*Dalea purpurea* Vent.], Black medic [*Medicago lupulina* L.]) were also

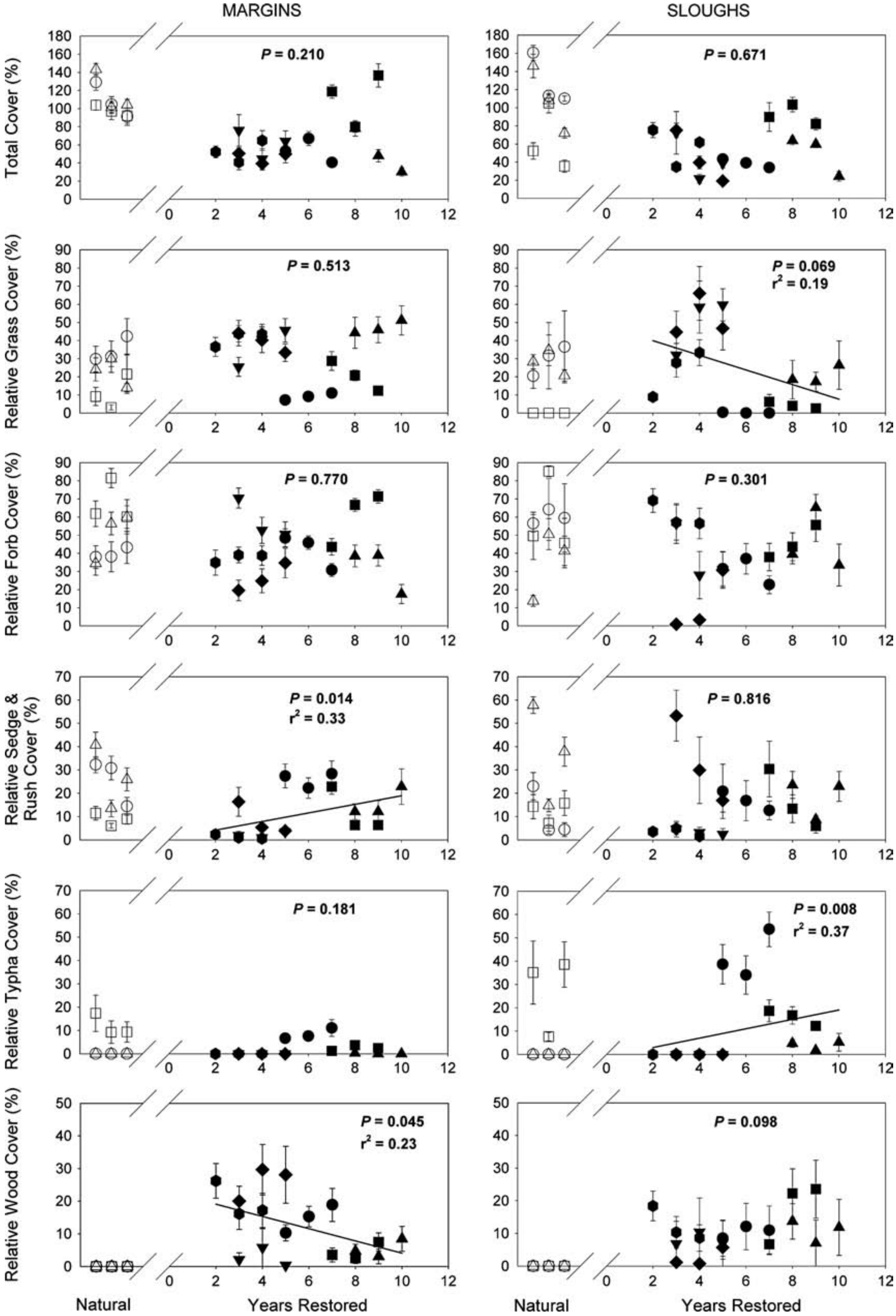

Figure 1. Average (±1 SE) total cover and relative cover of vegetation groups in natural and restored wetland margins and sloughs. Site symbols follow Table 1. Trajectory lines and coefficients of determination (r^2) accompany significant linear changes over time across the restored wetlands ($\alpha = 0.05$, p values <0.10 presented).

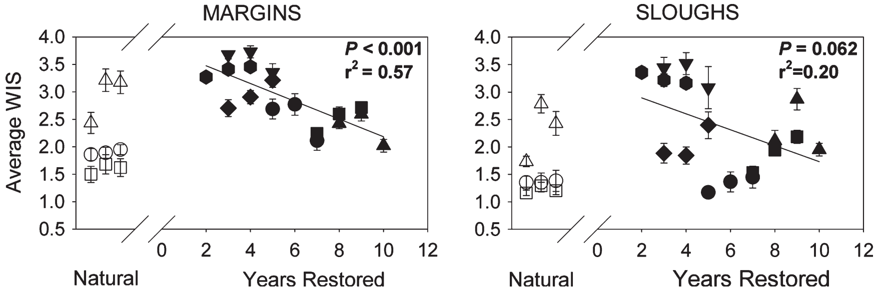

Figure 2. Average WIS of plants in natural and restored wetland margins and sloughs. Site symbols follow Table 1. Trajectory lines and coefficients of determination (r^2) accompany significant linear changes over time across the restored wetlands ($\alpha = 0.05$, p values <0.10 presented).

most abundant in the newest restorations (Meyer 2007). Likewise, species restricted to the wettest sites, such as Nodding beggartick (*Bidens cernua* L.) and Devil's beggartick (*B. frondosa* L.), were also likely to be found only in natural wetlands (Meyer 2007). Additionally, some taxa successfully established in margins of all restored sites (e.g., *Spartina pectinata*), whereas others were not present in margins of the newest restorations (e.g., *Carex emoryi*), and still others only occurred in natural sites (e.g., Broad-fruit bur-reed [*Sparganium eurycarpum* Engelm. ex Gray]) (Meyer 2007).

In sloughs, fitted vectors of maximum correlation were highly significant for hydrology ($r = 0.78$, $p < 0.0001$), site type ($r = 0.76$, $p < 0.0001$), and restoration age ($r = 0.72$, $p = 0.006$) (Fig. 5). The hydrology and site type vectors in the slough ordination were separated by approximately 43°, indicating that recovery with time in sloughs was related to hydrology but not as closely as in margins. However, taxonomic shifts along these vectors were still similar (Meyer 2007); species found only in the driest sites, such as Common yarrow (*Achillea millifoleum* L.) and American licorice (*Glycyrrhiza lepidota* Pursh), were also found only in the newest restorations; taxa that occurred in higher frequencies in wettest sloughs were also found in the natural sites (Meyer 2007). As in margins, some taxa, such as *Eleocharis* spp., were established in sloughs of restorations of all ages, some taxa only occurred in sloughs of natural and older restored systems (e.g., *P. lanceolata*), and others were unique to natural sites (e.g., Alkali buttercup [*Ranunculus cymbalaria* Pursh]) (Meyer 2007).

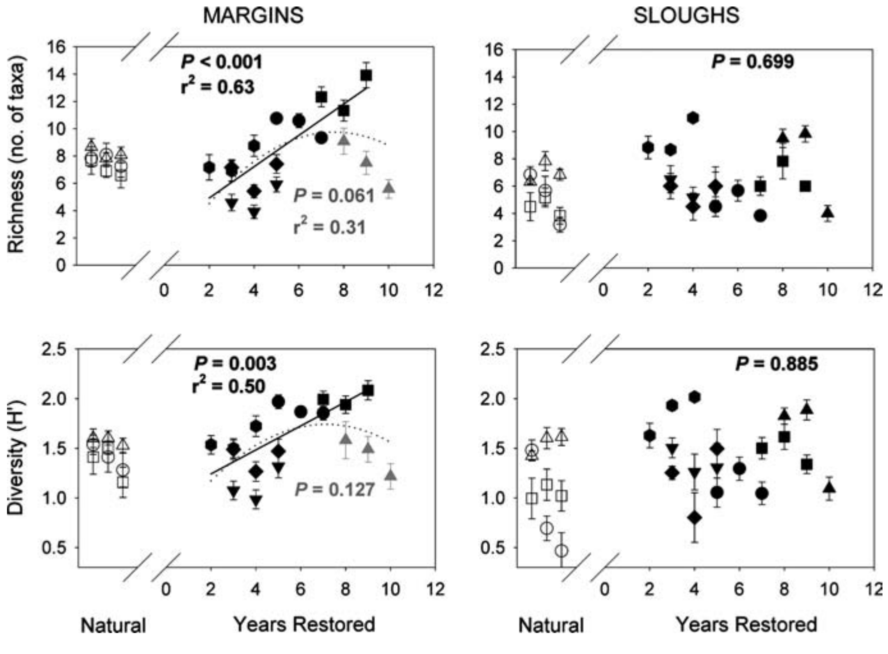

Figure 3. Average plant taxa richness (no.) and diversity (H') in natural and restored wetland margins and sloughs. Because one site (Uridil) may have been an outlier, richness and diversity were analyzed with both nonlinear regression of all data and with linear regression after removing data points from the Uridil site. Site symbols follow Table 1. Trajectory lines and coefficients of determination (r^2) accompany significant linear changes over time across the restored wetlands ($\alpha = 0.05$, p values <0.10 presented).

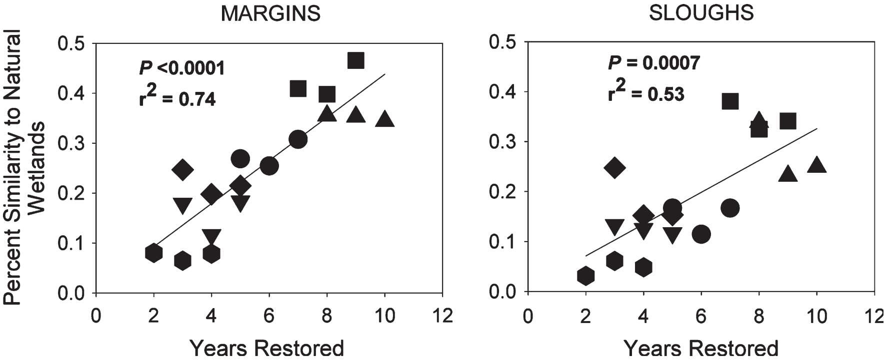

Figure 4. PS of plant communities in restored wetlands relative to the average of three natural sites during that year. Site symbols follow Table 1. Trajectory lines and coefficients of determination (r^2) accompany significant linear changes over time across the restored wetlands ($\alpha = 0.05$, p values <0.10 presented).

Discussion

Plant Community Recovery

Patterns of WIS values indicated that restored wetlands became increasingly dominated by wetland plants. Within both habitats, average WIS values showed that communities in newer restorations were not dominated by characteristic wetland plants, and this may be linked to site hydrology. Henszey et al. (2004) measured relationships between hydroperiod and frequency of plants in central Platte River wetlands and found that wetland obligates, species that were uncommon or absent in new restorations of our study (e.g., Rough bugleweed [*Lycopus asper* Greene]), peaked in abundance in areas that had a 7-day moving average high water level at or above the soil surface, and rapidly decreased along a gradient of depth to groundwater. Data from Spanish wetlands have shown that alterations in hydrology can have significant effects on species richness and cover (Alvarez-Cobelas et al. 2001). Hence, the lack of surface water and presumably corresponding increased depth to groundwater in newer restorations probably reduced establishment of wetland plants.

While no changes in richness and diversity were observed in sloughs, richness showed a weak quadratic relationship with time since restoration in margins. Furthermore, richness and diversity in margins were most similar between newer restorations and natural sites. Both of these patterns suggest that diversity and richness increase for 2–5 years and then decline and become representative of native systems. This resembled the short-term pattern documented by Reinartz and Warne (1993) (i.e., an increase in diversity in 3-year-old Wisconsin wetlands) and a similar response in tidal freshwater marshes (Baldwin 2004). Confer and Niering (1992) also observed a pattern of higher richness (although not statistically significant) in 3- to 4-year-old created emergent wetlands in Connecticut compared to natural systems. This “overshoot” in diversity may persist for some time; plant richness in over 50-year-old created wetlands was higher than that found in natural systems in New Jersey pineland

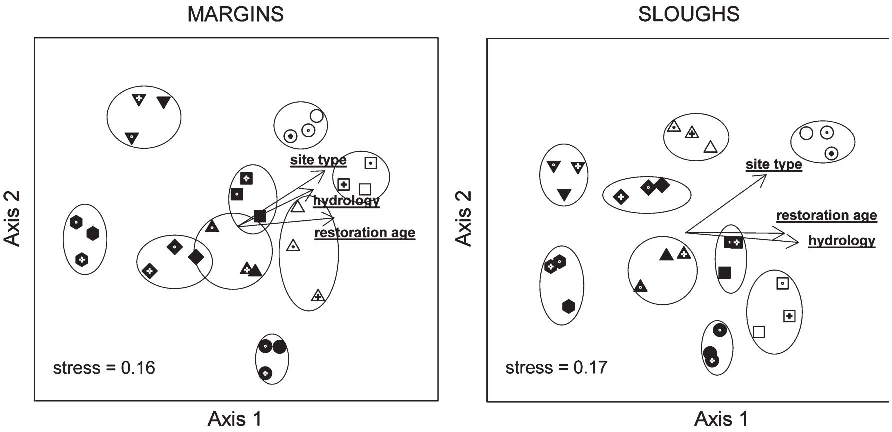

Figure 5. Two-dimensional NMDS ordination plots based on average relative cover of plant taxa in wetland margins and sloughs using the Bray–Curtis dissimilarity index. Sampling units are averages of community composition within subsample quadrats (12 in margins, 6 in sloughs) within a site for each year. Site codes follow Table 1 (symbols for 2004 contain a small + sign, symbols for 2005 contain a larger + sign). Significant vectors were fitted for hydrology, site type (natural vs. restored), and restoration age.

coastal plain ponds (Zampella & Laidig 2003). However, the prevalence of either linear or quadratic patterns is hard to assess because evaluations and/or restoration age classes are temporally restricted in many studies.

When we removed one study site from our analyses (Uridil), strong linear relationships between years restored and richness and diversity were evident. Uridil was the oldest restored site in our study and also one of the driest sites. It is possible that Uridil was disproportionately influenced by the prevailing drought conditions during our study, as it was the only site that decreased in diversity and richness consistently over the 3 years. This may indicate the presence of water limitation thresholds in these systems, beyond which species pools decline. If this is the case, stronger quadratic responses between time since restoration and richness and diversity may occur during more normal precipitation regimes. Perhaps this site was differentially affected by other factors (e.g., shallower depth to groundwater, management) and therefore exhibited relatively slower recovery than other sites.

Changes in plant cover over the restoration chronosequence indicated recovery of some groups. For example, sedge and rush cover in margins exhibited recovery patterns with years restored. Sedges and rushes are an important component of freshwater wetlands but are often slow to establish in restorations (e.g., Galatowitsch & van der Valk 1996*a*, 1996*b*, 1996*c*). Low cover of sedges and rushes in restored wetlands in our study and others may be related to specific germination and survival requirements (van der Valk et al. 1999; Budelsky & Galatowitsch 2000). Van der Valk et al. (1999) found that seed age, seed storage conditions, soil moisture, and soil amendments all potentially influenced germination success of three *Carex* species. Budelsky and Galatowitsch (2000) observed that seedling survival of Hairy sedge (*Carex lacustris* Willd.) was highly dependent on water levels during the first growing season. Ssegawa et al. (2004) also related patterns of sedge distribution found in wetlands in Uganda with several edaphic and geological factors and found that the most important were water levels, altitude, and rainfall. In our study, most of the sedges and rushes found in restorations were species other than *Carex* (e.g., *Eleocharis* and *Scirpus*), the dominant genus in most natural wetland systems in this region (Currier 1994, 1998), indicating a slower recovery of *Carex* in these sites. Although we did not test these factors, evidence from other studies suggests that hydrology and related aspects likely limited sedge recovery in the restorations we examined.

Although woody vegetation rarely occurred in the natural wetlands we examined, it was present in most restorations. Woody vegetation is undesirable in these systems because it shades herbaceous plants and reduces habitat quality for some focal wildlife species such as grassland birds and cranes (e.g., U.S. Fish and Wildlife Service 1981; Krapu et al. 1984). Woody encroachment into previously denuded sandbars and riparian areas in the central PRV since settlement has been attributed to river regulation and dewatering that collectively have altered seasonal flow patterns, reduced annual peak and mean flows, and decreased removal of saplings by scouring during high water events (Williams 1978; Eschner et al. 1983; U.S. Fish and Wildlife Service 1981; Sidle et al. 1989; Currier 1997). Fire suppression in wet meadows over the past century has compounded this problem and enhanced woody plant survival in riparian areas (U.S. Fish and Wildlife Service 1981). Higher abundance of mature trees in riparian areas represents abundant local sources for propagules of these historically uncommon wetland components. Land contouring for wetland restoration exposes soils that can then be readily colonized by woody species (Currier 1997). Therefore, methods to inhibit or remove woody vegetation such as clipping or burning should be considered in managing restored wetlands of the PRV.

Habitat-Specific Recovery

Recovery proceeded at different rates in margins and sloughs of the wetlands we studied. Most measures of ecosystem structure (e.g., richness, diversity) showed patterns of slow recovery in wetland margins, whereas these measurements were typically similar among restored sites, or did not show clear patterns, in sloughs. Specifically, many measures in recently restored sloughs were within the range of natural variation.

Elevational differences have been linked to gradients in hydrology, soil, and biota in this region (Henszey et al. 2004; Davis et al. 2006), and these in turn likely influence patterns of recovery following restoration. Depending on individual site morphology, margins and sloughs of our study sites varied in elevation from 10 to 25 cm, and these modest gradients can alter community structure (e.g., Rheinhardt & Fraser 2001), dominance (e.g., Galatowitsch & van der Valk 1996*c*), and successional trajectories (e.g., Edwards & Proffitt 2003) in wetlands. Differences of over 10 cm can influence the frequency of surface flooding in very low gradient systems (Bledsoe & Shear 2000). Henszey et al. (2004) examined the distribution of plants in Platte River wetlands along depth to groundwater gradients and found significant species-specific relationships with water levels. Odland (1997) studied vegetation composition following wetland creation within a permanently drawn-down lake system in Norway and found that after 4 years, vegetation exhibited distinct zonation patterns based on differences in elevation. Kennedy et al. (2003) also showed that manipulation of water levels in greenhouse experiments caused morphological responses of wetland plants of British northern poor fens that help explain factors controlling the location of plants along hydrologic gradients. Wetter conditions in sloughs may increase potential for seed germination and seedling survival during recovery, processes that are crucial to establishment of wetland vegetation (e.g., Morgan 1990; van der Valk et al. 1999). Our results show clearly different recovery patterns across elevational gradients within sites. Thus, restoration and management efforts should consider even subtle elevational changes, and assessments of restoration success should focus on higher elevation habitats within wetlands because they are the limiting components to recovery.

Restoration Assessment Challenges: Climate, Soil, Management, and Moving Targets

Prevailing weather patterns prior to and during our study may have influenced observed recovery patterns. The standard precipitation index (SPI) quantifies deficit or excess moisture conditions for a specified time period by comparing measure of departure from 30-year averages of precipitation (McKee et al. 1993). According to data provided by the National Agricultural Decision Support Center (USDA Risk Management Agency 2006), weather stations in Kearney, Hastings, and Grand Island showed SPI (3-month time period ending in June) values of -0.98 to -2.2, indicating moderately dry to extremely dry conditions in both 2000 and 2002. This lack of moisture may have decreased germination and survival of some species (e.g., van der Valk et al. 1999) and/or altered competition for limiting resources that maintain community structure, particularly in the drier margins where differences in richness and diversity were more pronounced. Rainfalls totaling over 20 cm during the month of May in 2005 in some locations within the central Platte region resulted in standing water for substantial periods of time in sites that previously had rarely (if ever) been inundated, and this may have resulted in germination of plants that had previously not been subjected to proper conditions (e.g., Morgan 1990; van der Valk et al. 1999). These extreme temporal differences in precipitation likely drove the interannual variability in plant community structure observed during the study period.

In addition to the potential influences of weather, differential water retention among restoration sites may have also influenced recovery patterns. In particular, two of the older restorations held water at least briefly during spring, while none of the newer restorations held water for more than a few days in 2003 or 2004, and only one recently restored site held water for at least 2 weeks in 2005. High site-specific variability in hydrology has been documented even among similar wetland types in the PRV (Whiles & Goldowitz 2001), and hydrologic patterns we observed may be related to some aspect of the restoration approach or location (e.g., differences in morphology, depth to groundwater, or soil characteristics in restoration sites), resulting in generally drier conditions in restorations. In particular, soil organic matter development influences water holding capacity and may potentially limit hydrologic recovery. Observations during a companion study indicated that soils in restorations contained substantially less organic matter than natural sites (Meyer et al. 2008). Measures within the range of natural variation in the moister slough habitats further support our hypothesis that moisture, including inputs and holding capacity, plays a critical role in the recovery of these systems.

Site-specific differences in management (e.g., grazing, burning) may have driven changes in plant community structure, thereby overriding recovery following restoration. Despite some evidence that grazers decrease diversity, particularly in arid regions (Belsky 1992; Bahre 1995; Wilcove et al. 1998), grazing has been shown to increase diversity in mesic grassland systems (Collins 1987; Knapp et al. 1999; Hayes & Holl 2003; Pykälä 2004). However, the effect depends on plant traits (Olff & Ritchie 1998; Hayes & Holl 2003) and is mediated by plant productivity and grazing pressure (Bakker 1989; Hodgson & Illius 1996). For example, Osem et al. (2002) found that diversity of the plant community in a Mediterranean rangeland was driven by the interaction between grazing and spatiotemporal variation in plant productivity. Prescribed fire is an important management tool in grasslands as well, and some generalized effects of burning include decreased woody vegetation, increased C_4 grass rhizome development and tillering, decreased C_3 grass flowering and tillering, and decreased forb abundance (Hartnett & Fay 1998, and references therein). However, significant interactions also exist between fire, large grazers, and plant community responses (Vinton et al. 1993). Recent work in PRV restorations has investigated these interactions (Helzer & Steuter 2005), but much work is still needed to understand these complex relationships. Site-specific management must be taken into account to fully understand factors influencing recovery of these systems.

A final challenge in the evaluation of restoration success was the ability to quantify structural aspects of the target system or restoration goal (Bradshaw 1996). A unique aspect of our study was the multiyear assessment across a range of restoration ages. This approach captured some of the natural interannual variation in the target natural systems and illuminated the complexity of evaluating restoration success. We observed high temporal variability in some plant cover groups in the natural wetlands. Hence, natural systems in this region were "moving targets," thereby making comparisons with restored systems (i.e., measuring "success") difficult. Additionally, other factors (e.g., precipitation) driving variability in ecosystem structure may override restoration processes. Thus, assessments should be performed for multiple years to encompass interannual variability in climate and characterize temporal variability in structure of the target system to improve adequacy of assessing restoration trajectories and success.

Implications for Practice

- Restoration efforts should consider even subtle differences in elevation.
- The influence of hydrology is likely overriding other aspects of recovery and should be a major focus of restoration efforts; enhancing soil organic matter accrual will likely positively influence plant germination and survival.

- Because of high temporal variability in plant community structure, conduct assessments within these and similar systems by including long-term sampling, particularly during periods of precipitation extremes.
- Site-specific differences in restoration effort and subsequent management may further override changes with restoration age.

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