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LOCATED ON RESTORED AND NATIVE PRAIRIE**

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Abstract

This study evaluated the biological and functional characteristics of restored and native Prairie Pothole Region (PPR) wetlands. The biological characteristics of study sites were evaluated through extensive analyses of the wetland and upland plant community composition using the Index of Plant Community Integrity (IPCI) approach, a transect method, and a Floristic Quality Index (FQI). Functional characteristics of the wetland ecosystems were evaluated using the Hydrogeomorphic (HGM) approach. Statistical analyses employed Nonmetric Multidimensional Scaling ordination and Multi-Response Permutation Procedure. The statistical analyses of the biological characteristics of the wetland ecosystems yielded several significant differences between native and restored ecosystems. Interestingly, the statistical analyses of the functional characteristics of the wetland ecosystems yielded contradictory results. All of the ecosystems evaluated in this study were found to function at relatively high capacities based on the HGM model reference standards. The inconsistent results of the statistical analyses of the biological and functional datasets indicate that biologically distinct ecosystems may be functionally very similar. Also, the discrepancies between the HGM approach and the biological approaches indicate that the HGM approach may overlook certain relationships that the biological methods are more appropriate for detecting.

Acknowledgements

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Introduction

The wetlands and grasslands of the PPR perform many diverse and valuable functions that serve to benefit humans, wildlife, and livestock. Examples of services performed by PPR wetlands include: the provision of habitat and forage for wildlife and livestock; the maintenance or improvement of water quality; recharge of aquifers; and flood attenuation (Burbridge 1994; Kirby et al 2002a,b). Prairie Pothole Region wetland functions are dependent on the composition and condition of the wetland plant community (Seabloom and van der Valk 2003a). Thus, anthropogenic impacts to PPR wetlands and their adjacent uplands, in concert with the alteration of environmental conditions, have limited the ability of PPR wetlands to perform valuable functions (Kantrud and Newton 1996).

Historically, the PPR existed as a complex of wetland and prairie ecosystems, with wetlands comprising 20% to 60% of the landscape (Seabloom and van der Valk 2003b). Currently, the PPR is dominated by agricultural land-uses (Schumacher and Rickerl 2004) and wetland and prairie ecosystems have been lost throughout the PPR due

to their direct conversion to agricultural systems. Remaining PPR wetlands and native prairie patches have become isolated within a matrix of agricultural lands and are thus impacted by adjacent land-use and management practices. In the past few decades, laws that effectively call for the improvement of both prairie and wetland ecosystem conditions throughout the PPR have been enacted. These laws, mainly the Clean Water Act and the Food Security Act which contained the Conservation Reserve Program and the Wetland Conservation Provision, have sparked conservation and restoration efforts throughout the PPR.

Wetland and prairie ecosystems have been restored throughout the PPR in order to improve the amount of natural services performed by PPR ecosystems and to increase the benefits received from natural systems. There are many benefits associated with prairie and wetland restoration including the preservation or improvement of biodiversity; habitat improvement or replacement; reduced erosion; improved water, sediment, and nutrient cycles; improved water quality; decreased risk of flood damage; increased recreational opportunities; improved weed control; and the detoxification of polluted areas (Mitsch et al. 1998; Zedler 2000; Blumenthal et al. 2003, Blumenthal et al. 2005).

Wetland restorations in the PPR have generally focused on restoring the physical characteristics of a wetland rather than the biotic components (Galatowitsch and van der Valk 1996a, b; Seabloom and van der Valk 2003a, b). In the PPR it is commonly believed that wetland plant communities will quickly reestablish themselves after hydrologic functions have been restored. Thus, there have been few attempts to return native plant species to restored wetlands. It has been found that the restoration of the abiotic components of a wetland in the southern PPR, without any attempt to return

native species to a wetland, often results in wetland plant communities that are distinct from those found in native wetlands in the same area (Galatowitsch and van der Valk 1996a; Seabloom and van der Valk 2003a, b). Since the composition and structure of restored wetland plant communities may be distinct from their native counterparts, it is likely that the restored wetlands may not function at the same level as undisturbed native wetlands.

Objectives

The specific objectives of this study include:

- 1) Evaluate plant community composition of prairie pothole wetlands and their adjacent uplands.
- 2) Compare the plant community composition of native and restored sites.
- 3) Determine the functional capacity of native and restored wetland ecosystems.
- 4) Relate ecosystem structure and function to plant community composition.

Methods and Analysis

Study area

This study was conducted during 2006 and 2007 on wetlands located at the Tewaikon National Wildlife Refuge near Cayuga in Sargent County, ND and at the Lostwood National Wildlife Refuge near Bowbells in Burke County, ND (Figure 1). Wetlands were selected based on wetland classification (according to Stewart and Kantrud 1971) and suitability for the study. Wetlands located within previously cropped areas of each NWR that had undergone restoration were selected for this study, as were wetlands located within the native (never cropped) areas of each NWR.

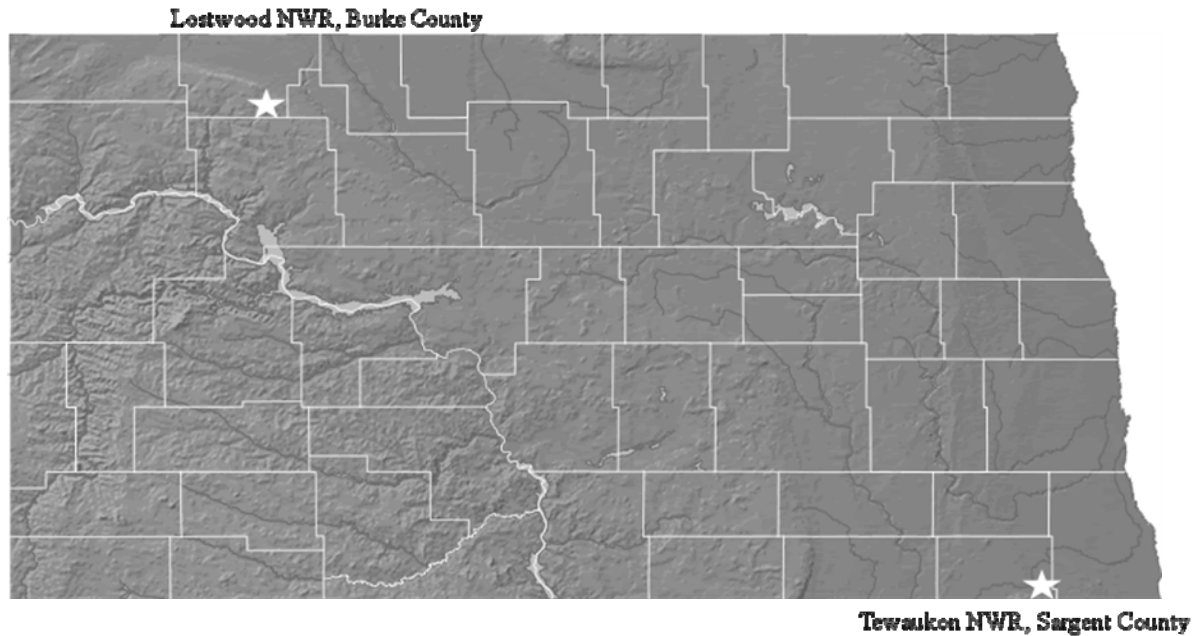


Figure 1. Map of North Dakota showing the location of Lostwood National Wildlife Refuge and Tewaukon National Wildlife Refuge.

A total of 18 temporary, seasonal, and semi-permanent wetlands were included in this study. Nine wetlands were selected at both Tewaukon NWR and Lostwood NWR. Of the nine total wetlands at each NWR, seven were located within restored areas while two were located within native areas. At Tewaukon NWR and Lostwood NWR, three restored temporary wetlands, three restored seasonal wetlands, and one restored semi-permanent wetland were selected for inclusion in this study. Two native wetlands from each NWR, one seasonal and one temporary, were also included in this study. All nine of the wetlands located at Tewaukon NWR were assessed during the summer of 2006. At Lostwood NWR, the seven restored wetlands were assessed during the summer of 2006, while the two native wetlands were assessed during the summer of 2007. The upland area of each wetland site was assessed during the summer of 2007.

This study was conducted in two ecoregions of North Dakota. Tewaukon NWR is located within the Northern Glaciated Plains Ecoregion (NGP), while Lostwood NWR is located within the Northwestern Glaciated Plains Ecoregion (NWGP) (Bryce et al. 1998). Bryce et al. (1998) characterize the NGP as having a flat to gently rolling landscape composed of glacial drift, and possessing fertile till soil. The NGP has a sub-humid climate; agricultural success is thus subject to climatic fluctuations (Bryce et al. 1998). The potential native vegetation for the NGP is transitional between tallgrass prairie to the east and mixed grass prairie to the west. The NGP typically has a high concentration of temporary and seasonal wetlands, providing favorable conditions for duck nesting and migration. The dominant land-use for the sub-ecoregion in which Tewaukon NWR is located is the cultivation of crops (small grains) or hay (Bryce et al. 1998).

Bryce et al. (1998) characterize the NWGP as a morainal landscape with significant surface variation and a high concentration of wetlands. The NWGP marks the westernmost extent of glaciation in the continental United States. Land use in the NWGP is transitional between intensive dryland agriculture to the east and extensive cattle ranching and farming to the west. The dominant land-uses for the sub-ecoregion in which Lostwood NWR is located are cattle grazing and haying, although flatter areas are cultivated (Bryce et al. 1998).

Sampling techniques

The wetland vegetation at each site was evaluated using the Index of Plant Community Integrity (IPCI) method, following DeKeyser et al. 2003 and Hargiss et al. 2008. Following this method, 8 1 m² quadrats were distributed evenly throughout the center of the low prairie zone, 7 throughout the wet meadow zone, and 5 each throughout

the shallow marsh and deep marsh zones (Figure 2). For the wetlands sampled in 2006, 15 total quadrats were sampled in each temporary wetland, 20 in each seasonal wetland, and 25 in each semi-permanent wetland. The IPCI for the two native wetlands at Lostwood NWR was completed during the summer of 1999 during the development of the IPCI method. In order to ensure sample size adequacy, 15 1 m² quadrats were sampled in each zone, resulting in 30 total quadrats for the temporary wetland and 45 total quadrats for the seasonal wetland.

Plant species found within the 1 m² quadrats were recorded as primary species and assigned a modified Daubenmire (1959) cover class (Table 1). Since the 1 m² IPCI quadrats are much larger than the standard 0.1 m² Daubenmire quadrats, an additional cover class was created for use with the IPCI method. Species found outside the quadrats were recorded as secondary species although no cover classes were assigned. Additional data collected at each quadrat include litter thickness, water depth, percent standing dead, and percent bare ground or open water.

The Hydrogeomorphic (HGM) model adapted for the Northern Great Plains was conducted at each wetland site in order to assess the level of ecosystem function. Data collected at each wetland site included soil information, land-use characteristics, wetland and catchment perimeter and area, buffer zone characteristics, and average litter depth. The HGM model utilizes the physical and landscape data collected in the field, along with additional GIS and management information to assess the level of function performed at each wetland site relative to a reference standard.

Several functions are assessed by the HGM model through the use of a Functional Capacity Index (FCI). The FCI of a wetland ranges from 0.0-1.0 and measures the level

of function of a wetland relative to a reference standard (Gilbert et al. 2006). An FCI of 1.0 indicates that the evaluated wetland performs the function at a level equivalent to that of the reference wetland, while an FCI lower than 1.0 indicates that the evaluated wetland performs the function at a lower level than the reference wetland.

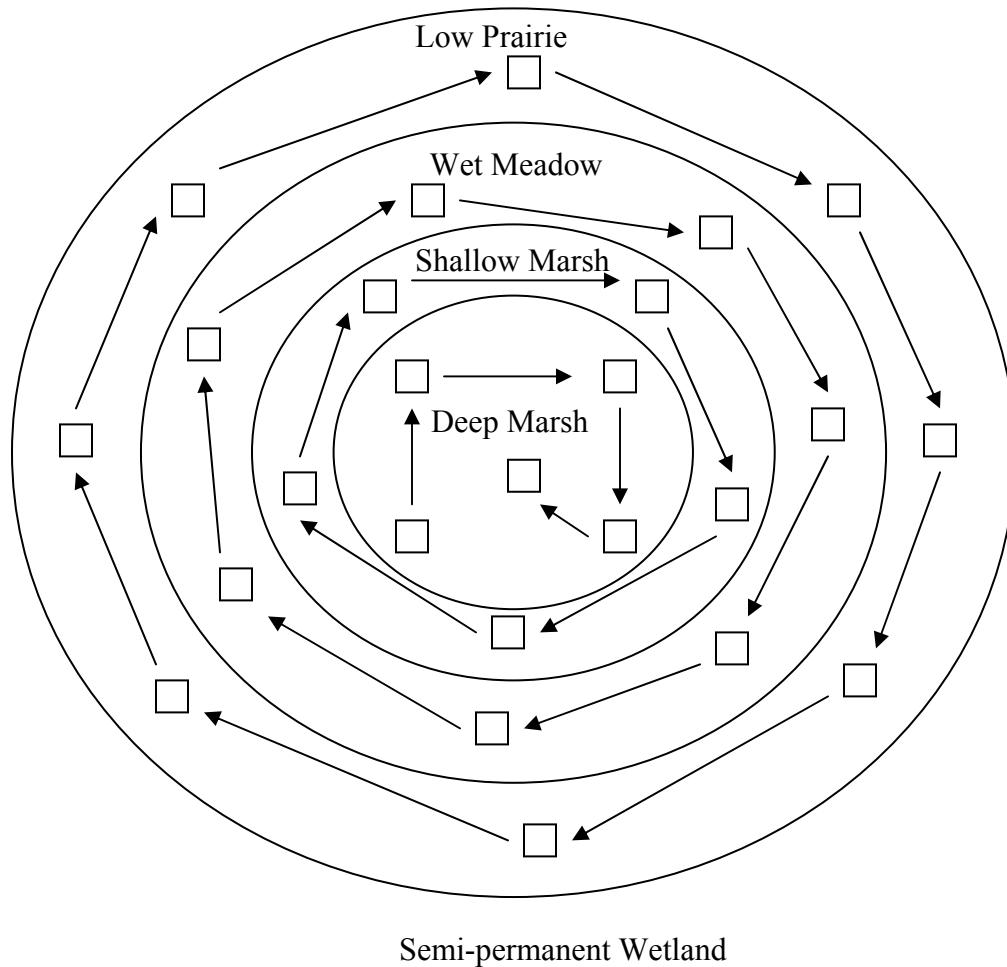


Figure 2. Index of Plant Community Integrity 1 m² quadrat distribution for a semi-permanent wetland.

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1.0 indicates that the evaluated wetland performs the function at a level equivalent to that of the reference wetland, while an FCI lower than 1.0 indicates that the evaluated wetland performs the function at a lower level than the reference wetland.

Table 1. Daubenmire (1959) and Index of Plant Community Integrity (DeKeyser et al. 2003) cover classes utilized for 0.1 m² and 1 m² quadrats.

Daubenmire Cover Class	Class Boundaries (%)	IPCI Cover Class	Class Boundaries (%)
1	0-5	1	0-1
2	5-25	2	1-5
3	25-50	3	5-25
4	50-75	4	25-50
5	75-95	5	50-75
6	95-100	6	75-95
		7	95-100

A Floristic Quality Index (FQI) was used in order to measure and to directly compare the overall floristic quality of the various plant communities evaluated in this study. The FQI is dependent on the identification of native plant species within the study area; thus, the vegetation data collected for the IPCI and upland transect methods were used to calculate the FQI for each plant community. This study used the FQI method developed by the Northern Great Plains Floristic Quality Assessment Panel (NGPFQAP 2001). The NGPFQAP assigned a coefficient of conservatism (C value) to each native plant species typically encountered throughout the Northern Great Plains Region. Non-native species are not assigned C values and are not used in FQI calculations. C values range from 0 to 10; 0 is assigned to native plants able to flourish in highly disturbed or degraded sites, while 10 is assigned to native plants limited to the most undisturbed, and purely native sites. Plants assigned C values ranging from 1-4 are found in natural areas, but are also able to tolerate highly degraded habitats. Plants with a C-value ranging from

5-9 are usually found in natural areas and have a decreasing tolerance to disturbance.

The FQI for a plant community is calculated by determining the average C value of the native species present and multiplying that number by the square root of the number of native species present. Non-native species are not utilized in the calculation of the FQI.

Data analysis

The vegetation data for each wetland site were divided into four subsets: wetland (including the wet meadow, shallow marsh, and deep marsh zones); low prairie; mid-slope; and top-slope. These subsets were chosen to represent a gradient of landscape positions, recognizing that plant community composition and structure is reflective of landscape position. For the statistical analysis of the vegetation data, each site was described by location (Tewaukon NWR or Lostwood NWR) and land use history (restored or native). The same descriptions were applied to the analysis of all subsets of the data.

As part of the Index of Plant Community Integrity (IPCI) method, nine metric values were calculated for each wetland site (DeKeyser et al. 2003; Hargiss et al. 2008). Metric values were determined based on the plant community data collected at each quadrat. A score for each of the nine metrics was determined for the wetland sites based on the range of values developed by Hargiss et al. 2008. The nine scores for the individual metrics were then added to produce a total IPCI score for each wetland site. Potential IPCI scores for an individual wetland range from 0 to 99, with 99 representing the most ideal condition for PPR wetland plant communities.

IPCI scores were compared using the Multiresponse Permutation Procedure (MRPP) (Mielke and Berry 2001). MRPP for the IPCI data was conducted in PC-Ord,

using the Euclidian distance measure at a significance level of $p < 0.05$. The Hochberg procedure for multiple comparisons was used since the p-values from the pair-wise comparisons of the MRPP are not corrected for multiple comparisons (Legendre and Legendre 1998). The Hochberg procedure applied in this study was implemented in the PROC MULTTEST SAS software procedure, Version 9.1.3 of the SAS System for Windows (Copyright © 2000-2004 SAS Institute Inc. SAS and all other SAS Institute Inc. product or service names are registered trademarks or trademarks of SAS Institute Inc., Cary, NC, USA).

Six Functional Capacity Index (FCI) scores were calculated for each wetland site following the HGM approach. The FCI scores were then compared by MRPP in PC-Ord, using the Euclidian distance measure (and the Hochberg procedure in SAS), in order to determine significant differences in the six functional capacities of the different wetland types included in this study. In addition to the comparison of the six FCI scores for each wetland, each FCI was also considered individually in order to determine the effects of restoration on various wetland functions. Functional capacity indexes were compared at the $p < 0.05$ level.

The vegetation datasets were analyzed using Nonmetric Multidimensional Scaling (NMS) (Mather 1976) in PC-Ord. For the NMS analysis of each dataset, the Sorensen (Bray-Curtis) distance measure was used (McCune and Grace 2002). User-supplied random numbers were employed in the starting configurations. Fifty runs were conducted using real data. Five hundred randomized runs were conducted. Final solutions were selected for low final stress and final instability. MRPP was then used to

test for significant differences ($p < 0.05$) between sites as described by location and land-use history using the Sorenson (Bray-Curtis) distance measure.

Lists of native species encountered during the evaluation of the plant communities included in this study were compiled in order to determine the FQI of each site. An FQI was calculated for the entire ecosystem at each study site, including all the native plant species encountered within the wetland, low prairie, mid-slope and top-slope areas. In addition, an FQI was calculated separately for the wetlands (including the wet meadow, shallow marsh, and deep marsh zones) and the uplands (including the low prairie, mid-slope, and top-slope areas). FQIs were compared by MRPP in PC-Ord using the Euclidian distance measure at the $p < 0.05$ significance level (McCune and Grace 2002).

Results

Wetland

The IPCI scores for the wetlands included in this study ranged from 0 to 95, indicating that there was wide variability in the condition of the various plant communities of the wetlands sampled (Table 2). When the IPCI scores for each wetland were compared using MRPP in PC-Ord, two significant differences were found ($p < 0.05$) (Table 3). The IPCI scores of restored wetlands at Tewaukon NWR were found to be lower than the IPCI scores of both the restored ($p = 0.01$) and native wetlands ($p = 0.03$) at Lostwood NWR.

Functional Capacity Index (FCI) scores were calculated for all 18 wetlands using the HGM model (Table 4). The six functions described by the model include: water storage; groundwater recharge; retention of particulates; removal, conversion, and sequestration of dissolved substances (biochemical processes); plant community

resilience and carbon cycling; and provision of faunal habitat. FCI scores for the wetlands included in this study ranged from 0.55-0.99. MRPP was used to identify significant differences in FCI scores between wetland types. When the six FCI scores for each wetland were combined, there were no significant differences ($p < 0.05$) among the four wetland categories.

Table 2. Index of Plant Community Integrity (IPCI) individual metric values and total IPCI score for each wetland.

Wetland Category	Wetland ID	Sp. Rich. ¹	# Gen. ²	# Grass like ³	% intro ⁴	#Nat. WM ⁵	#C \geq 5 ⁶	#C \geq 4 WM ⁷	Avg C ⁸	FQI ⁹	IPCI ¹⁰
TR ¹¹	TS061	4	4	4	4	4	0	4	7	7	38
	TT062	0	0	0	0	0	0	0	0	0	0
	TS063	0	4	7	4	4	0	0	4	4	27
	TT064	4	4	0	4	7	0	4	0	0	23
	TS065	4	4	7	4	7	0	4	0	4	34
	TT066	0	4	0	4	4	0	4	0	0	16
	TSP067	0	0	0	0	0	0	0	0	0	0
TN ¹²	TNS068	7	7	4	7	7	0	4	4	7	47
	TNT069	4	7	0	7	4	4	4	4	4	38
LR ¹³	LT061	4	4	0	7	4	4	0	4	4	31
	LS062	11	11	11	7	7	7	7	11	11	83
	LSP063	4	7	7	7	4	7	7	11	7	61
	LT064	7	7	0	4	7	7	4	7	4	47
	LS065	11	11	7	7	11	7	7	11	11	83
	LT066	7	11	7	7	11	7	4	4	4	62
	LS067	7	7	7	4	7	4	4	7	7	54
LN ¹⁴	LNT078	11	11	7	11	11	11	11	11	11	95
	LNS079	11	11	11	11	11	11	7	11	11	95

¹Species richness of native perennials.

²Number of genera of native perennial species.

³Number of grass and grass-like species (Poaceae, Juncaceae, and Cyperaceae).

⁴Percent of introduced, annual, and biennial species.

⁵Number of native species in wet meadow zone.

⁶Number of plant species with a C-value ≥ 5 .

⁷Number of plant species with a C-value ≥ 4 in wet meadow zone.

⁸Average C-value .

⁹Floristic Quality Index = average C-value multiplied by the square root of the total number of species.

¹⁰Total IPCI score for each wetland.

¹¹Restored wetland located on Tewaukon National Wildlife Refuge.

¹²Native wetland located on Tewaukon National Wildlife Refuge.

¹³Restored wetland located on Lostwood National Wildlife Refuge.

¹⁴Native wetland located on Tewaukon National Wildlife Refuge.

Table 3. Average total Index of Plant Community Integrity (IPCI) score for Tewaukon and Lostwood National Wildlife Refuge (NWR) sites showing significant differences ($p < 0.05$).

Location	Land-use History	Average Total IPCI Score
Tewaukon NWR	Restored	20.0a
	Native	42.5ab
Lostwood NWR	Restored	60.1b
	Native	95.0b

NMS analysis of the wetland vegetation dataset produced a final solution with 3 dimensions (Figures 3 and 4). The 3 dimension solution had a final stress of 8.79, indicating a good ordination with no real risk of drawing false inferences (McCune and Grace 2002). There were 114 iterations for the final solution and final instability was 0.00041. Each of the three axes of the final solution is important in explaining the variation within the wetland dataset. Axis 1 accounted for 28.9% of the variation, axis 2 accounted for 20.6%, and axis 3 accounted for 36.9%.

Axis 1 of the wetland NMS ordination was found to separate the wetland plant communities into those where reed canarygrass (*Phalaris arundinacea* L.) is present from those where quackgrass (*Elymus repens* (L.) Gould) is more likely to be present. (The United States Department of Agriculture PLANTS database was used as the primary reference for all of the plant species identified in this document (USDA, NRCS 2008).) The majority of the wetlands located far to the right of the ordination were located on Tewaukon NWR, indicating that Tewaukon wetlands possessed a relatively high amount of reed canarygrass. In contrast, the majority of the wetlands located to the left of the ordination were located at Lostwood NWR, indicating that Lostwood wetlands were more likely to contain quackgrass than reed canarygrass, although Lostwood wetlands were not invaded to the same extent as Tewaukon wetlands.

Table 4. Functional Capacity Index (FCI) scores as calculated by the Hydrogeomorphic (HGM) model for each wetland at Tewaukon and Lostwood National Wildlife Refuges.

Location	Land-Use History	Wetland ID	W.S. ¹	G.R. ²	P.R. ³	B.P. ⁴	P.C. ⁵	F.H. ⁶
Tewaukon National Wildlife Refuge	Restored	TS061	0.97	0.87	0.93	0.95	0.92	0.87
		TT062	0.97	0.96	0.86	0.90	0.81	0.77
		TS063	0.94	0.84	0.86	0.89	0.82	0.79
		TT064	0.58	0.64	0.68	0.61	0.58	0.55
		TS065	0.64	0.63	0.84	0.62	0.61	0.61
		TT066	0.97	0.87	0.87	0.88	0.80	0.81
	TSP067	0.97	0.81	0.89	0.90	0.84	0.82	
	Native	TNS068	0.97	0.87	0.93	0.93	0.89	0.89
		TNT069	0.97	0.91	0.88	0.90	0.83	0.83
Lostwood National Wildlife Refuge	Restored	LT061	0.97	0.93	0.88	0.89	0.81	0.78
		LS062	0.94	0.91	0.95	0.95	0.95	0.88
		LSP063	0.97	0.88	0.98	0.98	0.98	0.94
		LT064	0.97	0.96	0.90	0.91	0.86	0.83
		LS065	0.97	0.88	0.93	0.95	0.91	0.87
		LT066	0.97	0.87	0.92	0.91	0.87	0.85
		LS067	0.97	0.93	0.91	0.93	0.88	0.85
	Native	LNT078	0.97	0.98	0.98	0.98	0.98	0.96
		LNS079	0.97	0.95	0.98	0.99	0.99	0.97

¹ Functional Capacity Index scores for water storage within wetland.

² Functional Capacity Index scores for groundwater recharge.

³ Functional Capacity Index scores for particulate retention.

⁴ Functional Capacity Index scores for biochemical processes.

⁵ Functional Capacity Index scores for plant community resilience.

⁶ Functional Capacity Index scores for provision of faunal habitat.

Axis 2 of the wetland NMS ordination separated the wetland sites into plant communities with mostly native components from those with more introduced components. The wetland sites possessing plant communities containing many native species were located to the right of zero on the ordination axis, while the plant communities with more introduced species were located to the left of zero on the ordination axis. Axis 3 of the wetland NMS ordination was focused on typical shallow marsh vegetation, and separated out the wetland sites located in idle (no grazing or fire) or introduced grasslands. Wetland sites possessing a plant community similar to that of

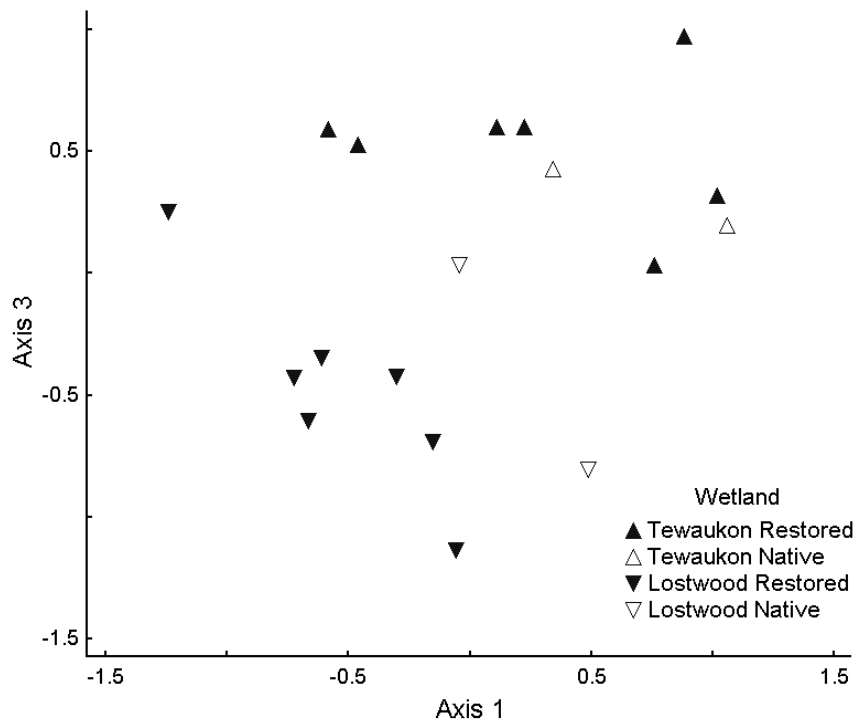


Figure 3. Nonmetric Multidimensional Scaling ordination of Tewaukon and Lostwood National Wildlife Refuge wetland sites showing axes 1 and 3. (Points in ordination space represent individual wetland sites.)

idle introduced grassland areas were located above zero on axis 3 while those with a plant community not typical of idle introduced grassland areas were located below zero.

Tewaukon wetlands were found to occupy positions above zero on axis 3, indicating that these wetlands possessed plant communities more similar to idle introduced grasslands.

Lostwood wetlands were generally found to occupy positions below zero on axis 3, indicating that these wetlands possessed plant communities distinct from idle introduced grasslands.

MRPP analysis of the wetland vegetation dataset revealed a significant difference ($p < 0.05$) between two groups. The plant communities of the restored wetlands at Tewaukon NWR were found to be significantly different from those of the restored wetlands at Lostwood NWR ($p = 0.01$). Similarly, the plant communities of the native

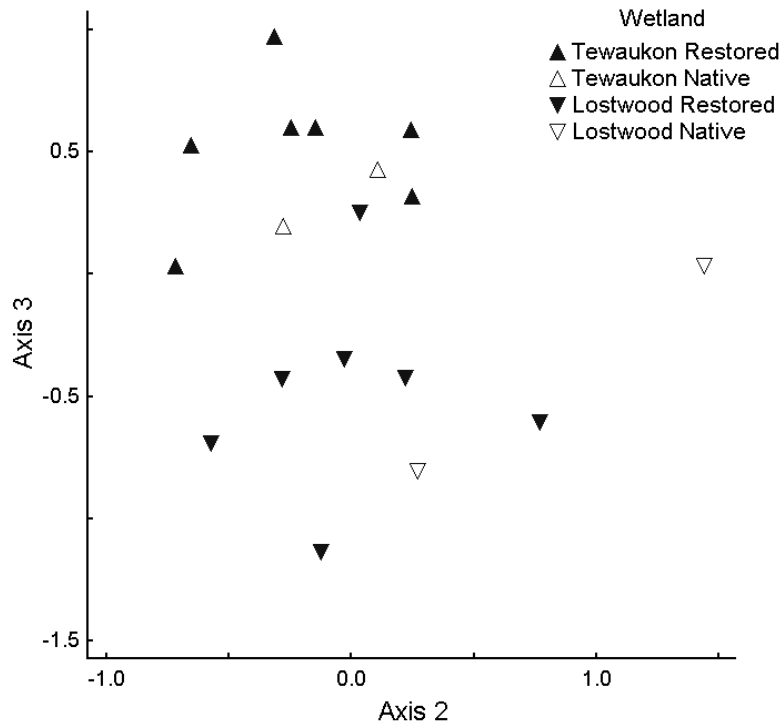


Figure 4. Nonmetric Multidimensional Scaling ordination of Tewaukon and Lostwood National Wildlife Refuge wetland sites showing axes 2 and 3. (Points in ordination space represent individual wetland sites.)

wetlands at Tewaukon NWR were found to be significantly different from those of the restored wetlands at Lostwood NWR ($p = 0.02$). There was no difference in the composition of the plant communities of restored and native wetlands located on the same refuge.

Low Prairie

NMS analysis of the low prairie vegetation dataset produced a final solution with 3 dimensions. The 3 dimension solution had a final stress of 6.88, indicating a good ordination with no real risk of drawing false inferences (McCune and Grace 2002).

There were 123 iterations for the final solution and final instability was 0.00044. Axis 3 explained 76% of the variation in the dataset, while axes 1 and 2 accounted for 2% and

13% respectively. NMS results are depicted in Figure 5; only axes 2 and 3 are shown since these axes explain 88% of the variation.

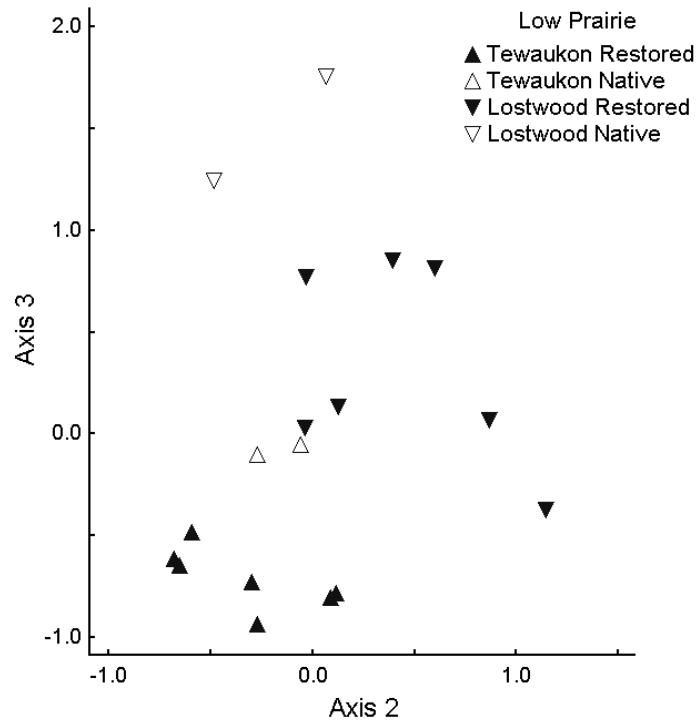


Figure 5. Nonmetric Multidimensional Scaling ordination of Tewaukon and Lostwood National Wildlife Refuge low prairie sites. (Points in ordination space represent individual wetland sites.)

Examination of the low prairie NMS ordination revealed that axis 2 separated the low prairie areas into sites dominated by a handful of introduced species (located to the left of zero on the ordination axis) from sites possessing plant communities dominated by several native species (located to the right of zero on the ordination axis). The low prairie areas included in this study were visibly divided along axis 2 by location. Tewaukon NWR low prairie areas were predominately found to possess plant communities dominated by introduced species and the handful of native grass species planted during restoration. Lostwood NWR low prairie areas were generally found to possess a lower proportion of introduced species and a higher proportion of native

species. Axis 3 was found to be very similar to axis 2. Axis 3 separated the sites in a similar manner to axis 2. Tewaukon NWR sites were predominately found below zero, while Lostwood NWR sites were generally located above zero on axis 3.

MRPP analysis of the low prairie dataset revealed that there were five significant differences in the plant community composition of the low prairie communities ($p < .05$). Restored low prairie plant communities at Tewaukon NWR were found to be significantly different from (1) the native low prairie plant communities at Tewaukon NWR ($p = 0.01$), (2) the restored low prairie plant communities at Lostwood NWR ($p < 0.01$), and (3) the native low prairie plant communities at Lostwood NWR ($p = 0.01$). Restored low prairie plant communities at Lostwood NWR were found to be significantly different from (1) the native low prairie plant communities at Tewaukon NWR ($p = 0.01$) and from (2) the native low prairie plant communities at Lostwood NWR ($p = 0.03$).

Mid-Slope

NMS analysis of the mid-slope vegetation dataset produced a final solution with 2 dimensions (Figure 6). The 2 dimension solution had a final stress of 9.93, indicating a good ordination with no real risk of drawing false inferences (McCune and Grace 2002). There were 116 iterations for the final solution and final instability was 0.00021. Axis 1 accounted for 62% of the variation in the dataset while axis 2 accounted for 26% of the variation.

Axis 1 of the mid-slope NMS ordination separated the mid-slope sites possessing a plant community typical of planted grasslands (located to the right of zero on the ordination axis) from those with more native components (located to the left of zero on the ordination axis). Tewaukon NWR sites were predominately located to the right on

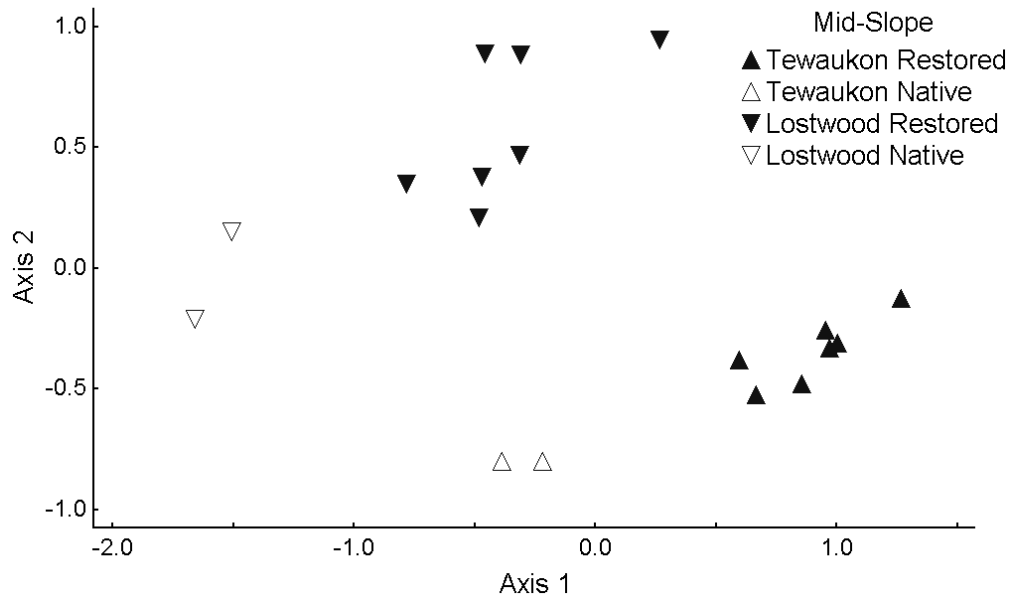


Figure 6. Nonmetric Multidimensional Scaling ordination of Tewaukon and Lostwood National Wildlife Refuge mid-slope sites. (Points in ordination space represent individual wetland sites.)

axis 1 while Lostwood NWR sites were predominately to the left. Axis 2 of the mid-slope NMS ordination separated the sites in a similar fashion to axis 1. Mid-slope sites were separated into sites possessing communities with more native components (located above zero on the ordination axis) and communities with more introduced components (located below zero on the ordination axis). All Tewaukon NWR sites were found below zero on axis 2 while the Lostwood NWR sites were generally found above zero on axis 2.

Similar to the results of the MRPP analysis of the low prairie dataset, MRPP analysis of the mid-slope dataset revealed significant differences in the plant communities of five groups ($p < .05$). Restored mid-slope plant communities at Tewaukon NWR were found to be significantly different from (1) the native mid-slope plant communities at Tewaukon NWR ($p = 0.01$), (2) the restored mid-slope plant communities at Lostwood NWR ($p < 0.01$), and (3) the native mid-slope plant

communities at Lostwood NWR ($p = 0.01$). Restored mid-slope plant communities at Lostwood NWR were found to be significantly different from (1) the native mid-slope plant communities at Tewaukon NWR ($p = 0.01$) and (2) from the native mid-slope plant communities at Lostwood NWR ($p = 0.01$).

Top-Slope

NMS analysis of the top-slope vegetation dataset produced a final solution with 2 dimensions (Figure 7). The 2 dimension solution had a final stress of 9.06, indicating a good ordination with no real risk of drawing false inferences (McCune and Grace 2002). There were 115 iterations for the final solution and final instability was 0.00035. Axis 1 accounted for 68% of the variation in the dataset, while axis 2 accounted for 19% of the variation.

The ordination axes of the top-slope NMS ordination function very similarly to the ordination axes 1 and 2 of the mid-slope dataset. As with the mid-slope ordination, axis 1 of the top-slope ordination separated the top-slope areas into sites possessing communities typical of planted grasslands (located to the right of zero on the ordination axis) and sites with more native components (located to the left of zero on the ordination axis). Axis 2 of the top-slope ordination, separated the sites into plant communities possessing more native components and those possessing more introduced components, as did axis 2 of the mid-slope ordination. Top-slope sites were separated into sites possessing communities with more native components (located above zero on the ordination axis) and communities with more introduced components (located below zero on the ordination axis). All Tewaukon NWR sites were found below zero on axis 2 while the Lostwood NWR sites were generally found above zero on axis 2.

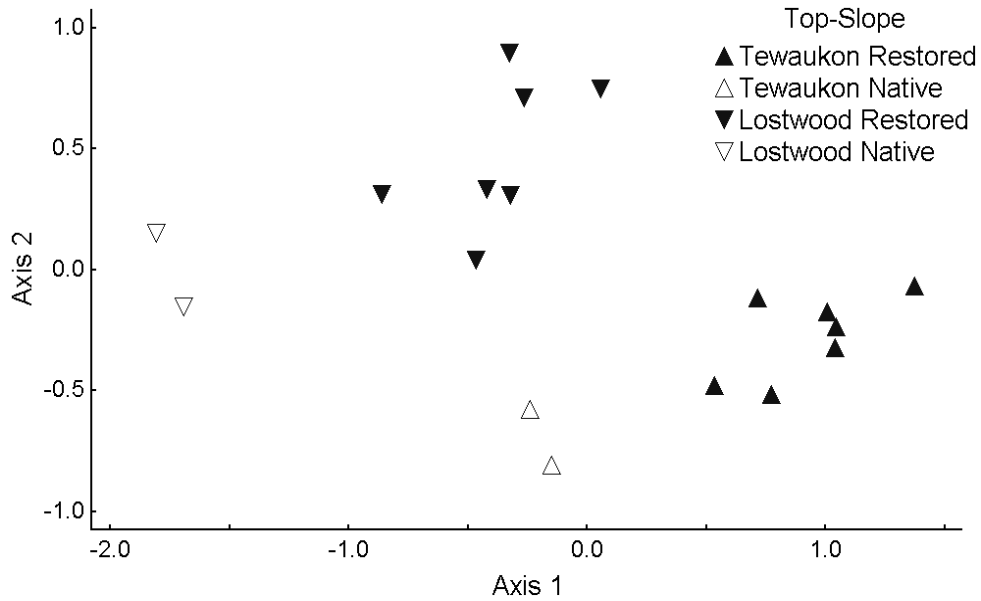


Figure 7. Nonmetric Multidimensional Scaling ordination of Tewaukon and Lostwood National Wildlife Refuge top-slope sites. (Points in ordination space represent individual wetland sites.)

Similar to the results of the MRPP analysis of the low prairie and mid-slope datasets, MRPP analysis of the top-slope dataset revealed that there were significant differences in the plant communities of five groups ($p < 0.05$). Restored top-slope plant communities at Tewaukon NWR were found to be significantly different from (1) the native top-slope areas at Tewaukon NWR ($p = 0.01$), (2) the restored top-slope areas at Lostwood NWR ($p < 0.01$), and (3) the native top-slope areas at Lostwood NWR ($p = 0.01$). Restored top-slope areas at Lostwood NWR were found to be significantly different from (1) the native top-slope areas at Tewaukon NWR ($p = 0.01$) and (2) the native top-slope areas at Lostwood NWR ($p = 0.01$).

Floristic Quality Index

FQI values were calculated for the entire ecosystem evaluated at each study site. The FQI values for the sites included in this study ranged from a minimum of 12.00 for a restored temporary wetland located at Tewaukon NWR to a maximum of 56.72 for a

native seasonal wetland located at Lostwood NWR (Table 5). There was a wide range in the average C value for each study site. The minimum average C value was 2.59 for a restored seasonal wetland located at Tewaukon NWR while the maximum average C value was 5.80 for a native temporary wetland located at Lostwood NWR. MRPP analysis of the ecosystem scale data revealed that each of the four groups (determined by location and land-use history) was significantly different from every other group ($p < 0.05$). P values for the pair-wise comparisons are presented in Table 6.

Table 5. Average Coefficient of Conservatism (C value) and Floristic Quality Index scores for National Wildlife Refuge study sites showing location and land-use history.

Location	Land-Use History	Site ID	Average C Value	Floristic Quality Index
Tewaukon National Wildlife Refuge	Restored	TS061	3.79	23.36
		TT062	3.77	21.01
		TS063	3.08	15.69
		TT064	2.62	12.00
		TS065	2.59	14.67
		TT066	2.94	12.49
		TSP067	3.03	18.41
	Native	TNS068	3.81	26.41
		TNT069	4.24	25.81
Lostwood National Wildlife Refuge	Restored	LT061	4.69	34.43
		LS062	4.36	37.55
		LSP063	4.38	42.20
		LT064	4.58	37.51
		LS065	4.52	41.95
		LT066	4.20	33.86
		LS067	4.31	33.91
	Native	LNT078	5.80	53.47
		LNS079	5.51	56.72

Separate FQI values were calculated for the wetland and upland plant communities at each study site (Table 7). The FQI calculations for the wetland plant communities included all native plants encountered within the wet meadow, shallow

Table 6. P values of the pair-wise comparisons resulting from MRPP analysis of the total plant community Floristic Quality Index values showing location and land-use history of Tewaukon and Lostwood National Wildlife Refuge study sites.

Group A	Group B	p value
Tewaukon restored	Tewaukon native	0.03
Tewaukon restored	Lostwood restored	<0.01
Tewaukon restored	Lostwood native	0.02
Tewaukon native	Lostwood restored	0.02
Tewaukon native	Lostwood native	*
Lostwood restored	Lostwood native	0.02

* MRPP analysis could not be completed for the comparison of these two groups since they had too few members to produce reliable results.

marsh, and deep marsh vegetation zones. The FQI calculations for the upland plant communities included all plants encountered within the low prairie, mid-slope, and top-slope vegetation areas. The FQI values for the wetland plant communities ranged from 3.00 for a restored temporary wetland located at Tewaukon NWR to 31.29 for a native temporary wetland located at Lostwood NWR. The average C values for the wetland plant communities ranged from 1.50 for a restored temporary wetland located at Tewaukon NWR to 5.53 for a native temporary wetland located at Lostwood NWR.

The FQI values for the upland plant communities ranged from 10.10 for a restored upland area located at Tewaukon NWR to 54.83 for a native upland area located at Lostwood NWR (Table 7). The average C values for the upland plant communities ranged from 2.6 for a restored upland area located at Tewaukon NWR to 5.80 for a native upland area located at Lostwood NWR. Similar to the ecosystem scale FQI data, MRPP analysis of the wetland and upland data revealed that each of the four groups (determined by location and land-use history) was significantly different from every other group ($p <$

0.05 level). P values for the pair-wise comparisons are presented in Table 8.

Table 7. Average Coefficient of Conservatism (C value) and Floristic Quality Index scores for the wetland and upland communities at national wildlife refuge study sites showing location and land-use history.

Location	Land-Use History	Site ID	Average C Value		Floristic Quality Index (FQI)	
			Wetland	Upland	Wetland	Upland
Tewaukon National Wildlife Refuge	Restored	TS061	2.96	3.96	14.18	19.39
		TT062	1.50	3.96	3.00	20.98
		TS063	2.42	3.15	8.37	14.09
		TT064	2.54	2.92	9.15	10.10
		TS065	2.41	2.60	12.51	11.63
		TT066	2.40	3.33	7.59	12.91
	Native	TSP067	2.24	3.41	11.20	15.99
		TNS068	2.83	4.21	13.55	25.96
		TNT069	2.58	4.45	8.95	25.59
Lostwood National Wildlife Refuge	Restored	LT061	2.33	5.02	8.08	35.14
		LS062	3.32	4.82	19.38	35.73
		LSP063	3.38	4.93	22.66	40.32
		LT064	3.00	4.62	10.82	36.11
		LS065	3.00	4.96	16.43	40.87
		LT066	2.59	4.41	10.67	33.85
		LS067	2.85	4.73	14.51	33.14
	Native	LNT078	5.53	5.80	31.29	52.57
		LNS079	3.76	5.75	20.24	54.83

Table 8. P values of the pair-wise comparisons resulting from MRPP analysis of the wetland and upland plant community Floristic Quality Index values at each site showing location and land-use history.

Group A	Group B	p value
Tewaukon restored	Tewaukon native	0.03
Tewaukon restored	Lostwood restored	<0.01
Tewaukon restored	Lostwood native	0.02
Tewaukon native	Lostwood restored	0.03
Tewaukon native	Lostwood native	*
Lostwood restored	Lostwood native	0.02

* MRPP analysis could not be completed for the comparison of these two groups since they had too few members to produce reliable results.

Discussion

Analyses of the biological assessment methods yielded several significant differences in the composition of the various plant communities assessed during this study. For instance, analysis of the wetland IPCI scores revealed significant differences between the restored wetlands located on Tewaukon NWR and both the restored and the native wetlands at Lostwood NWR. Since the IPCI focuses on the quality of the entire wetland plant community, the significant differences found in this study indicate that the quality of the plant communities varies by NWR and with land-use history. Analyses of the vegetation datasets utilizing NMS and MRPP also produced multiple significant differences in the composition of the wetland, low prairie, mid-slope, and top-slope plant communities. The significant differences detected by NMS and MRPP analyses indicate that there are structural differences in the restored and native plant communities included in this study.

The significant differences detected through the analyses of the FQI scores of the various plant communities reinforce the results of the analyses of the wetland IPCI scores, as well as, the results of the analyses of the vegetation datasets using NMS and MRPP. Analyses of the FQI data again indicated inherent differences in the composition of the wetland and upland communities included in this study. MRPP analyses of the whole community scale (including the deep marsh, shallow marsh, wet meadow, low prairie, mid-slope, and top-slope communities) FQI data also indicated significant differences in the composition of the various restored and native plant communities. In addition to compositional differences, the analyses of the FQI data also indicated significant differences in the quality of the plant communities encountered, both between

native and restored plant communities, and between the plant communities located at the two refuges. Differences in the quality of the plant communities are explained, in part, by the differences in the restoration and management techniques employed at each refuge. Other important contributing factors include the success of cultivation and agriculture in the region surrounding the refuge, the degree of habitat degradation prior to ecological restoration, and the extent of habitat fragmentation and isolation of restored and native plant communities.

Essentially all of the wetlands included in this study were found to function at high levels relative to the reference standards by the HGM model. Many of the wetlands performed functions at or above 90% of the functional capacity of the reference wetlands used to develop the HGM approach for the Northern Great Plains Region. Interestingly, no significant differences ($p < 0.05$) were found when the FCIs were compared using MRPP. The absence of statistically significant differences in the FCI scores for our wetland categories indicates that the restored wetlands included in this study function similarly to the native wetlands included in this study, and that the wetlands function similarly at both refuge locations.

The finding of no significant differences in the functional capacities of the wetlands included in this study is not unexpected since the HGM model relies heavily on the physical and landscape characteristics of wetlands rather than on the biological characteristics. It is likely that the restored wetlands included in this study function similarly to the native wetlands (and the HGM model's reference wetlands) since these restored wetlands are physically similar to native wetlands, i.e., this study selected wetlands that were located in previously cropped restored areas rather than previously

drained wetlands. The restored wetlands located in previously cropped areas were undoubtedly physically altered from their native states, but not to the extent that it significantly lowered the functional capacity of the wetland to perform the physical and hydrological functions as measured by the HGM model.

The disagreement in the results of the statistical analyses of the biological assessment methods and the HGM model implies that the HGM model is not an entirely holistic approach to wetland assessment. In certain instances, the HGM model may fail to detect biological differences in wetland plant communities that a biological model may be more apt to find. Thus, one should include a biological assessment method in addition to the HGM model when assessing the condition of restored wetland plant communities in the PPR in order to adequately assess all aspects of the wetland ecosystem.

In general, the management and restoration techniques employed at Lostwood NWR have been more intensive and proactive than those employed at Tewaukon NWR. Lostwood NWR has a longer history of prairie restoration entailing reseeding areas with a locally harvested seed mix. Lostwood NWR also has had better control of introduced and invasive species, implemented more frequent and intensive burning and grazing programs, and has a lower frequency of leaving areas idle (Smith personal communication 2006). In addition, prairie and wetland areas at Lostwood NWR may never have been degraded to the same extent as many of those at Tewaukon NWR, and the prairie habitat in and around the Lostwood NWR is more contiguous throughout the landscape surrounding Lostwood NWR than that surrounding Tewaukon NWR. These factors help to create and maintain higher quality plant communities at Lostwood NWR relative to those at Tewaukon NWR since the environment in and around Lostwood

NWR is more conducive to the persistence of higher quality prairie and wetland habitats at the landscape scale.

Conclusion

Prairie and wetland ecosystems throughout the PPR are adapted to many types of disturbance, having evolved within the harsh and often unpredictable conditions of the Northern Great Plains. For example, the prairie ecosystems of the Great Plains Region have evolved to withstand alternating periods of drought and deluge, as well as grazing by native ungulate species, and periodic fire (Fuhlendorf and Engle 2001; Gurevitch et al. 2006). Prairie pothole wetlands have persisted through the same conditions, and are well adapted to withstand many of the same disturbance factors affecting the prairie ecosystems (Kantrud 1986; Kantrud and Newton 1996).

In today's human dominated landscapes, disturbances continue to mold and shape natural and anthropogenic ecosystems (Vitousek et al. 1997). However, many of the characteristics of natural disturbances have been impacted by human practices and human actions have advertently and inadvertently introduced new disturbance factors to natural systems (Vitousek et al. 1997; Ellis and Ramankutty 2007). Examples of anthropogenic disturbances to both the prairie and wetland ecosystems of the PPR are numerous. Lands have been directly converted to agriculture at a high rate, leading to the current domination of the PPR by agricultural land uses (Schumacher and Rickerl 2004). Fire suppression, wetland alteration and drainage, habitat degradation and fragmentation, the eradication of native ungulate grazers, and the introduction of numerous species quickly followed the expansion of agriculture into the PPR, effectively producing the mosaic of natural and anthropogenic ecosystems we see today.

The alteration of landscape scale processes, including various natural disturbance patterns, has had many negative consequences for PPR grassland and wetland ecosystems. For example, fire suppression has altered the structure and composition of plant communities and contributed to a buildup of litter within wetlands (Kantrud et al. 1989; Howe 1994); the prevalence of wetland drainage has led to a dramatic decline in wetland area across the PPR (Dahl 1990; Schumacher and Rickerl 2004); and species introductions have changed the dynamics of wetland and grassland systems alike (Christian and Wilson 1999).

Leaving areas idle for long periods of time has also altered native plant communities throughout the PPR in manners similar to the direct anthropogenic disturbances listed above. In PPR ecosystems, when grazing is removed and fire is suppressed, introduced species often come to dominate wetland and prairie systems resulting in a plant community that is different in structure and function from the native communities that have evolved in the PPR. Thus, it is vital that remaining native areas and restored areas be managed in ways that mimic natural disturbances in order to maintain healthy communities of native plants.

This study has shown that restoration has the potential to improve the plant community composition of wetlands and grasslands in the PPR when properly managed. Although the community composition of restored areas may not be identical to that of native areas, many of the restorations evaluated in this study possessed plant communities with several native components – a marked improvement over the degraded systems that formerly occupied these areas. With time and active management, the

restored ecosystems evaluated in this study will likely continue to improve and to converge with native ecosystems.

It is apparent that restoration and management practices could be improved through the implementation of a holistic, landscape level approach. Wetlands and uplands are inextricably linked; patterns and processes affecting the uplands (both negatively and positively) will undoubtedly reach the wetlands. In order to improve wetland composition and function, adjacent uplands must be considered and managed concordantly. Similarly, wetlands exist in relation to their landscape. Prairie potholes located within wetland complexes are able to perform functions at higher levels than those isolated from other wetlands. Thus, large-scale restorations of wetland and grassland complexes are necessary to achieve a higher level of potential benefits from ecosystem restorations throughout the PPR.

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