

# Colonization during early succession of restored freshwater marshes

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**Abstract:** Little is known about the importance of initial colonization in the successional development of restored wetlands. We compared plant communities of two lightly planted restorations (water levels restored + planted and seeded), three hydrologic restorations (water levels restored), and two undrained sites. Measurements typically used in monitoring (richness, diversity, aboveground biomass) indicated that 2–3 years after restoration, restored wetlands showed only small differences from the plant community structure of undrained wetlands in the saturated zone. In contrast, analysis of vegetation based on species composition indicated differences in vegetation communities among all wetland types. Plant communities of planted restorations and reference sites were dominated by emergent species, while hydrologic restorations had a more variable plant community. These results indicate a small effect of initial planting and seeding at low densities and show that colonization is rapid during early succession of restored marshes. It was not clear whether either restoration method would eventually result in vegetation communities similar to reference sites. These results indicate that current monitoring periods of 3–5 years are insufficient to allow time for an accurate assessment of the successional development in each wetland.

*Key words:* dispersal, germination, monitoring, plant biomass, plant community, wetland.

**Résumé :** On connaît peu de choses sur l'importance de la colonisation initiale dans le développement de la succession des terres humides restaurées. Les auteurs ont comparé les communautés végétales de deux sites de restauration avec plantations (restauration des niveaux d'eau + plantation et ensemencement), de trois sites de restauration hydrologique (restauration des niveau d'eau) et de deux sites non-drainés. Les mesures typiquement utilisées pour faire le suivi (richesse, diversité, biomasse épigée) indiquent que 2-3 ans après la restauration, les terres humides régénérés ne montrent que de petites différences par rapport à la structure des communautés végétales des terres humides non-drainées dans la zone saturée. Au contraire, l'analyse de la végétation basée sur la composition en espèces montre des différences dans les communautés végétales entre tous les types de terre humide. Les communautés végétales des sites restaurés avec plantation et des sites de référence sont dominés par des espèces émergentes, alors que les sites de restauration hydrologique comportent une communauté végétale plus variable. Ces résultats indiquent que l'effet de plantations et ensemencements à faible densité, au départ, est peu marqué et montrent également que la colonisation est rapide au début de la succession dans les marais restaurés. Il n'est pas clair si une des méthodes de restauration conduirait éventuellement à des communautés végétales semblables à celles de sites de référence. Ces résultats indiquent que les suivis usuels sur des périodes de 3-5 ans sont insuffisants pour permettre une évaluation précise du développement de la succession dans chaque terre humide.

*Mots clés :* dispersion, germination, suivi, biomasse végétale, communauté végétale, terre humide.

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## Introduction

The loss of over one half of the original wetlands in the conterminous United States (Dahl and Johnson 1991) has focused attention on the value of wetlands. The importance of functions such as habitat, water quality, groundwater recharge, and flood prevention (National Research Council 1992) have led to efforts to restore many previously drained wetlands. Attempts at restoration are often ecologically and legally unsuccessful when compared with nearby undrained

reference sites. These failures are often due to the colonization and subsequent dominance of plant communities by invasive species (Galatowitsch and van der Valk 1996a; Race and Fonseca 1996). Despite the environmental and economic consequences of efforts to restore wetlands, very little long-term monitoring to evaluate the ecological consequences of these efforts has occurred (Kusler and Kentula 1989; Zedler 1996).

The ultimate aim of restoration is to produce a self-sustaining wetland that will approximate the structural and functional attributes of undrained, relatively undisturbed wetlands (Zedler 1996; Niering 1997). To evaluate progress toward this goal, permitting agencies require monitoring based on the idea of rapid, predictable succession in 5–10 years (Zedler and Callaway 1999). These expectations are based on the assumption of a directional recovery resulting in a single successional endpoint (MacMahon 1987; Zedler 1996). However, this assumption is unrealistic because of the complex successional paths taken by different wetlands

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(Zedler and Callaway 1999). To fashion more appropriate ways of evaluating success of restorations, there is a critical need for research on the impact of individual species during succession of plant communities (Edwards et al. 1997), the persistence of plant species and biomass accumulation (Zedler 1996), and the capacity of plants to recolonize wetlands (Wheeler 1995). Restoration of wetlands with differing initial conditions offers a set of ecosystem-level manipulations (Werner 1987) capable of addressing these research needs in the context of successional theory (MacMahon 1987).

Although restoration may be viewed as a process of actively directing succession (Luken 1990; Dobson et al. 1997), others emphasize the importance of natural colonization in the succession of restored ecosystems (Mitsch and Wilson 1996). The importance of colonization in succession has long been recognized, although predictions of community changes during succession are debatable (e.g., Gleason 1926; Clements 1936). In the absence of established vegetation, succession in wetlands is initially dependent on seed dispersal and establishment (van der Valk 1981, 1992), but subsequent spread within a site is primarily by vegetative means (van der Valk 1992). Thus, differences in colonization and establishment lead to initial differences in the vegetation of a wetland, which are expected to have a great impact on the plant community that becomes established during succession (van der Valk 1981; Glenn-Lewin and van der Maarel 1992).

Seed banks are an important factor in the successional trajectory of wetlands (van der Valk 1981). However, at the initiation of secondary succession in restored marshes, the seed bank is often depauperate as a result of the site being intentionally drained for long periods (Weinhold and van der Valk 1989). Additionally, recent studies have found that vegetation communities in restored marshes have little relationship to the initial seed bank (Galatowitsch and van der Valk 1995; Brown 1998) and are primarily derived from colonization (Galatowitsch and van der Valk 1996a, 1996b; Brown 1998). Therefore, initial differences in established vegetation due to planting would be expected to have large effects on development of the plant community.

Despite the differences in wetland restoration methods of freshwater marshes (ranging from no introduction of plant material to intensive planting), few studies have examined the results of differences in initial colonization on plant community development during succession of freshwater wetlands. Reinartz and Warne (1993) found higher species richness in seeded freshwater marsh restorations than in unseeded, hydrologic restorations, indicating dispersal limitation during plant community development. The proportion of the vegetation represented in various plant guilds can also differ between hydrologically restored freshwater marshes and reference sites (Galatowitsch and van der Valk 1996a, 1996b), indicating that early colonizers form different communities than found in later succession. Mitsch et al. (1998) found few differences between plant communities of a planted and unplanted wetland, although the proximity of the two sites and the use of river water in the sites enhance colonization opportunities. These studies show the importance of dispersal and early colonization, but none examined the effect of established plants on successional patterns beyond 3 years.

This study addresses the effect of differences in early colonization on vegetation establishment during early (6–7 years) succession in restored freshwater marshes in northern Indiana. We addressed this problem by comparing hydrologic, naturally colonized restorations (water levels restored), planted restorations (water levels restored + planted and seeded), and undrained reference sites. By comparing initially uncolonized wetlands (hydrologic restorations) with wetlands initially colonized by a small number of known species (planted restorations), one can measure the effect of early colonization on the establishment of vascular macrophytes during succession. Our first hypothesis was that species richness, diversity, and aboveground biomass in the saturated zone would be lowest in hydrologic restorations, intermediate in planted restorations, and highest in reference sites. These expectations were based on the higher initial colonization of the planted sites and the longer period of colonization in reference sites. Our second hypothesis was that the above patterns would not be apparent in flooded zones, due to suppressed germination under flooded conditions. Reference sites were expected to have higher species richness, diversity, and aboveground biomass than restored sites in the flooded hydrologic zone due to (i) historic low water periods that allowed seed germination and (ii) longer periods of time to allow vegetative ingrowth from the shallow areas. Our third hypothesis was that restored wetland types would have different plant communities and guild dominance, due to differences in initial colonization. Furthermore, we expected that neither type of restoration would be similar to reference sites, due to the age differences.

## Materials and methods

This study was conducted in seven freshwater marshes in northern Indiana, U.S.A. (41°14′–41°32′N, 85°52′–86°26′W). The sites consisted of three hydrologic restorations (hydrology restored, mean area 2 ha) with natural colonization only, two planted restorations (hydrology restored + planted and seeded, mean area 2 ha), and two reference wetlands that were never drained (mean area 7 ha). Planted and hydrologic restorations were restored 2–3 years before the start of this study. Water regimes were restored by removal of drainage tiles, construction of earthen berms, and installation of water control structures. Both hydrologic and planted restorations took place on previously drained wetlands that had been cultivated for at least 45 years. Historical photographs, documents, and personal interviews confirmed that there were no remaining areas of wetland vegetation prior to restoration. All sites lacked surface inlets and had plant communities dominated by herbaceous wetland vegetation at the beginning of the study. When selecting restored sites, we intentionally excluded restorations that did not retain water sufficient for wetland hydrology or were dominated by monotypic stands of invasive plant species. All restored sites were sampled in areas away from the earthen dam to avoid areas disturbed by dam construction. All three hydrologic restoration sites had hydrology restored in 1994. The reference sites had never been drained or cultivated and were chosen to be as near as possible to the restorations. All sites were within a 30-km radius and were selected for similarity in duration and frequency of inundation, assessed by visits

**Table 1.** Species and numbers of plants introduced in planted restorations.

Guild and species	1993 restoration	1994 restoration	
		1994 planting	1996 planting
Wet prairie and sedge meadow species			
<i>Angelica atropurpurea</i> L.	1.4 kg		
<i>Iris versicolor</i> L.		25	
<i>Iris virginica</i> L.		25	
<i>Leersia oryzoides</i> (L.) Sw.	20		
<i>Scirpus atrovirens</i> Willd.		109	
Emergent species			
<i>Sagittaria latifolia</i> Willd.	20		0.5 kg
<i>Scirpus acutus</i> Bigelow		109	
<i>Scirpus cyperinus</i> (L.) Kunth	2.3 kg	109	0.5 kg
<i>Scirpus validus</i> Vahl		109	
Floating aquatic species			
<i>Nelumbo lutea</i> (Willd.) Pers.	10	50	
<i>Nymphaea odorata</i> Aiton	15	50	
<i>Pontedaria cordata</i> L.	20		
Woody species			
<i>Acer rubrum</i> L.			30
<i>Betula nigra</i> L.		160	80
<i>Cephalanthus occidentalis</i> L.	25	25	
<i>Cornus amomum</i> Miller		160	80
<i>Cornus stolonifera</i>	40	160	80
<i>Nyssa sylvatica</i> Marsh.			20
<i>Platanus occidentalis</i> L.		160	30
<i>Quercus bicolor</i> Willd.			80
<i>Quercus palustris</i> Muenchh.	10	160	

**Note:** Seeded species are listed in kg; all other species were planted.

to the sites during the year prior to the study. Soils in all restored sites were loam or clay loam, while reference sites were histosols.

The first planted restoration was performed in 1993 (10 species) and the second in 1994 (14 species) by the same consulting firm (J.F. New and Associates, Inc., Walkerton, Ind.). In addition to restoring hydrology, all planted restorations had a small introduction of herbaceous plants in a 0.5-ha area of shallower water at the edges of the restoration (see Table 1 for planting list). Woody species from the 1994 restoration were planted over a 1.6-ha area. This minimal effort was typical of planted restorations at the time in this area, and both were judged to be regulatory successes by the U.S. Army Corps of Engineers. Records from the consulting firm verified that all planted and seeded species in the 1993 restoration were present at the end of the first growing season (J.F. New and Associates, Inc. 1993). The 1994 planted site had 10 of the original 14 planted species (loss of *Iris versicolor*, *Iris virginica*, *Scirpus atrovirens*, *Scirpus validus*) present in three 4-m<sup>2</sup> quadrats at the end of the first growing season (J.F. New and Associates, Inc. 1994). *Scirpus validus* may have been present in the 1994 restoration and identified as *Scirpus acutus*. These two species are difficult to identify without seeds and often hybridize (Voss 1980). Additionally, no overall site survey of vegetation was performed for the 1994 restoration, so planted species not found in quadrats may still have been present in the restoration. The 1994 planted restoration site had higher water levels than designed, and the water level was lowered 15 cm after the first

year (by removal of boards from the drainage structure). This higher than anticipated water level caused some mortality in the tree species planted at the site, requiring an additional planting of tree seedlings in April 1996 (J.F. New and Associates, Inc. 1996). During this additional planting, seeds of *Sagittaria latifolia* and *Scirpus cyperinus* were also seeded in the wetland (although both species were present in the wetland at the end of the first growing season in 1994). Both planted wetlands were also seeded with a nurse crop of *Secale cereale* (26 kg mean per site) during the first year to prevent initial establishment of invasives.

In 1996, six permanent 1-m<sup>2</sup> cover plots were placed in each wetland. In the reference sites, areas dominated (greater than 50% cover) by *Cephalanthus occidentalis* (approximately 20% of total area of each reference site) were excluded to better compare the herbaceous vegetation typical of restored and reference marshes. Three plots were randomly placed in each of two hydrologic zones defined at peak growing season during the first year of the study as saturated (0 to +5 cm water depth) and flooded (+20 to +25 cm water depth). In 1998, five additional 1-m<sup>2</sup> cover plots were randomly sampled in each hydrologic zone. Because plots were selected randomly, they were not necessarily near initial plantings in planted restorations. Seeded species were widespread, and our plots were likely in seeded areas. The species from these cover plots were indicative of the most common species in each wetland. Water depth in the middle of each permanent plot was measured with a metre stick during annual sampling at peak growing season. Monthly re-

**Table 2.** Mean percent cover of species used in PCAs.

Guild and species	Hydrologic		Planted		Reference	
	Saturated	Flooded	Saturated	Flooded	Saturated	Flooded
Wet prairie and sedge meadow						
<i>Carex lurida</i> Wahl.	10 (2)	7 (1)				
<i>Carex vulpinoidea</i> Michaux ( <b>Cavu</b> )	6 (3)					
<i>Impatiens capensis</i> Meerb.	10 (1)					
<i>Juncus effusus</i> L.	11 (3)	22 (1)				
<i>Leersia oryzoides</i> (L.) Sw. ( <b>Leor</b> ) <sup>a</sup>	50 (3)	1 (1)	35 (2)	20 (2)		59 (1)
<i>Polygonum pensylvanicum</i> L. ( <b>Pope</b> )					10 (2)	
<i>Scirpus atrovirens</i> Willd. ( <b>Scat</b> ) <sup>a</sup>	16 (2)	15 (1)				
Emergent						
<i>Alisma plantago-aquatica</i> L.	1 (1)		5 (2)	6 (1)		2 (2)
<i>Calamagrostis canadensis</i> (Michaux) Beauv. ( <b>Caca</b> )	1 (1)				26 (2)	13 (2)
<i>Carex lasiocarpa</i> Ehrh.					31 (1)	50 (1)
<i>Eleocharis obtusa</i> (Willd.) Schultes	2 (2)		9 (2)	1 (1)		
<i>Eleocharis smallii</i> Britton			51 (1)	12 (1)		15 (1)
<i>Lythrum salicaria</i> L.					33 (2)	
<i>Phalaris arundinacea</i> L. ( <b>Phar</b> )	39 (3)		8 (2)		56 (2)	32 (2)
<i>Polygonum hydropiperoides</i> Michaux			1 (1)		2 (2)	1 (1)
<i>Proserpinaca palustris</i> L.					2 (1)	21 (1)
<i>Sagittaria latifolia</i> Willd. ( <b>Sala</b> ) <sup>a</sup>			2 (2)	1 (1)	8 (2)	16 (2)
<i>Scirpus acutus</i> Bigelow <sup>a</sup>					9 (2)	6 (2)
<i>Scirpus cyperinus</i> (L.) Kunth ( <b>Scy</b> ) <sup>a</sup>	24 (2)	24 (1)				
<i>Scirpus validus</i> Vahl ( <b>Scva</b> ) <sup>a</sup>	13 (2)		10 (2)			3 (1)
<i>Typha</i> spp.	21 (2)	23 (2)	18 (2)	5 (1)	10 (2)	14 (1)
Floating aquatic						
<i>Potamogeton natans</i> L.	30 (1)	8 (1)		2 (2)		1 (2)
Mudflat annuals						
<i>Bidens connatus</i> Willd.	4 (2)	32 (1)	3 (2)	12 (1)		1 (1)
<i>Lindernia dubia</i> (L.) Pennell			23 (2)	1 (1)	1 (1)	1 (1)
Woody						
<i>Cephalanthus occidentalis</i> L. <sup>a</sup>					8 (2)	12 (2)

**Note:** Percent cover determined as mean of plots where species appeared during any year of study. Number in parentheses indicates number of sites containing species within a hydrologic zone. Species abbreviations used in Fig. 1 are bolded.

<sup>a</sup>Planted or seeded in planted restorations.

gional precipitation data from NOAA climatic data stations within 10 km of the sites (Lakeville and Warsaw, Ind., <http://www.nndc.noaa.gov/> [site last accessed October, 2002]) were used to assess differences in precipitation between years from 1996 to 1998.

Cover was visually estimated (as a percentage) for all rooted plant species by two or three observers, and the observations were averaged for each species. Permanent plots in each wetland were sampled annually during peak growing season (July 15 – August 1) from 1996 to 1998 (2–5 years after restoration). Plant species richness and the Shannon–Weiner diversity (base 10) were determined for each permanent plot annually. Total richness in each wetland and for each hydrologic zone was determined using a cumulative species list from the cover plots for all three years of the study, including the additional plots sampled in 1998. Cumulative richness includes species that both appeared and disappeared from plots during the study. This total richness is only an indication of the richness of the entire wetland, as the wetlands were not completely sampled. Nonvascular plant species, such as algae, were present in all sites but were not sampled because there was no expectation of dispersal limitation in these species.

Aboveground biomass was destructively sampled each year in plots located within 1 m of the permanent cover plots by clipping all living vegetation to ground level. Plots were sampled at the same time as cover was taken in permanent plots. After clipping and sorting by species, vegetation was dried at 65°C for 48 h and weighed. Vegetation was sorted by species in 1997 and 1998. In 1996, a 1-m<sup>2</sup> plot was sampled. In 1997 and 1998, two random 0.04-m<sup>2</sup> subplots from a 1-m<sup>2</sup> plot were sampled to minimize sampling effort. Different biomass plots were used each year. Voucher specimens are on file at the University of Notre Dame Herbarium. Nomenclature follows Voss (1980, 1985, 1996).

Cumulative richness in the cover plots (all years of the study) for the entire wetland (all hydrologic zones combined) and within each hydrologic zone was compared among treatments (hydrologic restoration, planted restoration, reference) using ANOVA. Annual richness, Shannon–Weiner diversity, and aboveground biomass from permanent plots were analyzed by repeated measures ANOVA (ANOVAR) with plots nested by hydrologic zone within each site. Diversity and biomass values were log transformed prior to analysis to provide a normal distribution. After significant year × treatment interactions were detected

in the ANOVAR, ANOVA (plots nested by hydrologic zone within each site) and Tukey post hoc tests were performed on plot data from each year to identify differences. Because of nesting, no interaction term between treatment and hydrologic zone was possible. Significance of all analyses was assessed as  $p \leq 0.05$ .

Principal components analysis (PCA), a multivariate method of comparing plant communities, was used to analyze vegetation patterns based on species cover and aboveground biomass in each plot. The variance-covariance matrix was used in the PCA because, in this method, clustering is done with respect to the original descriptors, preserving their differences in magnitude (LeGendre and LeGendre 1998). All species present in less than 5% of the plots were excluded prior to analysis, and outliers (over 2 SD) were removed from all data sets (Gauch 1986) (Table 2). Differences from the PCA were confirmed using multiresponse permutation procedures (MRPP). MRPP is a nonparametric procedure for testing a priori differences between two or more groups (McCune and Mefford 1999). Because each MRPP analysis of a hydrologic zone required three tests, the  $p$  values were evaluated using a Bonferroni correction and only found to be significant if  $p < 0.017$ . MRPP analysis of the plant community cover data showed significantly different communities between hydrologic zones ( $p < 0.001$ ), so PCAs were done separately for each hydrologic zone. The year sampled and water level at time of sampling did not affect the ordination, so data from all years were used in each PCA. PCA confirmed that additional plots sampled in 1998 did not change results of the community analysis, so all community analyses in these zones were conducted on permanent plots only. Species typical of plant communities were determined based on species eigenvectors from each PCA. All community comparisons were analyzed using PC-ORD, version 4 (McCune and Mefford 1999).

Species were assigned to guilds based on germination characteristics and hydrologic tolerance of mature plants (Galatowitsch and van der Valk 1996b). This type of guild designation allows comparisons between wetland types based on life history characteristics of the plant community. Guilds consisted of (i) wet prairie and sedge meadow, (ii) emergents, (iii) floating aquatics, (iv) mudflat annuals, and (v) woody species. Guild designation was based on prior designations (Galatowitsch and Van der Valk 1996b) and information from the flora of Michigan (Voss 1980, 1985, 1996). Guild aboveground biomass for 1997 and 1998 was analyzed for effects of hydrologic zone, wetland type, and year using ANOVAR with plots nested by hydrologic zone within each site. Significant effects were analyzed within each year by ANOVA and Tukey tests as above.

## Results

### Species richness, diversity, and aboveground biomass

There were no differences in cumulative richness among wetland treatments for both hydrologic zones pooled (mean ( $\pm$ SD) richness per site  $22 \pm 2$ ) or in the saturated zone (mean richness per site  $19 \pm 2$ ) (Table 3). In the flooded zone, hydrologic restorations (mean richness per site  $4 \pm 5$ ) had lower richness than reference sites ( $p = 0.049$ ), whereas planted restorations (mean richness per site  $7 \pm 3$ ) were not

different from reference sites ( $p = 0.12$ , mean richness per site  $20 \pm 6$ ) or hydrologic restorations ( $p = 0.75$ ).

In the permanent plots, richness was different between hydrologic zones and treatments (ANOVAR, Table 3). There was also an indication of a year  $\times$  treatment interaction. Plots were analyzed by year to be consistent with analysis of diversity and biomass, which had significant year  $\times$  treatment interactions. Reference sites were richer than either restoration treatment in the first two years of the study (Table 4). In 1998, planted restorations did not differ from hydrologic restorations or reference sites, whereas hydrologic restorations remained less rich than reference sites (Table 4). Flooded plots were less rich than saturated plots during 1996 and 1997. However, saturated and flooded zones were equally rich in 1998 (Table 4).

Shannon-Weiner diversity in permanent plots was affected by hydrologic zone and a year  $\times$  treatment interaction (ANOVAR, Table 3). During 1996, there were no differences in diversity among treatments (Table 4). In 1997 and 1998, restoration treatments did not differ and were less rich than reference sites. Flooded plots had lower diversity than saturated plots in all years (Table 4).

Aboveground biomass had a significant year  $\times$  treatment and year  $\times$  hydrologic zone interactions (ANOVAR, Table 3). Reference sites had greater biomass than restored sites in all years, and restoration treatments did not differ from each other (Table 4). Flooded plots had lower biomass than saturated plots in 1996 and 1997, while the two hydrologic zones did not differ in 1998.

### Plant communities

Seven planted species were common enough in the sites to be included in PCAs (Table 2). *Sagittaria latifolia* was present in planted restorations but absent in hydrologic restorations. *Leersia oryzoides* was much more common in the flooded zone of planted restorations than in hydrologic restorations. *Scirpus validus* was present in the saturated zone of both restoration treatments with similar abundance. *Scirpus atrovirens* and *Scirpus cyperinus* were only found in hydrologic restorations. *Cephalanthus occidentalis* and *Scirpus acutus* were only found in reference sites.

Ordination of plant cover data (21 species) in saturated permanent plots (Fig. 1) revealed differences in communities between the two restoration treatments (MRPP,  $p = 0.007$ ) and showed that reference sites were different from both restoration treatments (MRPP,  $p < 0.001$ ). Axes I and II explained 36 and 24%, respectively, of variation in the covariance matrix. Axis I separated reference sites from restored sites. Reference sites had greater cover of *Phalaris arundinacea* (eigenvector axis I (E1) =  $-0.76$ , eigenvector axis II (E2) =  $0.59$ ), *Polygonum pennsylvanicum* (E1 =  $-0.08$ , E2 =  $0.05$ ), *Calamagrostis canadensis* (E1 =  $-0.08$ , E2 =  $0.03$ ), and *Sagittaria latifolia* (E1 =  $-0.05$ , E2 =  $0.02$ ). Axis II separated restoration treatments. Hydrologic restorations were separated from planted restorations by greater cover of *Leersia oryzoides* (E1 =  $0.63$ , E2 =  $0.75$ ), *Phalaris arundinacea* (E1 =  $-0.76$ , E2 =  $0.59$ ), and *Carex vulpinoidea* (E1 =  $0.02$ , E2 =  $0.02$ ). Hydrologic restorations were more variable than the planted restorations and were spread on axis II due primarily to differences in cover of *Leersia oryzoides*. Two outlier plots from the planted restorations

**Table 3.** ANOVA and ANOVAR results for all analyses (A–E).

		Treatment			Hydrologic zone (site)			Year × treatment			Year × hydrologic zone (site)			
		F	df	p	F	df	p	F	df	p	F	df	p	Error df
<b>(A) ANOVA cumulative richness.</b>														
Both zones		1.76	2	ns										
Saturated zone		3.63	2	ns										4
Flooded zone		6.73	2	*										4
<b>(B) ANOVAR structural traits.</b>														
Richness		9.71	2	***	5.51	7	***	2.27	2	ns	1.24	14	ns	64
Shannon–Weiner diversity		8.08	2	***	6.85	7	***	3.03	2	0	0.77	14	ns	64
Aboveground biomass		9.78	2	***	5.78	7	***	2.72	4	0	3.19	14	***	62
<b>(C) ANOVA structural traits.</b>														
Richness		5.77	2	**	5.35	7	***							32
1996		9.34	2	***	7.48	7	***							32
1997		5.91	2	***	1.33	7	ns							32
Diversity		1.29	2	ns	7.44	7	***							32
1996		8.53	2	***	6.34	7	***							32
1997		7.30	2	**	2.59	7	0							32
1998		17.85	2	***	6.60	7	***							31
Biomass		10.61	2	***	9.88	7	***							32
1996		4.45	2	0	1.72	7	ns							32
1997														
1998														
<b>(D) ANOVAR functional group aboveground biomass.</b>														
Wet prairie and sedge meadow		3.00	2	ns	0.36	7	ns	0.37	2	ns	1.30	7	ns	32
Emergent		1.14	2	ns	0.60	7	ns	0.38	2	ns	1.50	7	ns	32
Floating aquatic		1.03	2	ns	1.41	7	ns	0.94	2	ns	1.65	7	ns	32
Mudflat annual		3.88	2	0	3.10	7	**	6.13	2	**	3.24	7	**	32
Woody		0.57	2	ns	1.01	7	ns	1.63	2	ns	1.01	7	ns	32
<b>(E) ANOVA mudflat annual functional group.</b>														
1997		4.35	2	0	3.56	7	**							32
1998		4.92	2	**	3.15	7	**							32

**Note:** Sources in parentheses indicate nesting. \* $p \leq 0.05$ ; \*\* $p \leq 0.01$ ; \*\*\* $p \leq 0.001$ ; ns,  $p > 0.05$ .

**Table 4.** Mean (1 SE) plant richness, Shannon–Weaver diversity, and aboveground biomass in saturated and flooded zones for each year of the study.

Treatment	Richness (species/m <sup>2</sup> )		Diversity		Biomass (g/m <sup>2</sup> )	
	Saturated	Flooded	Saturated	Flooded	Saturated	Flooded
1996						
Hydrologic	3.9 (0.8) <i>aA</i>	1.2 (0.4) <i>aB</i>	0.9 (0.2) <i>aA</i>	0.2 (0.1) <i>aB</i>	309 (92) <i>aA</i>	96 (62) <i>aB</i>
Planted	3.7 (0.5) <i>aA</i>	0.4 (0.2) <i>aB</i>	0.8 (0.1) <i>aA</i>	0.2 (0.1) <i>aB</i>	168 (62) <i>aA</i>	14 (14) <i>aB</i>
Reference	3.6 (0.8) <i>bA</i>	4.5 (0.4) <i>bB</i>	0.4 (0.1) <i>aA</i>	0.7 (0.1) <i>aB</i>	457 (38) <i>bA</i>	570 (90) <i>bB</i>
1997						
Hydrologic	3.8 (0.7) <i>aA</i>	1.0 (0.4) <i>aB</i>	0.6 (0.1) <i>aA</i>	0.2 (0.1) <i>aB</i>	1221 (368) <i>aA</i>	255 (209) <i>aB</i>
Planted	5.2 (0.3) <i>aA</i>	1.2 (0.7) <i>aB</i>	0.6 (0.1) <i>aA</i>	0.2 (0.2) <i>aB</i>	667 (347) <i>aA</i>	1 (1) <i>aB</i>
Reference	4.2 (0.5) <i>bA</i>	5.0 (0.5) <i>bB</i>	0.8 (0.2) <i>bA</i>	1.1 (0.1) <i>bB</i>	530 (113) <i>bA</i>	533 (123) <i>bB</i>
1998						
Hydrologic	3.1 (0.8) <i>aA</i>	1.1 (0.5) <i>aA</i>	0.5 (0.2) <i>aA</i>	0.2 (0.1) <i>aB</i>	581 (163) <i>aA</i>	983 (605) <i>aA</i>
Planted	4.3 (0.8) <i>abA</i>	3.0 (1.4) <i>abA</i>	0.5 (0.1) <i>aA</i>	0.3 (0.3) <i>aB</i>	384 (158) <i>aA</i>	277 (180) <i>aA</i>
Reference	4.5 (0.3) <i>bA</i>	5.0 (0.6) <i>bA</i>	0.8 (0.1) <i>bA</i>	1.0 (0.1) <i>bB</i>	625 (106) <i>bA</i>	846 (116) <i>bA</i>

**Note:** Lowercase letters following values indicate significant differences in a single year; uppercase letters following values indicate significant differences in a single year between the saturated and flooded zones.

were also due to an unusually high cover (mean cover = 98%) of *Leersia oryzoides*. To determine if this species was the only difference between the restoration treatments, the communities were compared after removal of *Leersia oryzoides* from the data set. Without *Leersia oryzoides*, the communities were still significantly different (MRPP,  $p < 0.001$ ; data not shown) between restoration treatments. Ordination of species' biomass in 1997 and 1998 showed a distribution similar to cover data (data not shown).

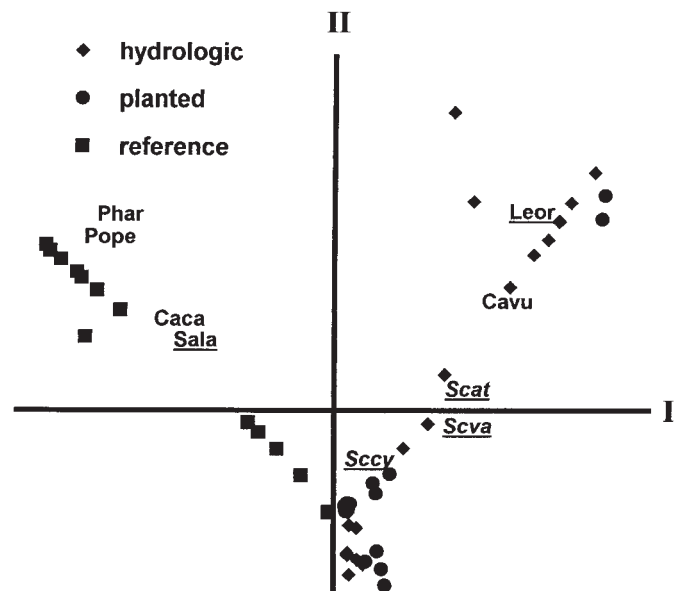
Ordination of plant cover data (15 species) from flooded permanent plots (data not shown) showed that reference sites had a plant community different from that of both restoration treatments (MRPP,  $p < 0.001$ ) but indicated no difference between restoration treatments. Axes I and II explained 37 and 21%, respectively, of variation in the covariance matrix. The reference sites had greater cover of *Carex lasiocarpa* ( $E1 = -0.17$ ,  $E2 = 0.94$ ), *Phalaris arundinacea* ( $E1 = 0.92$ ,  $E2 = 0.08$ ), and *Sagittaria latifolia* ( $E1 = 0.29$ ,  $E2 = 0.15$ ). The communities of restored sites were more influenced by *Bidens connatus* ( $E1 = -0.07$ ,  $E2 = -0.11$ ), *Leersia oryzoides* ( $E1 = -0.05$ ,  $E2 = -0.06$ ), and *Scirpus cyperinus* ( $E1 = -0.13$ ,  $E2 = -0.23$ ). Ordination of species' biomass in 1997 and 1998 showed a distribution similar to cover data (data not shown).

### Plant guilds

Aboveground biomass of mudflat annuals differed due to a year  $\times$  treatment and year  $\times$  hydrologic zone interaction (ANOVAR, Table 5). In 1997, both restoration treatments had lower biomass than reference sites. In 1998, planted restorations had greater biomass than hydrologic restorations and did not differ from reference sites. In 1997, the saturated zone had greater biomass, while in 1998, the flooded zone had greater biomass.

Aboveground biomass of wet prairie and sedge meadow species had an indication of differences among wetland treatments, indicating that there was greater biomass of this functional group in hydrologic restorations (ANOVAR, Table 5), but did not differ among years or hydrologic zone. There were no differences in aboveground biomass of emergent, floating aquatic, or woody species.

**Fig. 1.** PCA of plant species cover in saturated zone permanent plots for all years. Species codes are defined in Table 2. Nonitalicized species listed strongly affected the ordination. Underlined species indicate planted or seeded in at least one of the planted restorations. Italicized and underlined species were planted or seeded in at least one of the planted restorations but did not strongly affect the ordination. Species are plotted based on eigenvectors from PCA.



### Precipitation and water depth

Monthly precipitation data from the two nearest NOAA weather stations were used to measure differences in precipitation among years. During the active growing season prior to sampling (May–July), mean precipitation totals for both stations were 44.3% lower in 1998 than the average rainfall for 1996 and 1997. This precipitation difference was evident in the measurements of standing water depth of each plot taken during annual sampling at peak standing crop. Saturated plots remained within our definition of saturated (0 to +5 cm stand-

ing water depth) with an average ( $\pm$ SE) depth of  $4.4 \pm 0.6$  cm during the three years of the study. Flooded plots had an average depth of  $19.3 \pm 0.9$  cm during 1996 and 1997, but in 1998 the average depth decreased 58% to  $8.2 \pm 1.9$  cm.

During annual sampling in 1996 and 1997, 88% of our permanent saturated plots had 5 cm or less of standing water, and 98% of our permanent flooded plots had 20 cm or greater of standing water, indicating that hydrology was similar among sites. In 1998, 95% of our permanent saturated plots had 5 cm or less of standing water, and only 10% of our permanent flooded plots had 20 cm or greater of standing water, showing the effects of drought. The similarity in water depth changes also indicates that hydroperiods were similar among all sites.

## Discussion

Planting of wetland restorations at the low densities found in these planted restorations offers no clear advantages over hydrologic restoration. The only indication that plant community structure (richness, diversity, biomass) was affected by planting was equivalent richness to reference sites during the final study year, possibly due to greater on-site seed production immediately following planting. The main plant community differences between restoration treatments were due to increased abundance of *Leersia oryzoides* and *Phalaris arundinacea* in the saturated zone of hydrologic restorations. Hydrologic restorations also had a greater number of wet prairie and sedge meadow species. The nurse crop of annual rye may cause community differences in planted restorations by competitively limiting establishment of other grasses, such as *Leersia oryzoides* and *Phalaris arundinacea*, in planted restorations. Additionally, annual rye would increase initial shade levels, which limits germination of wet prairie and sedge meadow species such as *Carex vulpinoidea* (Baskin and Baskin 1998) and *Scirpus atrovirens* (Isely 1944). The absence of floating aquatic species in planted restorations is likely due to waterfowl herbivory (Kubichek 1933; J.F. New and Associates, Inc. 1993), whereas the limited spread of planted woody species is attributable to limited seed production by plants this young. The minimal plantings of these restorations are analogous to remnant wetland vegetation, which was found to only slightly affect vegetation community development in restored marshes (Brown 1998). Because hydrologic restorations dominated by monotypic communities (e.g., *Phalaris arundinacea*, *Typha* spp.) were excluded from the study, the differences between hydrologic and planted restorations may be greater than these results suggest. However, because the plant communities of hydrologic restorations were so strongly affected by the presence of two grass species, it is unlikely that the conclusions would change fundamentally in most restorations. These results refute the expected differences in species richness, diversity, and aboveground biomass between restoration treatments of our first hypothesis.

Although there were significant differences between restored and reference sites in plant community structure (richness, diversity, biomass), these differences were of a small magnitude in the saturated zone. Small differences in plant community structure among restoration treatments and reference wetlands indicate rapid colonization during early

**Table 5.** Mean (1 SE) aboveground biomass for plant guilds in saturated and flooded zones for 1997 and 1998.

Guild	Aboveground biomass (g/m <sup>2</sup> )		
	Hydrologic	Planted	Reference
Wet prairie and sedge meadow			
1997	403 (220)	32 (21)	1 (1)
1998	304 (122)	139(72)	10(10)
Mudflat annual			
1997	1 (0) <i>a</i>	0 <i>a</i>	8 (5) <i>b</i>
1998	0 <i>a</i>	38 (21) <i>b</i>	6 (6) <i>ab</i>
Emergent			
1997	302 (120)	317 (201)	523 (79)
1998	478 (302)	209 (85)	675 (74)
Floating aquatic			
1997	9 (7)	0	0
1998	0	0	0
Woody			
1997	2 (2)	0	0
1998	0	0	4 (4)

**Note:** Letters following values indicate significant differences among treatments in a single year.

secondary succession in restored freshwater marshes. The rapid increases in these community indices in the saturated zone are in contrast with the results of Reinartz and Warne (1993), who found higher richness in seeded freshwater marsh restorations than in unseeded, hydrologic restorations 1–3 years after initiation of restoration. This difference is likely due to the increased richness of seeding (22 species) of that study over ours. Similar to our sites, rapid recovery of biomass has been found in restored salt marshes (Broome et al. 1982, 1988), although other salt marshes show slower accumulations of biomass (Boyer and Zedler 1998).

In the flooded zone, increased richness and aboveground biomass in response to drought indicate that germination limitation is responsible for differences in structural traits between restored and reference wetlands. Increases in richness and biomass of restored sites in the flooded zone during 1998 show the dramatic response that can occur when normally flooded areas experience mudflat conditions. Lack of favorable germination conditions has a great effect on plant communities during succession (van der Valk 1981), and water drawdowns are essential for germination of many wetland species (Galinato and van der Valk 1986; Weiher et al. 1996; Toner and Keddy 1997). That these changes are a response to drought, rather than to changes in seed availability or successional trends, is indicated by the presence of mudflat annual (*Bidens connatus*, *Lindernia dubia*) and wet prairie (*Leersia oryzoides*) species growing in normally flooded zones of reference sites, which were only present in 1998 (Table 2). Due to the drought, the plant community in the flooded zone may increase quickly as plants that germinated during the drought spread vegetatively. These results support our second hypothesis by showing the importance of germination limitation in deeper water zones in slowing rates of increase of species richness, diversity, and biomass in both restoration treatments.

Although there were differences in communities between restoration treatments, the most striking differences were between restored sites as a group and reference sites. The differences in community composition between re-

stored and reference sites imply the importance of colonization during secondary succession in these systems. Some differences resulting from lack of colonization into restored sites were the absence of species such as *Polygonum pensylvanicum* and *Calamagrostis canadensis* in all restorations. Increasing dominance of *Phalaris arundinacea* in reference sites may be due to competitive spread of the invasive grass. The greater presence of sedge meadow and wet prairie species in restorations compared with reference sites differs from hydrologically restored prairie potholes (Galatowitsch and van der Valk 1996a, 1996b), possibly indicating greater colonization and restoration potential of these species in this area. This may be due to a greater number of small relict wetlands in the study area that provide a source of seeds for dispersal but is more likely due to the inhibitive effect of *Phalaris arundinacea* in reference sites. Community differences between restored and reference wetlands were driven by differences in species and not guilds, as shown by the minor differences in guild biomass. These results support our third hypothesis that plant communities would differ among wetland treatments.

These results clearly show the difficulties in predicting the rate and direction of plant community development during early succession. When commonly monitored structural indices such as species richness, diversity, and aboveground biomass were compared, both types of restorations had only small differences from reference sites 5–6 years after initiation of restoration, particularly in the saturated zone. However, the small number of wetlands used in this study may have reduced our power to detect differences among treatments. Despite the small differences in structural characteristics, the differences in species composition of plant communities between restored and reference wetlands contradict expectations of easy re-establishment of plant communities (National Research Council 1992). These results indicate the need for longer monitoring periods to allow time for stochastic events, such as droughts, to structure the plant communities in restored marshes. This study also emphasizes the need for longer-term data sets on which to set realistic monitoring requirements (Zedler and Callaway 1999).

Increased abundance of *Phalaris arundinacea* in reference sites indicates the need for ongoing management of plant communities in restored wetlands. Active management has been proposed for sedge meadow and wet prairie species in prairie potholes (Galatowitsch and van der Valk 1995), and it appears that *Phalaris arundinacea* may be particularly important in inhibition of species from this guild, although this was not explicitly tested. Our results indicate that some species, such as *Sagittaria latifolia*, benefit from even low levels of introduction during restoration. However, the planting of other species, such as *Leersia oryzoides*, *Scirpus atrovirens*, and *Scirpus cyperinus*, appears unnecessary. More intensive planting and careful selection of species introduced may limit the effects of colonization and reduce the variability inherent in hydrologic restorations. An initial reduction in variability of succession may lessen the oft-noted difficulties of permitting agencies in judging success of restorations.

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