RELATIVE CONTRIBUTIONS OF ADJACENT SPECIES SET AND ENVIRONMENTAL CONDITIONS TO PLANT COMMUNITY RICHNESS AND COMPOSITION IN A GROUP OF CREATED WETLANDS

Sharon M. Ashworth[1,3], Bryan L. Foster[1], and Kelly Kindscher[2]
[1]*Department of Ecology and Evolutionary Biology*
University of Kansas
Lawrence, Kansas, USA 66045

[2]*Kansas Biological Survey*
University of Kansas
Lawrence, Kansas, USA 66047

[3]*Present address: Environmental Studies Program*
University of Kansas
Lawrence, Kansas, USA 66045

Abstract: A major topic of discussion in community ecology is the relative influence of proximate seed sources and environmental variability on local plant species diversity. We investigated the effect of adjacent seed sources and environmental factors on initial plant species richness and composition in sixty wetland basins created in central Kansas, USA in 1998. We defined the adjacent seed source for each basin as the list of plant species found within a 10-m radius around each basin, filtered for those species capable of growing in wetland conditions. Basin water levels were monitored biweekly over three growing seasons, starting in 1999, as were soil moisture, temperature, and conductivity. Soil samples were analyzed for total nitrogen, total phosphorus, pH, and soluble salts in 2001. We found that in the three-year-old basins, the species richness of the adjacent areas had contributed significantly to basin species richness, as did basin area, soil pH, and water-level fluctuation. After three years, 61% of the species found in the adjacent areas were also found in the basins. While we found that proximate seed sources did influence initial species richness and composition in newly created wetlands, we cannot conclude that any differences in initial plant communities will ultimately result in different successional trajectories for the wetlands in our system. However, given the potential sensitivity of vegetation richness and composition in these newly created wetlands to proximate seed sources, the location of future wetland creations may need to be considered.

Key Words: Cheyenne Bottoms, colonization, Kansas, restoration, species richness, wetlands

INTRODUCTION

Numerous factors influence vascular plant diversity in wetland systems, including hydrology, salinity, nutrient availability, disturbance, and resource competition (Mitsch and Gosselink 1993). Establishing the dominant abiotic factors, in addition to hydrology, that determine the characteristics of a wetland plant community has been the subject of many papers (see for example Ovenden and Brassard 1988, Weiher and Keddy 1995, Ashworth 1997, Tsuyuzaki 1997, Dickinson and Mark 1999). As for biotic influences, the role of species competition in determining the distribution of vegetation in wetlands has been addressed specifically (Grace and Wetzel 1981, Keddy et al. 1994, Gaudet and Keddy 1995). The importance of seed source proximity for the revegetation of wetland areas (Salonen and Setälä 1992, Seabloom and van der Valk 2003) and for influencing species richness and composition in established systems (Cantero et. al. 1999) has also been examined. Borgegård (1990) found that surrounding vegetation strongly influenced vegetation in abandoned gravel pits undergoing primary succession in Sweden. Futhermore, the species pool hypothesis (Taylor et al. 1990) states that the most important determinant of plant species richness is the number of species available for local colonization (Pärtel and Zobel 1999). Stated another way, local (small scale) richness is primarily determined by the size of the regional (large scale) species pool and is independent of biotic interactions at the local level (Zobel 1997). There has been discussion in the ecological literature about the potential, possibly overriding, influence of the regional species pool on local

plant species diversity (Eriksson 1993, Pärtel et al. 1996, Zobel 1997, Pärtel and Zobel 1999). Identifying and quantifying the factors that influence wetland plant diversity are of special interest to those who seek to restore wetlands and re-establish or create particular plant communities.

In this study, we investigated the relative importance of proximate seed sources and several abiotic factors on the development of plant species richness and composition in newly created wetlands within an abandoned agricultural field. If the adjacent vegetation has an overriding effect on the development of a plant community, the location of newly created wetlands in a heterogeneously vegetated landscape is critical. Multiple pathways of plant community succession on similar sites have been attributed to proximity of a seed source (Fastie 1995). Inouye and Tilman (1988) found successional divergence over four years among grassland plots because of differing initial abundances of three dominant species. Recently, the relative influence of initial plant assemblies on subsequent plant assemblies and successional trajectories has been highlighted in debates about community assembly theory in the restoration literature (Lockwood 1997, Palmer et al. 1997, Pritchett 1997, Young et al. 2001).

In 1998, The Nature Conservancy of Kansas created seasonally flooded basins at its Cheyenne Bottoms Preserve in central Kansas, USA as part of a landscape restoration effort aimed at increasing shorebird habitat. The first phase of this restoration effort consisted of excavating 60 shallow basins in a 50-hectare, former agricultural field. The basins are topographically and environmentally distinct from the surrounding landscape. The basin seed banks were removed during excavation, and all recruitment was dependent upon dispersal from outside the basins and, in 30 of the basins, from two deliberately introduced native species. The interstitial area between the basins, the seed and propagule source, is seasonally flooded and populated with species tolerant of wet conditions (obligate to facultative). The basins provided a unique opportunity to establish and document initial conditions and, subsequently, to assess the environmental parameters and adjacent vegetation that may influence plant community development over time. We expect that environmental factors, namely hydrology, will prove more influential than adjacent vegetation. If, however, adjacent vegetation is a significant factor in establishing the initial plant community of a newly created basin, the placement of that wetland in the heterogeneously vegetated landscape becomes important. Such a finding may alter the design of future wetland complexes at Cheyenne Bottoms, specifically, and inform the placement decisions of wetland restorations in general. Establishing which factors most influence the devel-opment of a plant community is crucial for successful ecosystem restoration.

METHODS

Study Site and Data Collection

The study site is located in Barton County, Kansas (98° 41′ N. 38° 30′ W) at the Nature Conservancy's Cheyenne Bottoms Preserve. The experimental area is an abandoned agricultural field last cropped in 1995 and was, for the period of the study, dominated by *Bromus japonicus* (Thunb.), *Eriochloa contracta* (Hitchc.), *Hordeum pusilum* (Nutt.), *Hordeum jubatum* (L.), and *Aster subulatus* (Michx.). The seed bank was dominated by *Leptochloa fascicularis* (Lam.) (unpublished data). Soils at the site are somewhat poorly drained Drummond silt loams and Tabler-Drummond silt loams, with a subsoil slightly to moderately affected by sodium and soluble salts (Dodge et al. 1981). Water inputs to the site consist of both precipitation and overland, seasonal sheet flow across the study site from the NW to the SE. The experimental area is immediately surrounded by more abandoned agricultural fields, pasture, and further to the northwest (4.8 km) and south (6.4 km), by deeper marshes with large populations of *Typha domingensis* (Pers.).

In the fall of 1998, the Nature Conservancy randomly excavated sixty rectangular basins across 50 hectares of the site (Figure 1). The excavated material was piled adjacent to each basin and was not removed until the fall of 2001 after the conclusion of the study. The basins were of two sizes, three maximum depths and either transplanted with two native clonal species or not, constituting a $3 \times 2 \times 2$ factorial design (Sokal and Rohlf 1995). The shortest distance between the basins was approximately 14 m, and there may have been limited and sporadic hydrologic connections between the wetlands during seasonal rains (Rob Penner, personal communication). The basins were inundated with water before the start of the first growing season in the spring of 1999. We classified thirty of the basins as 'small,' ranging in size from 28 m² to 129 m² (average 63 m²), and thirty of the basins as 'large,' ranging in size from 193 m² to 603 m² (average 382 m²). We also classified the basins as shallow (4.6–12.1 cm deep), intermediate (12.6–17.0 cm deep), and deep (17.4–29.7 cm deep). In May 1999, we transplanted six, 26 cm² plugs of *Distichlis spicata* (L.) and *Eleocharis xyridiformes* (Fern. & Brackett), dug from visually uniform stands found near the experimental site, into fifteen large and fifteen small, randomly chosen, basins. Both species were present on the site prior to the construction of the basins. We transplanted these species in an attempt to reestablish the historic vege-

(a)

(b)

Figure 1. Small (a) and large (b) wetland basins created in 1998 at the Cheyenne Bottoms Nature Reserve in Barton County, Kansas, USA.

tative structure of these shallow basins (Zimmerman 1990) and as part of another investigation. No other deliberate seeding, planting, or soil amendments were conducted. Our study design ensured that we created all possible combinations of size, depth, and presence/absence of transplants at the site.

A team of botanists monitored the vegetation over three days in both June and September in 1999, 2000,

and 2001. Two people, walking the entire basin, re-corded each species present and visually estimated ab-solute species-specific vegetation cover for each basin; due to overlap of individual species, total cover values could exceed 100%. Nomenclature followed the Flora of the Great Plains (Great Plains Flora Association 1986), and voucher specimens were deposited in the R. L. McGregor Herbarium at the University of Kan-sas. We defined the list of species found within 10 m of the edge of the basin in June of 2000 and in June and September of 2001 as the adjacent vegetation. We only had complete data (spring and fall surveys) on the adjacent area species richness from 2001 because the interstitial area between the basins was not com-prehensively surveyed in 1999 and had been mowed in the fall of 2000 prior to sampling. The 10-m dis-tance ensured that there was no overlap between the defined adjacent areas of vegetation. We defined the importance of each species found in the basins and adjacent areas as the sum of their relative cover and relative frequency, a modification of Curtis' measure of importance (Curtis and McIntosh 1951). The list of species found within 10 m of each basin was then filtered (Zobel 1997, Pärtel and Zobel 1999) to include only those species capable of inhabiting a temporarily flooded system, defined for the purposes of this study as a plant with a wetland index number of four or less (Reed 1988).

We chose to focus on various measures of hydrol-ogy and soil condition in the basins as the most po-tentially influential environmental variables. To mea-sure these factors, we numbered and identified each basin with a steel post placed in the center of the basin and attached a staff gauge to each post to record the water level (cm) in each basin biweekly for three growing seasons (1999–2001). We also took biweekly measurements of basin soil ionic conductivity (cS/m) (a measure of soil salinity), temperature (°C), and moisture (%) one meter from the edge of each basin using an AQUATERR EC-200 soil probe. To capture the hydrologic conditions of the basins, we then cal-culated the maximum water level (cm), the mean water level (cm), and the coefficient of variation (CV) for the water level (a measure of the fluctuation in water level throughout the growing season; SD/Mean) for each year. Similarly, we summarized soil conditions sampled in each year by calculating the maximum, minimum, mean, and coefficient of variation for soil conductivity (cS/m), moisture (%), and temperature (°C). Additionally, we took soil samples from the ba-sins in July 2001 and had them analyzed for pH, total soluble salts (mS/cm) as measured by conductivity, to-tal nitrogen (ppm), and total phosphorus (ppm) at the Kansas State University Soil Testing Laboratory. Wa-ter samples were also taken from each basin in July

of 2001 and analyzed for turbidity using a Spectronic 601 spectrophotometer. We used one-way ANOVA, with Tukey HSD *post hoc* tests, to determine signifi-cant differences between means of environmental pa-rameters across basin depth categories.

Data Analyses

Influence of Adjacent Area Species Richness on Basin Species Richness. We ran a correlation analysis (Pearson correlation) between basin and adjacent area richness for 2001 and plotted $\log_{10}$ basin richness against $\log_{10}$ adjacent area richness for all basins. We accounted for any differences between transplanted and non-transplanted basins by first including a vari-able indicating whether a basin had been transplanted or not and an interaction term between transplantation and adjacent area richness. This allowed us to test if the intercept and slope of the regression line were sig-nificantly different between transplanted and non-transplanted basins. This regression indicated that nei-ther the intercept nor the slope of the regression was significantly different between transplanted and non-transplanted basins when considered individually and jointly (p = 0.729, p = 0.795, and p = 0.174, respec-tively).

Because the areas of the basins and their associated adjacent areas were not uniform, we needed to account for the species-area effect (i.e., larger basins and their associated adjacent areas were likely to have more spe-cies). A positive relationship between species richness and area could bias the results of the correlation anal-ysis between basin and adjacent area richness. To test for any effect of area, we regressed $\log_{10}$ basin richness on $\log_{10}$ basin area. Once again, we directly addressed the issue of transplantation by first including a term indicating transplant status and an interaction term in the regression equation. When considered individually and jointly, neither the intercept nor the slope of the regression was significantly different between trans-planted and non-transplanted basins. The residuals cal-culated from the regression of $\log_{10}$ basin richness on $\log_{10}$ basin area represented the variance in basin spe-cies richness that could not be explained by basin sur-face area. These residuals were then regressed on ad-jacent area richness and area in order to identify any effect generated by adjacent area richness.

Influence of Adjacent Area Species Composition on Basin Species Composition. To address the influence of adjacent area species composition on basin species composition, we determined what percentage of the species had successfully colonized the basins from the pool of adjacent species (potential seed banks within the basins had been removed with excavation). We

calculated the percentage of species from the adjacent area occurring in each basin in each year and analyzed between-year differences using repeated measures AN-OVA. This analysis indicated the degree to which basin species composition might be limited by the species composition of the pool of species immediately adjacent to the basin.

Influence of Environment on Basin Species Richness and Composition. To examine the influence of the basin environment on basin species richness and composition, we assessed how much of the variation in basin plant communities could be explained by the measured environmental factors. For this assessment, we used Canonical Correspondence Analysis (CCA) and treated spring and fall percent cover data separately. CCA is an appropriate multivariate technique for addressing questions of species-environment relationships when species show unimodal, rather than linear, responses to environmental gradients (McCune and Grace 2002). A test of three of the species with the highest importance values [sum of relative frequency and cover (Bray and Curtis 1957)] present in our system confirmed that they responded unimodally to the measured environmental factors. CCA uses two matrices, a plant community matrix of species percent cover and an environmental matrix, and tests the null hypothesis that there is no linear relationship between the matrices (McCune and Mefford 1999). We used all 60 basins for this analysis and the environmental data from 2001, the only year that water turbidity, soil total nitrogen, phosphorus, and soluble salts were sampled. We reduced the number of independent variables in the environmental matrix before running CCA by including only those variables not highly intercorrelated [variance inflation factor (VIF) > 10]. Remaining variables with skewed distributions (skew > $^\pm1$) were $\log_{10}$-transformed (McCune and Grace 2002). Soil total nitrogen, total phosphorus, and soluble salts were $\log_{10}$- transformed in an attempt to linearize non-linear relationships between plant growth and resource levels (Palmer 1993). All environmental variables were then relativized by their standard deviation. Outliers were identified, and those basins distributed further than 2.3 standard deviations from the mean of average distances among basins were removed (McCune and Grace 2002). As for the species matrix, species occurring in fewer than three basins were removed because CCA exaggerates the uniqueness of samples containing rare species (McCune and Grace 2002). All species cover values were arcsin squareroot transformed (Sokal and Rohlf 1995). Again, outlying basins were identified and removed.

Resource competition among the plant species might also have limited basin species richness, and if so, we would expect richness to decrease as total plant cover increased (Foster 2001). We used correlation analysis (Spearman's rho) to test the relationship between basin richness and total plant cover.

Regression of Basin Richness. Once we established which environmental variables were most highly correlated with species richness and composition in the basins, we included those variables as independent regressors (all $\log_{10}$-transformed with the exception of soil pH) with basin richness ($\log_{10}$-transformed) as the dependent variable. Also included as independent regressors (each $\log_{10}$-transformed) were basin surface area and adjacent area richness. Once again, we directly addressed the presence or absence of transplants by first including a term indicating transplant status and an interaction term in the regression equation. When considered individually and jointly, neither the intercept nor the slope of the regression was significantly different between transplanted and non-transplanted basins. Our system is not top-censored (Greene 1993) since basin richness can exceed adjacent area richness. Large scale (adjacent area) richness in our system does not depend upon small scale (basin) richness since the basins were constructed within an area of established vegetation. Adjacent area richness can therefore be used as an independent regressor.

Any environmental variables established as significantly related to basin species richness by the regression analysis were further analyzed for significant differences across basin depth using one-way ANOVA and between basin sizes using *t*-tests. We conducted the data analyses for this paper using PCORD (McCune and Mefford 1999), SAS (2000), and SPSS (SPSS Inc. 2000).

RESULTS

Results from Environmental Monitoring and Vegetation Surveys

All 60 basins were inundated at the start of hydrologic monitoring in March 1999. The mean of the measured environmental parameters for all three growing seasons are summarized in Table 1. The mean water level (cm), water-level variation, mean soil moisture, and soil moisture variation (%) were all significantly different (F = 66.69, 47.42, 29.52, and 13.58 respectively; df = 2, p < 0.01) between the three basin depth categories. Additionally, the basins classified as deep were significantly different than the shallow and intermediate depth basins, having higher maximum water levels, lower mean soil salinity, and lower maximum soil salinity (F = 14.41, 10.62, and 4.02 respectively; df = 2, p < 0.01). Deep basins were also significantly different than shallow basins, having lower mean tem-

Table 1. Summary of mean environmental parameters for basins of different depths over three growing seasons. Mean environmental parameters of different basin depths followed by the same letter are significantly different based on Tukey's *post hoc* tests (p < 0.05).

Basin Depth	Water Level			
	Mean (cm)	Minimum (cm)	Maximum (cm)	CV[1] (cm)
shallow	3.66[a]	0	19.15[a]	168.50[a]
intermediate	4.97[a]	0	19.68[b]	144.12[a]
deep	9.67[a]	0	26.65[ab]	106.34[a]
	Soil Salinity			
	Mean (cS/m)	Minimum (cS/m)	Maximum (cS/m)	CV (cS/m)
shallow	67.69[a]	12.04	157.39[a]	60.46
intermediate	67.93[b]	14.84	156.41[b]	57.56
deep	57.18[ab]	13.77	138.07[ab]	57.80
	Soil Moisture			
	Mean (%)	Minimum (%)	Maximum (%)	CV (%)
shallow	58.69[a]	9.98	96.21	51.60[a]
intermediate	62.26[a]	12.44	97.08	47.25[a]
deep	67.43[a]	10.80	96.87	43.33[a]
	Soil Temperature			
	Mean (°C)	Minimum (°C)	Maximum (°C)	CV (°C)
shallow	19.34[a]	9.68	26.97	43.59
intermediate	19.21	9.38	26.72	43.63
deep	19.11[a]	9.52	26.54	43.48
	pH			
shallow	7.24[bc]			
intermediate	7.39[b]			
deep	7.41[c]			
	Soluble Salts (mS/cm)			
shallow	1.02			
intermediate	1.05			
deep	0.98			
	Total Nitrogen (ppm)			
shallow	1217.96[bc]			
intermediate	1099.64[b]			
deep	1041.57[c]			
	Total Phosphorous (ppm)			
shallow	522.24			
intermediate	519.47[b]			
deep	541.88[b]			

[1] Coefficient of Variation (SD/Mean): a measure of the fluctuation in water level, soil salinity, soil moisture, and soil temperature throughout the growing season.

peratures, higher pH values, and lower total nitrogen levels (F = 3.27, 4.99, and 13.277 respectively; df = 2, p < 0.05). Basins of intermediate depth had significantly lower total phosphorous (F = 4.35, df = 2, p < 0.05) than deeper basins.

We recorded a total of 109 species over the course of three growing seasons. Ninety-one species were recorded in 2001. Fifteen of these species have a wetland index value of five and were removed from the analysis. Eighty-one percent of the species found in the adjacent areas had a wetland index value of four or less. Within the basins, the five species with the highest importance values for each sampling period (fall and spring) in 1999 were all native annual grasses and forbs, with the exception of *Rumex stenophyllus* (Ledeb.), an introduced perennial forb (Table 2a). Each of these species, again with the exception of *R. stenophyllus*, has a wetland index value of three or less. In 2001, these species remained on the list of species (spring and fall) with the highest importance values,

Table 2. The relative cover and frequency of the five most important species found in the basins (1999 and 2001) and their adjacent areas (2001).

Species	Wetland Index	Relative Cover/Frequency	
		Spring	Fall
a. Basins in 1999 (initial colonizers)			
Polygonum ramosissimum	3		
Coreopsis tinctoria	3		0.05/0.97
Eriochloa contracta	4		
Leptochloa fascicularis	1	0.18/0.97	0.19/0.85
Rumex stenophyllus	2	0.10/0.95	
Echinochloa crusgalli	2	0.04/0.93	0.15/0.82
Aster subulatus	1	0.03/0.83	0.05/0.77
Panicum dichotomiflorum	3	0.02/0.83	0.19/0.57
b. Basins in 2001			
Eleocharis xyridiformes	1	0.45/0.97	
Hordeum jubatum	2	0.14/0.98	0.38/0.90
Coreopsis tinctoria	3	0.11/0.98	0.04/0.83
Rumex stenophyllus	2		
Aster subulatus	1		
Leptochloa fascicularis	1	0.03/0.97	0.15/0.90
Echinochloa crusgalli	2	0.14/0.98	0.09/0.87
c. Adjacent areas in 2001			
Bromus japonicus	4		0.27/0.97
Hordeum pusillum	3		
Hordeum jubatum	2		
Schedonnardus paniculatus	5	0.36/0.93	0.07/0.87
Rumex stenophyllus	2	0.25/0.90	
Eriochloa contracta	4	0.07/0.88	0.26/0.97
Aster subulatus	1	0.08/0.85	0.06/0.93
Kochia scoparia	4	0.02/0.90	0.03/0.88

Figure 2. Partial plot from the regression of the regression residuals ($\log_{10}$ basin richness on $\log_{10}$ basin area) on the plant species richness and size (m^2) of the adjacent areas surrounding each of the basins ($r^2 = 0.07$, $p = 0.044$).

with the exception of *Polygonum ramosissimum* (Michx.), *E. contracta*, and *Panicum dichotomiflorum* (Michx.), which were replaced by *H. jubatum* and *E. xyridiformes*, two native perennials (Table 2b). Species with high importance values found in the adjacent areas (2001) that were not found in any significant quantity in the basins included *B. japonicus*, *H. pusillum*, and *Kochia scoparia* (L.) (Table 2c).

Results from the Data Analyses

Influence of Adjacent Area Species Richness on Basin Species Richness. Correlation analysis of basin and adjacent area plant species richness revealed that the relationship between these two factors was significant and positive (Pearson correlation = 0.358, $p = 0.005$). We also found a significant and positive relationship ($p < 0.001$, $r^2 = 0.198$) between basin species richness and basin area. Regressing the resulting residuals from that regression on adjacent area richness and area, done to remove the effect of basin area and test for
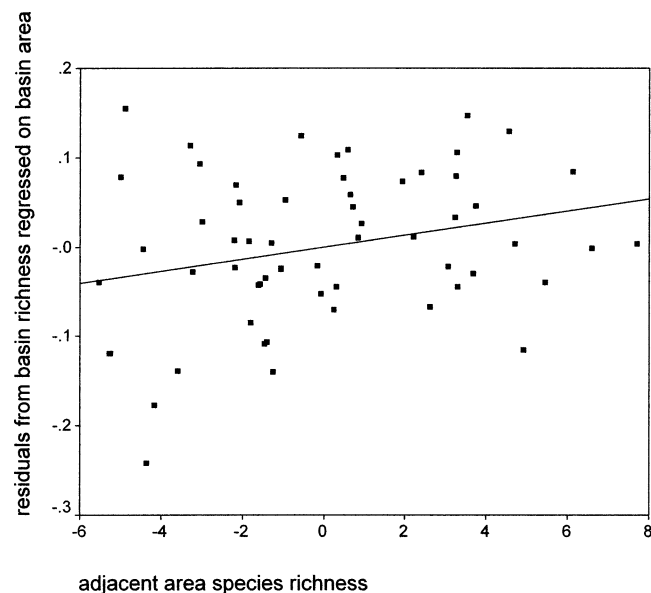
any effect of adjacent area richness, revealed a significant and positive ($p = 0.044$, $r^2 = 0.07$) relationship to adjacent area richness and no significant relationship ($p = 0.426$) to the size of the adjacent area (Figure 2).

Influence of Adjacent Area Species Composition on Basin Species Composition. The potential contribution of the adjacent area plant community to basin plant species composition was not limiting. Fifty-two percent of the species successfully colonizing the basins in 1999 were found in the adjacent areas. The species found in common increased significantly to 61% in 2001. The remaining species found in any basin are assumed to have been contributed by the remainder of the interstitial area or from the regional species pool.

Influence of Environment on Basin Species Richness and Composition. Canonical Correspondence Analysis indicated that there was a statistically significant relationship between the species (percent cover) and environmental matrices. For spring data the eigenvalue for axis 3 was significantly ($p < 0.05$) greater than or equal to that expected by chance and for the fall, eigenvalues for all 3 axes were significantly ($p < 0.05$) greater than or equal to that expected by chance. The first three axes of the CCA explained 19.9% of the total variance in spring species cover data and 24.2% of the total variance in fall species cover data for 2001. The environmental variables most highly correlated with the CCA axes in 2001 (spring and fall) were pH, maximum water level, and the coefficient of variation

Table 3. Results of the regression analysis of basin species richness on adjacent area richness, basin size, and environmental variables highly correlated with axes of the Canonical Correspondence Analysis ($r^2 = 0.572$).

Regressor	β	p
$\log_{10}$ CV[1] for water level	0.453	0.002
soil pH	−0.269	0.032
$\log_{10}$ basin area	0.286	0.017
$\log_{10}$ adjacent area richness	0.253	0.020
$\log_{10}$ soil total nitrogen	0.071	0.587
$\log_{10}$ CV for soil conductivity	0.059	0.606
$\log_{10}$ mean soil conductivity	0.167	0.227
$\log_{10}$ minimum soil conductivity	0.056	0.623
$\log_{10}$ maximum water level	0.209	0.100
$\log_{10}$ soil soluble salts	−0.232	0.069

[1] Coefficient of Variation (SD/Mean).

Table 4. Differences among basin depths and sizes for species richness and the environmental factors found to significantly influence basin species richness.

| | Mean Value for 2001 | | |
	Basin Richness	pH	CV[1]-Water Level
Basin Depth			
shallow	17.16**	7.24	154.95*
intermediate	15.48	7.39	136.84*
deep	14.20**	7.41	110.41**
Basin size			
small	14.17**	7.32	122.11**
large	17.00**	7.37	145.42**

[1] Coefficient of Variation (SD/Mean).
* Significant at $p < 0.05$, ** significant at $p < 0.01$.

(CV) of water level. These three environmental variables, as well as mean soil conductivity, CV soil conductivity, soil total nitrogen, and soil total soluble salts also highly correlated with the CCA axes, were included as independent regressors in the regression analysis of basin plant species richness. Plant species competition for resources was not likely related to basin richness because basin species richness and total plant cover were positively and significantly correlated (Spearman's rho = 0.390, p = 0.002) in 2001.

Regression of Basin Richness. Regression analysis of basin species richness on basin surface area, adjacent area richness, and selected environmental variables indicated that adjacent area richness was significantly and positively related to basin richness (p = 0.02, β = 0.253) (Table 3). Basin size and the seasonal fluctuation in water level (CV water level) were also significantly and positively related to basin plant species richness (p = 0.017, β = 0.286; p = 0.002, β = 0.453 respectively). Soil pH was significantly but negatively related (p = 0.032, β = −0.269) to basin plant species richness. Using one-way ANOVA and *t*-tests, we found that shallow basins had significantly more species (F = 4.53, df = 2, p < 0.01) than deep basins and large basins had significantly (p < 0.01) more species than small basins (Table 4). Seasonal fluctuation in water level was significantly different across basin depths (F = 13.978, df = 2, p < 0.001) and size (p = 0.019) with the shallow and large basins having a greater degree of fluctuation (there was no significant interaction between size and depth). Basin pH was not significantly different across basin depth.

DISCUSSION

Our examination of the earliest stages of this restoration suggested that the degree to which adjacent

seed and propagule sources and measured environmental variables explained variation in the initial plant species richness and composition among the basins. While we did conclude that environmental factors were influential, adjacent area species richness was also a significant factor, contrary to our expectations. Additionally, we found that species composition in a basin was not limited by the species composition of the adjacent area but that a majority of a basin's species were found in the adjacent area. We found that variation in species richness among the basins was explained by adjacent area richness, basin area, water-level fluctuations, and basin soil pH. Competition for resources did not seem to be a significant factor during this early stage of succession.

The measured environmental variables explained a maximum of 24.2% of the variation in plant communities (species presence and percent cover) among the basins according to CCA. The bulk of the explainable variation was related to a number of edaphic factors, as well as basin hydrology. The influence of hydrology on the richness and composition of wetland vegetation is well-established (Kadlec 1962, Harris and Marshall 1963, Meeks 1969, Mitsch and Gosselink 1993). In our system, the degree of seasonal fluctuation in basin water levels proved to be a more significant factor in determining species richness than maximum basin water levels according to our regression analysis. This can be expected, since alternating dry and wet conditions can allow a greater diversity of species to exist at a site (Mitsch and Gosselink 1993). Soil conditions in wetlands, such as salinity (Ungar 1965), nutrient availability, pH, and moisture (Polley and Collins 1984), have also been found to influence plant community structure. Although CCA found a number of soil factors to be significantly related to variation in the basin plant communities, pH proved to be the only significant edaphic factor in the regression with species richness. While Glaser et. al. (1990) found plant spe-

cies richness to increase with increasing soil water pH in surveys of a peatland in Minnesota, USA, there was a peak in species richness at pH levels of 6.5 to 7. The pH values in the basins of our system range from 6.5 to 7.9, and species richness is negatively correlated with these higher pH values, a finding supported by Pärtel's (2002) overview of the relationship between soil pH and plant species richness. At pH extremes, Pärtel found that physiological tolerance has a local effect on species richness (i.e., there is lower richness at pH extremes). Most of the variation in the plant communities examined for this study remained unexplained and may be attributed to unmeasured abiotic variables, unmeasured biotic factors, the fact that these are young systems still undergoing transient dynamics, and according to our analysis, the species richness of the adjoining areas.

The significance of these findings for wetland restoration at Cheyenne Bottoms is that, for basins created in a heterogeneous old field, the location of the basins may result in different initial plant communities based on the species found adjacent to the basin. Borgegård (1990), Salonen and Setälä (1992), Cantero et. al. (1999), and Seabloom and van der Valk (2003) all found that adjacent or local vegetation was a significant factor in determining the plant species richness and composition in their target communities. These differences were sustained over the course of several years. Differing initial species composition in similar ecosystems may ultimately result in divergent successional trajectories, as Inouye and Tilman (1988) and Fastie (1995) found. However, we cannot conclude that any differences in initial plant communities will ultimately result in different successional trajectories for the wetlands in our system. Unlike Seabloom and van der Valk (2003), who found that dispersal limitation was the primary cause of vegetative differences between restored and natural wetlands, there appear to be no barriers to wind or water dispersal in our system. Consequently, species access to the basins is likely not limited and the ultimate configuration of species diversity in the basins is likely to be determined by environmental factors. Hatton and West (1987) and Myster and Pickett (1990), for example, found that while the early successional trajectories of their respective surface mine and abandoned agricultural fields varied according to initial floristic conditions (and time of abandonment in the case of the agricultural fields), such variation affected the rate of convergence but not the ultimate outcome of site species composition. Further examination of a maturing Cheyenne Bottoms wetland complex is necessary to reach any conclusions about the drivers of succession in this system.

Despite the limitations of studying such a young system, we can make some observations that may in-

form future wetland restoration projects in general and those planned for Cheyenne Bottoms specifically. Evaluations of restoration success are often made within the first five years and are generally based solely on plant community composition (Zedler et al. 2001). Given the potential sensitivity of vegetation richness and composition in newly created wetlands to proximate seed sources and the uncertainty of how this will impact future community development, it is premature to judge the success of restoration or creation projects based solely on vegetation within the initial years of development. The appropriate time frame, necessarily, will depend upon the unique circumstances and goals of each project. In the case of the restoration project at Cheyenne Bottoms, if maximizing plant species richness is a desirable feature, future wetland construction activities should include excavating shallow (4–17 cm) basins with larger surface areas. It may also be advisable to locate future basins in proximity to desired vegetation if transplanting of preferred vegetation proves to be of limited success or is limited by available resources.

The establishment of desired plant communities in restored systems is critical for attaining compliance with restoration goals. Moreover, ''understanding what regulates diversity is central for guiding strategies for habitat preservation, and for restoration ecology'' (Lubencho et al. 1991). Further research should evaluate the impact that alternative initial plant communities and environmental variability might have on the successional development of these and other restored systems.

ACKNOWLEDGMENTS

LITERATURE CITED

Ashworth, S. M. 1997. Comparison between restored and reference sedge meadow wetlands in south-central Wisconsin. Wetlands 17: 518–527.

Borgegård, S. O. 1990. Vegetation development in abandoned gravel pits; effects of surrounding vegetation, substrate and regionality. Journal of Vegetation Science 1:675–682.

Bray, R. J. and J. T. Curtis. 1957. An ordination of the upland forest

communities of southern Wisconsin. Ecological Monographs 27: 325–349.

Cantero, J. J., M. Pärtel, and M. Zobel. 1999. Is species richness dependent on the neighbouring stands? An analysis of the community patterns in mountain grasslands of central Argentina. Oikos 87:346–354.

Curtis, J. T. and R. P. McIntosh. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology 32:476–496.

Dickinson, K. J. M. and A. F. Mark. 1999. Interpreting ecological patterns in an intact estuary, South-West New Zealand World Heritage Area. Journal of Biogeography 26:913–932.

Dodge, D. A., W. A. Wehmueller, B. R. Hoffman, and T. D. Grimwood. 1981. Soil survey of Barton County, Kansas. USDA Soil Conservation Service, Manhattan, KS, USA.

Eriksson, O. 1993. The species-pool hypothesis and plant community diversity. Oikos 68:371–374.

Fastie, C. L. 1995. Causes and ecosystem consequences of multiple pathways of primary succession at Glacier Bay, Alaska. Ecology 76:1899–1916.

Foster, B. L. 2001. Constraints on colonization and species richness along a grassland productivity gradient: the role of propagule availability. Ecology Letters 4:530–535.

Gaudet, C. L. and P. A. Keddy. 1995. Competitive performance and species distribution in shoreline plant communities: a comparative approach. Ecology 76:280–291.

Glaser, P. H., J. A. Janssens, and D. I. Siegel. 1990. The response of vegetation to chemical and hydrological gradients in the Lost River Peatland, Northern Minnesota. The Journal of Ecology 78: 1021–1048.

Grace, J. B. and R. G. Wetzel. 1981. Habitat partitioning and competitive displacement in cattails (*Typha*): experimental field studies. The American Naturalist 118:463–474.

Great Plains Flora Association. 1986. Flora of the Great Plains. University Press of Kansas, Lawrence, KS, USA.

Greene, W. H. 1993. Econometric Analysis. Prentice Hall, Englewood Cliffs, NJ, USA.

Harris, S. W. and W. H. Marshall. 1963. Ecology of water-level manipulations on a northern marsh. Ecology 44:331–343.

Hatton, T. J. and N. E. West. 1987. Early seral trends in plant community diversity on a recontoured surface mine. Vegetatio 73:21–29.

Inouye, R. S. and D. Tilman. 1988. Convergence and divergence of old-field plant communities along experimental nitrogen gradients. Ecology 69:995–1004.

Kadlec, J. A. 1962. Effects of a drawdown on a waterfowl impoundment. Ecology 43:267–281.

Keddy, P. A., L. Twolan-Strutt, and I. C. Wisheu. 1994. Competitive effect and response ranking in 20 wetland plants: are they consistent across three environments? Journal of Ecology 82:635–643.

Lepš, J. 2001. Species-pool hypothesis: limits to its testing. Folia Geobotanica 36:45–52.

Lockwood, J. L. 1997. An alternative to succession: assembly rules offer guide to restoration efforts. Restoration & Management Notes 15:45–50.

Lubchenco, J., A. M. Olson, L. B. Brubaker, S. R. Carpenter, M. M. Holland, S. P. Hubbell, S. A. Levin, J. A. MacMahon, P. A. Matson, J. M. Melillo, H. A. Mooney, C. H. Peterson, H. R. Pulliam, L. A. Real, P. J. Regal, P. G. Risser. 1991. The Sustainable Biosphere Initiative: an ecological research agenda: a report from the Ecological Society of America. Ecology 72:371–412.

McCune, B. and J. B. Grace. 2002. Analysis of Ecological Communities. MjM Software Design, OR, USA.

McCune, B. and M. J. Mefford. 1997. PC-ORD. Multivariate Analysis of Ecological Data, version 3.0. MjM Software Design, OR, USA.

Meeks, R. 1969. The effect of drawdown date on wetland plant succession. Journal of Wildlife Management 33:817–821.

Mitsch, W. J. and J. G. Gosselink. 1993. Wetlands, second edition. Van Nostrand Reinhold, New York, NY, USA.

Myster, R. W. and S. T. A. Pickett. 1990. Initial conditions, history and successional pathways in ten contrasting old fields. American Midland Naturalist 124:231–238.

Ovendum, L. and G. R. Brassard. 1988. Wetland vegetation near Old Crow, northern Yukon. Canadian Journal of Botany 67:954–960.

Palmer, M. W. 1993. Putting things in even better order: the advantages of canonical correspondence analysis. Ecology 74:2215–2230.

Palmer, M. A., R. F. Ambrose, and N. L. Poff. 1997. Ecological theory and community restoration ecology. Restoration Ecology 5:291–300.

Pärtel, M. 2002. Local plant diversity patterns and evolutionary history at the regional scale. Ecology 83:2361–2366.

Pärtel, M. and M. Zobel. 1999. Small-scale plant species richness in calcareous grasslands determined by the species pool, community age and shoot density. Ecography 22:153–159.

Pärtel, M., M. Zobel, K. Zobel, and E. vander Maarel. 1996. The species pool and its relation to species richness: evidence from Estonian plant communities. Oikos 75:111–117.

Polley, H. W. and S. L. Collins. 1984. Relationships of vegetation and environment in buffalo wallows. American Midland Naturalist 112:178–186.

Pritchett, D. A. 1997. Maybe, sometimes: a practitioner replies. Restoration & Management Notes 15:51.

Reed, P. B. Jr. 1988. National list of plant species that occur in wetlands: Central Plains (Region 5). U.S. Fish and Wildlife Service, National Wetlands Inventory, Washington, DC, USA. Biological Report 88.

Salonen, V. and H. Setälä. 1992. Plant colonization of bare peat surface—relative importance of seed availability and soil. Ecography 15:199–204.

SAS Inc. 2000. SAS user's guide version 8.1, Cary, NC, USA.

Seabloom, E. W. and A. G. van der Valk. 2003. Plant diversity, composition and invasion of restored and natural prairie pothole wetlands: implications for restoration. Wetlands 23:1–12.

Sokal, R. R. and F. J. Rohlf. 1995. Biometry. W.H. Freeman and Company, New York, NY, USA.

SPSS Inc. 2000. SPSS release 10.0. Chicago, IL, USA.

Taylor, D. R., L. W. Aarsen, and C. Loehle. 1990. On the relationship between r/K selection and environmental carrying capacity: a new habitat template for plant life history strategies. Oikos 58: 239–250.

Tsuyuzaki, S. 1997. Wetland development in early stages of volcanic succession. Journal of Vegetation Science 8:353–360.

Ungar, I. A. 1965. An ecological study of the vegetation of the Big Salt Marsh, Stafford County, Kansas. University of Kansas Science Bulletin 46:1–99.

Young, T. P., J. M. Chase, and R. T. Huddleston. 2001. Community succession and assembly: comparing, contrasting and combining paradigms in the context of ecological restoration. Ecological Restoration 19:5–18.

Zedler, J. B. (ed). 2001. Compensating for Wetland Losses Under the Clean Water Act. National Academy of Sciences, National Academy Press, Washington, DC, USA.

Zimmerman, J. L. 1990. Cheyenne Bottoms: Wetland in Jeopardy. University Press of Kansas, Lawrence, KS, USA.

Zobel, M. 1997. The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence? TREE 12:266–269.

Appendix A. Plant species present in the basins and adjacent areas across a wetland creation site at Cheyenne Bottoms Wetland Preserve in central Kansas. The number of basins or adjacent areas in which an individual species was found is given.

Species	Basins 1999		Basins 2001		Adjacent areas 2001	
	Spring	Fall	Spring	Fall	Spring	Fall
Achillea millefolium L.	0	0	0	0	16	13
Aegilops cylindrica Host	3	0	0	0	8	0
Agropyron intermedium (Host) Beauv.	0	0	0	0	1	2
Agropyron smithii Rydb.	11	8	23	22	44	42
Agrostis hyemalis (Walt.) B. S. P.	0	0	0	0	0	0
Alopecurus carolinianus Walt.	2	1	7	0	1	0
Amaranthus blitoides S. Wats.—Rydberg	1	1	1	3	0	1
Amaranthus rudis Sauer	9	0	0	0	0	1
Ambrosia artemisiifolia L.	3	0	0	1	0	0
Ambrosia grayi (A. Nels.) Shinners	0	1	1	1	1	1
Ambrosia psilostachya DC.	13	8	20	21	32	32
Ammannia coccinea Rottb.	41	42	9	12	0	0
Andropogon saccharoides Sw.	0	0	0	0	0	1
Apocynum cannabinum L.	1	1	1	1	4	1
Aristida oligantha Michx.	0	0	0	1	0	6
Asclepias speciosa Torr.	0	0	0	0	6	5
Asclepias verticillata L.	0	1	1	2	11	21
Aster ericoides L.	4	5	9	13	53	53
Aster subulatus Michx.	46	46	59	59	51	56
Atriplex argentea Nutt.	0	0	0	0	0	5
Atriplex subspicata (Nutt.) Rydb.	6	2	1	0	1	4
Baccharis salicina T. & G.	1	0	0	0	0	1
Bacopa rotundifolia (Michx.) Wettst.	1	0	1	0	0	0
Bromus inermis Leyss.	0	0	0	0	2	2
Bromus japonicus Thunb.	21	18	28	21	56	58
Buchloë dactyloides (Nutt.) Engelm.	1	0	1	2	17	35
Carex brevior (Dew.) Mack.	0	0	0	1	5	4
Chenopodium pratericola Rydb.	24	2	0	2	34	7
Cirsium vulgare (Savi) Ten.	1	0	0	0	2	3
Convovulus arvensis L.	1	1	1	1	1	2
Conyza canadensis (L.) Cronq.	2	0	0	0	17	10
Conyza ramosissima Cronq.	2	0	0	0	3	0
Coreopsis tinctoria Nutt.	57	58	59	46	50	36
Cyperus acuminatus Torr. & Hook.	14	35	17	24	1	2
Cyperus esculentus L.	1	7	0	0	1	4
Descurainia pinnata (Walt.) Britt.	1	0	0	0	0	0
Desmanthus illinoensis (Michx.) MacM.	1	0	0	0	0	0
Distichlis spicata (L.) Greene	11	33	38	33	30	13
Echinochloa crusgalli (L.) Beauv.	28	49	27	52	5	35
Eleocharis xyridiformes Fern. & Brackett	29	41	58	54	27	11
Elymus canadensis L.	0	0	2	0	6	2
Elymus virginicus L.	0	0	0	2	0	0
Eragrostis cilianensis (All.) E. Mosher	0	0	0	0	0	3
Erigeron annuus (L.) Pers.	0	0	1	0	3	0
Erigeron strigosus Muhl.	0	0	0	0	6	0
Eriochloa contracta Hitchc.	56	40	3	32	2	58
Euphorbia geyeri Engelm.	16	19	0	18	0	13
Euphorbia marginata Pursh	4	3	1	1	4	13
Happlopappus ciliatus (Nutt.) DC.	8	3	12	20	37	50
Helianthus annuus L.	10	9	6	12	32	43
Heliotropium curassavicum L.	0	0	0	0	0	1

Appendix A. Continued.

Species	Basins 1999		Basins 2001		Adjacent areas 2001	
	Spring	Fall	Spring	Fall	Spring	Fall
Hibiscus trionum L.	3	1	0	0	0	3
Hordeum jubatum L.	41	24	59	50	53	29
Hordeum pusillum Nutt.	48	1	49	9	54	32
Ipomoea hederacea Jacq.	0	1	0	0	0	0
Iva annua L.	5	3	4	11	4	16
Juncus interior Wieg.	0	0	0	1	11	9
Kochia scoparia (L.) Schrad.	33	18	2	6	34	53
Lactuca ludoviciana (Nutt.) Ridd.	0	0	0	0	1	0
Lactuca serriola L.	0	0	0	1	37	26
Lepidium densiflorum Schrad.	36	1	4	2	25	5
Leptochloa fascicularis (Lam.) A. Gray	50	51	40	54	5	22
Lythrum californicum T. & G.	0	0	0	0	5	0
Marsilea vestita Hook. & Grev.	1	3	3	2	0	0
Medicago sativa L.	9	4	2	3	53	37
Melilotus alba Medic.	0	0	1	0	8	2
Melilotus officinalis (L.) Pall.	1	0	0	1	19	3
Mollugo verticillata L.	12	0	0	1	0	0
Oenothera albicaulis Pursh	7	0	1	0	0	0
Oenothera laciniata Hill	3	0	0	0	0	0
Opuntia macrorhiza Engelm.	0	0	0	0	1	1
Oxalis dillenii Jacq.	1	1	0	0	0	0
Panicum dichotomiflorum Michx.	16	34	0	20	0	33
Physalis longifolia Nutt.	8	5	3	1	9	14
Plantago elongata Pursh	7	0	1	0	2	0
Poa arida Vasey	1	0	5	5	46	38
Polygonum bicorne Raf.	6	4	1	1	2	2
Polygonum ramosissimum Michx.	58	41	45	45	24	45
Populus deltoides Marsh.	2	5	3	2	1	1
Portulaca oleracea L.	13	9	0	0	0	1
Quincula lobata (Torr.) Raf.	0	1	0	0	0	0
Rorippa sinuata (Nutt.) Hitchc.	20	16	18	3	2	0
Rumex stenophyllus Ledeb.	50	36	58	50	54	53
Salix nigra Marsh.	0	0	1	0	0	0
Schedonnardus paniculatus (Nutt.) Trel.	15	15	6	30	51	52
Scirpus pendulus Muhl.	0	0	0	1	0	0
Setaria glauca (L.) Beauv.	0	2	0	0	0	7
Solidago canadensis L.	0	0	0	0	1	1
Sporobolus airoides (Torr.) Torr.	1	0	0	0	22	18
Sporobolus asper (Michx.) Kunth	0	0	0	0	0	12
Sporobolus cryptandrus (Torr.) A. Gray	0	7	1	0	3	7
Sporobolus pyramidatus (Lam.) Hitchc.	0	0	0	4	19	35
Sporobolus vaginiflorus (Torr. ex Gray) Wood	0	0	0	0	0	9
Suaeda depressa (Pursh) S. Wats.	0	1	0	0	0	0
Taraxacum officinale Weber	6	3	0	0	6	0
Tragopogon dubius Scop.	0	0	1	0	12	0
Triticum aestivum L.	1	0	0	0	0	0
Typha domingensis Pers.	10	13	13	12	0	0
Verbena bipinnatifida Nutt.	1	0	0	0	0	0
Verbena bracteata Lag. & Rodr.	1	0	0	0	0	0
Veronica peregrina L.	3	0	16	0	4	0
Xanthium strumarium L.	10	11	11	15	8	13