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Author(s): Susan M. Galatowitsch and Arnold G. van der Valk
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THE VEGETATION OF RESTORED AND NATURAL PRAIRIE WETLANDS[1]

SUSAN M. GALATOWITSCH[2] AND ARNOLD G. VAN DER VALK
Department of Botany, Iowa State University, Ames, Iowa 50011 USA

Abstract. Thousands of wetland restorations have been done in the glaciated midcontinent of the United States. Wetlands in this region revegetate by natural recolonization after hydrology is restored. The floristic composition of the vegetation and seed banks of 10 restored wetlands in northern Iowa were compared to those of 10 adjacent natural wetlands to test the hypothesis that communities rapidly develop through natural recolonization. Restoration programs in the prairie pothole region assume that the efficient-community hypothesis is true: all plant species that can become established and survive under the environmental conditions found at a site will eventually be found growing there and/or will be found in its seed bank. Three years after restoration, natural wetlands had a mean of 46 species compared to 27 species for restored wetlands. Some guilds of species have significantly fewer (e.g., sedge meadow) or more (e.g., submersed aquatics) species in restored than natural wetlands. The distribution and abundance of most species at different elevations were significantly different in natural and restored wetlands. The seed banks of restored wetlands contained fewer species and fewer seeds than those of natural wetlands. There were, however, some similarities between the vegetation of restored and natural wetlands. Emergent species richness in restored wetlands was generally similar to that in natural wetlands, although there were fewer shallow emergent species in restored wetlands. The seed banks of restored wetlands, however, were not similar to those of natural wetlands in composition, mean species richness, or mean total seed density. Submersed aquatic, wet prairie, and sedge meadow species were not present in the seed banks of restored wetlands. These patterns of recolonization seem related to dispersal ability, indicating the efficient-community hypothesis cannot be completely accepted as a basis for restorations in the prairie pothole region.

Key words: colonization; dispersal; Iowa; life history strategies; plant communities; prairie potholes; revegetation; seed banks; species richness; succession; wetland restoration; zonation.

INTRODUCTION

LaGrange and Dinsmore (1989) concluded "that a high-quality wetland, with a plant and animal community very similar to unaltered wetlands, can be restored by removing or blocking tile lines." LaGrange and Dinsmore's (1989) study as well as other pioneering studies (Madsen 1986, 1988, Sewell and Higgins 1991) of restored wetlands in the prairie potholes region suggested that a drained wetland can be restored by either plugging its drainage ditch or destroying its drainage tile line(s), i.e., by restoring its hydrology. Once a wetland's hydrology was restored, wetland vegetation would become reestablished naturally within a few years. Consequently, no effort has been made to plant or seed appropriate wetland species in hydrologically restored prairie potholes. Thousands of such restorations have been done in the United States section of the North American prairie pothole region since the mid-1980s (Galatowitsch 1993). This is in sharp contrast to wetland restoration projects in other parts of the United States in which active revegetation is typically a major feature of a project (Committee on the Restoration of Aquatic Ecosystems 1992).

We will refer to the idea that the vegetation of restored prairie pothole wetlands will develop rapidly after their hydrology has been restored as the "efficient-community" hypothesis. Current restoration programs are based on the assumption that this hypothesis is true for prairie wetlands, although it has not been explicitly tested. According to the efficient-community hypothesis, all plant species that can become established and survive under the environmental conditions found at a site will eventually be found growing there and/or will be found in its seed bank. In other words, composition of the vegetation does not reflect dispersal ability. If the hypothesis is true, then all restored wetlands will develop plant communities resembling those of natural wetlands, regardless of location or efforts to plant or seed. On the other hand, if the hypothesis is false, then restoration recovery will be affected by proximity to propagule source and by deliberate introduction of propagules by planting or seeding.

Because prairie wetlands undergo cyclic changes in their vegetation in response to changes in water depth (van der Valk and Davis 1978, van der Valk 1981), the

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[2] Present address: Departments of Horticultural Science and Landscape Architecture, University of Minnesota, Saint Paul, Minnesota 55108 USA.

vegetation in the deeper sections of prairie potholes ranges from that in the drawdown phase when mudflat annuals are dominant to that of the regenerating phase when emergent species are dominant to that of the lake phase when submersed aquatics are dominant. Consequently, in a short-term study, not all the species present in a wetland will be found in the vegetation. Nearly all species in these wetlands that are found during the various vegetation phases are, however, present in their seed banks (van der Valk and Davis 1976, 1978, 1979). An examination of the species composition of the seed bank can be used to determine what species are present in a wetland that are not found in its vegetation at a given time.

For a wetland restoration, the efficient-community hypothesis implies that the success or failure of a restoration will depend primarily on how well pre-drainage environmental conditions are reestablished. If true, after successful restoration of the pre-drainage hydrology, the spread of refugial populations, recruitment from remnant seed banks, and/or dispersal of propagules to the restored basin will quickly reestablish vegetation that is identical in composition and structure to that of the pre-drainage period. Wienhold and van der Valk (1989) noted that some species, such as *Scirpus fluviatilis* and *Scirpus validus,* seem to be able to persist as marginal populations in drained wetlands. Wienhold and van der Valk (1989) also showed that seeds of some wetland species can persist in the seed banks of drained and cultivated wetlands. Seed density and species richness, however, declined with increasing duration of drainage. Very little is known about the role of dispersal in recolonizing restored wetlands. Waterfowl are suspected to be a primary vehicle of dispersal of many wetland species (deVlaming and Proctor 1968, Gill 1974, Powers et al. 1978).

To test the efficient-community hypothesis, we need to make operational "all plant species" and "eventually" in the definition. A survey of "all plant species" found in the seed banks and vegetation of comparable natural wetlands provides the best estimate of what species should be found in successfully restored wetlands. In such a survey, suitable comparable natural wetlands must be in close proximity to the restored wetlands, must be the same size and depth, and must have the same hydrology. Because the operating assumption of managers in the region is that vegetation reestablishes immediately (within 1 yr) from persistent seed banks and because the existing literature has supported this notion, it seems reasonable that "eventually" initially be defined as $\leq$3 yr after restoration. Previous surveys of the vegetation of restored prairie potholes did not compare the composition of the vegetation of restored wetlands to that of comparable natural wetlands. Nor did they examine the seed banks of restored wetlands to determine if species not represented in the vegetation were present in the restored wetland and if the seed banks of restored wetlands were similar to those of natural wetlands. After 3 yr it is unlikely that the vegetation of restored wetlands will resemble that of natural wetlands in all respects, but, at a minimum, a comparison of the species present in the seed banks and vegetation in restored and natural wetlands seems an appropriate initial test of the efficient-community hypothesis. At these initial stages of reestablishment, any effects of recolonization ability on community composition will be most pronounced and therefore detectable.

In this study we compare the overall floristic composition, distribution of species at four elevations, and composition of the seed banks of 10 recently restored wetlands that had been tile-drained and cultivated for >25 yr to those of 10 comparable natural wetlands. The objectives of the study are to determine (1) how closely the composition of the vegetation of restored wetlands after 3 yr of reflooding resembles that of natural wetlands and (2) how closely the composition of the seed banks of restored wetlands after 3 yr of reflooding resembles that of natural wetlands.

METHODS

Study sites

Ten restored wetlands in five counties in northern Iowa (42°30′–43°30′ N, 93°–95° W) were selected from 62 restored wetlands that were being monitored as part of a general study of restored prairie wetlands (Galatowitsch 1993). All 10 restored wetlands were on hydric soils that correspond to a pre-drainage seasonal or semipermanent water regime. Each basin had been tile-drained and completely cultivated for corn and soybean production for 25–75 yr, as confirmed from interviews with landowners and from federal crop compliance records (Galatowitsch 1993). Surveys of landowners established that none of the selected basins had areas predominated by residual wetland vegetation during cultivation. Each basin included in the study was thoroughly drained, without persistent ponding or saturation, throughout its agricultural usage. All 10 sites were restored in 1988 by disrupting tile lines leaving these wetlands. A nearby natural wetland of similar size and water regime was selected for each restored wetland (Fig. 1). All restored and natural wetlands were freshwater wetlands with mean specific conductance of water between 233 μS/cm and 748 μS/cm (Cowardin et al. 1979). Each of the 20 wetlands is an isolated basin, lacking surface water connections to other wetlands.

A topographic field survey was made of each basin to an accuracy of $\pm$3 cm using a surveying level. Topographic maps were produced by using SURFER (Golden Software, Inc., Golden, Colorado, USA). The high-water elevation was taken to be the level of the primary spillway or standpipe elevation for restored wetlands and the elevation of the water level in April 1991, when water levels were the highest, for natural wetlands. A staff gauge was installed in each wetland,

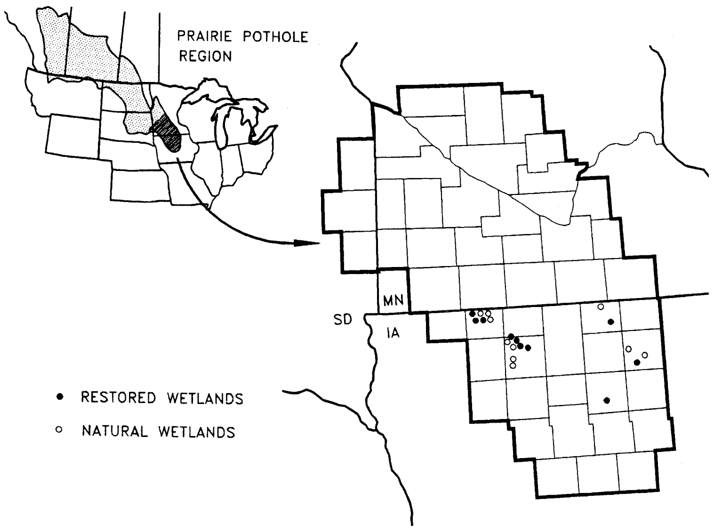

FIG. 1. The locations of the ten restored (●) and the 10 natural (○) wetlands in the prairie pothole region of northern Iowa, USA (IA = Iowa, MN = Minnesota, SD = South Dakota).

and water levels in each basin were recorded monthly from April to October 1991. For each basin, the proportion of the basin exposed when water levels dropped from the maximum to the minimum water level recorded in 1991 was estimated using SURFER.

Vegetation survey

A complete list of plant species was developed for each wetland from lists of species encountered during monthly surveys (April to October 1991) of the entire basin. During each survey the cover of each species was estimated using a standard cover-abundance scale (see *Species at different elevations,* below). Voucher specimens have been deposited in the Ada Hayden Herbarium of Iowa State University (Ames, Iowa). Nomenclature follows the Great Plains Flora Association (1986).

The floristic similarity of the vegetation in two wetlands was calculated for all pairs of basins using Sorenson's Index (Mueller-Dombois and Ellenberg 1974). The highest cover over the growing season of each species in a wetland was used in these calculations. The formula for Sorensen's Index of Similarity is $S = [2M_w/(M_a + M_b)] \times 100$, where M_w is the sum of smaller cover values of species common to wetlands A and B and where $M_{a,b}$ is the sum of all species cover values in stands A and B. Sorensen's Similarity Index (S) was converted to a Sorensen's Dissimilarity Index (D), a distance measure, using the following formula: $D = 1 - S$. Distance matrices were calculated for all pairs of restored wetlands, all pairs of natural wetlands, and all pairs of restored and natural wetlands.

The Mantel test, a nonparametric method for comparing two distance matrices, was used to determine if stand dissimilarities of pairs of restored and natural wetlands differed significantly from stand dissimilarities of pairs of either restored wetlands or pairs of natural wetlands (Fortin and Gurevitch 1993). The Mantel test measures the association between the elements in two matrices and gauges the significance of this association by comparison with the distribution of values found from randomly reallocating the elements of the second matrix (Manley 1991). Tests of the null hypothesis were made by randomizing the second matrix 1000 times and recalculating the "g" statistic (the index of matrix of similarity). The 1000 "g" values comprise the statistical distribution used to determine the significance of observed similarity.

Wetland plants were classified into eight guilds based on life history strategy (sensu van der Valk 1981 and Stewart and Kantrud 1971) and water-depth tolerance: wet-prairie perennials, sedge meadow perennials, shallow emergent perennials, deep emergent perennials, submersed aquatics, floating annuals, mudflat annuals, and woody plants. Species descriptions in floras and herbarium label information (from the Iowa State University collection) along with personal observations were used to obtain information used for the guild classification. The total numbers of species in each guild in restored and natural wetlands were compared with a Wilcoxon Rank Sum test.

Species at different elevations

Vegetation also was sampled using quadrats at four elevations in each wetland: 0 m (high-water line) and 0.15 m, 0.30 m, and 0.60 m below the high-water line. Five 1-m^2 quadrats were randomly located across the entire perimeter at each elevation. The vegetation within these quadrats was sampled in late July 1991 by estimating the total cover of each species. A seven-point cover scale (Mueller-Dombois and Ellenberg 1974) was used: (r ["rare"]) one individual with insignificant cover; (+) few individuals with insignificant cover; (1) 1–4%; (2) 5–24%; (3) 25–49%; (4) 50–74%; (5) 75–100%. For both restored and natural wetlands, the abundance of a species at an elevation was calcu-

TABLE 1. The mean size and depth of the 10 restored and 10 natural wetlands in northern Iowa, USA. Neither differs significantly between restored and natural wetlands (t test, $P > 0.05$).

Type of wetland	Size (ha)		Mean depth (cm)	
	Mean	Range	Mean	Range
Natural	2.3	1.1–6.0	33.5	18.6–54.5
Restored	2.4	0.5–6.6	45.4	16.1–83.3

lated by summing the cover classes of the species in the five quadrats at that elevation. The following six cover classes were used: "r" and "+" were designated "class 1," 1–4 % was class 2, class 3: 5–24%, class 4: 25–49%, class 5: 50–74%, and class 6: 75–100%. The abundance of a species at a given elevation can range from 0 (completely absent) to 30 (cover of 75 to 100%, cover class 6, in all five quadrats).

Seed bank survey

Seed bank samples were collected in each basin at the same four elevation ranges as used for the cover estimates at different elevations. Sediment was collected using a 7.5-cm-diameter core to a depth of 5 cm. Cores were taken at five random locations at each elevation in late April 1991. Sediment samples from each elevation were combined, mixed, bagged, and stored in a cold room (at 4°C) until late May 1991.

Each seed bank sample was sieved to remove litter, roots, and tubers and divided into two subsamples. Under greenhouse conditions, the soil in one set of subsamples was maintained at saturation (drawdown treatment) while the other set was shallowly flooded (flooded treatment) from May to September 1991. These seed bank subsamples (200 cm^3) were placed in plastic flats ($19.5 \times 19.5 \times 6$ cm) that had been filled with either 500 (drawdown) or 200 (flooded) cm^3 of sterilized sand. A water depth of 4–5 cm was maintained over the surface of the flooded flats by adding water as needed. Soil in saturated flats was watered once or twice daily. Flats within a treatment were completely randomized. Eight flats with sterile sand and soil were also placed at random on the bench to test for contamination of samples from greenhouse sources. No seeds germinated in these control flats.

Seedlings were counted and removed as they reached an identifiable stage. Most viable seeds should have germinated within the 4-mo assay period: past studies have shown that 90% of temperate wetland seedlings emerged within the first 3 mo (Pederson 1983). At the end of 4 mo, all remaining unknown seedlings were transferred to pots and grown to an identifiable stage. Seed densities are expressed as the number of seeds per square metre in a layer of soil 5 cm thick.

Seedling counts were used to estimate the number of viable seeds of a species in the drawdown and flooded treatments subsamples per unit area. The number of species in a given seed bank was the larger of the two estimates of its density from the drawdown and flooded treatments. Statistical analysis of seed bank data indicated no significant differences in density of species at different elevations. Subsequent analyses were done with pooled data. Seed bank dissimilarity between restored and natural wetlands was compared with a Mantel test, as previously described for floristic data. Wilcoxon rank-sum tests were used to test if the total number of seeds germinated and the total number of species differed in the natural and restored wetlands. All tests of significance were done at $\alpha=0.05$ (Hollander and Wolfe 1973). Species in the seed bank were also placed in guilds as described in *Vegetation survey,* above.

RESULTS

Wetland features

The 10 restored and 10 natural wetlands were similar in their mean size and mean water depth (Table 1). The mean difference between minimum and maximum water level from April to October 1991 was 0.39 m for both restored and natural wetlands (Table 2). The mean percentage of a basin exposed by seasonal drawdown also was similar, 56% for restored basins and 45% for natural basins.

Vegetation survey

Vegetation similarity was greater among restored wetlands or natural wetlands than between restored and natural wetlands ($P < 0.001$). Vegetation dissimilarity (Sorenson's Dissimilarity Index, D) between restored and natural wetlands ranged from $D = 56$ to $D = 88$; between restored wetlands from $D = 37$ to $D = 69$; and between natural wetlands from $D = 39$ to $D = 64$. Natural wetlands had a mean of 46 species per basin; restored wetlands had a mean of 27 species per basin. The vegetation of natural wetlands had significantly more wet-prairie, sedge meadow, shallow emergent,

TABLE 2. Drop in water level between April and October 1991 and basin exposure in the 10 natural and 10 restored wetlands in northern Iowa, USA. There is no significant difference between restored and natural wetlands (t test, $P > 0.05$).

	Water-level drop (m)		Proportion of basin exposed		Area exposed (m^2)	
	Restored	Natural	Restored	Natural	Restored	Natural
Mean	0.39	0.39	0.56	0.45	12 909	8721
SD	0.22	0.27	0.22	0.25	12 437	7650
Minimum	0.17	0.04	0.20	0.05	3359	557
Maximum	0.88	0.76	0.83	0.78	42 610	19 444

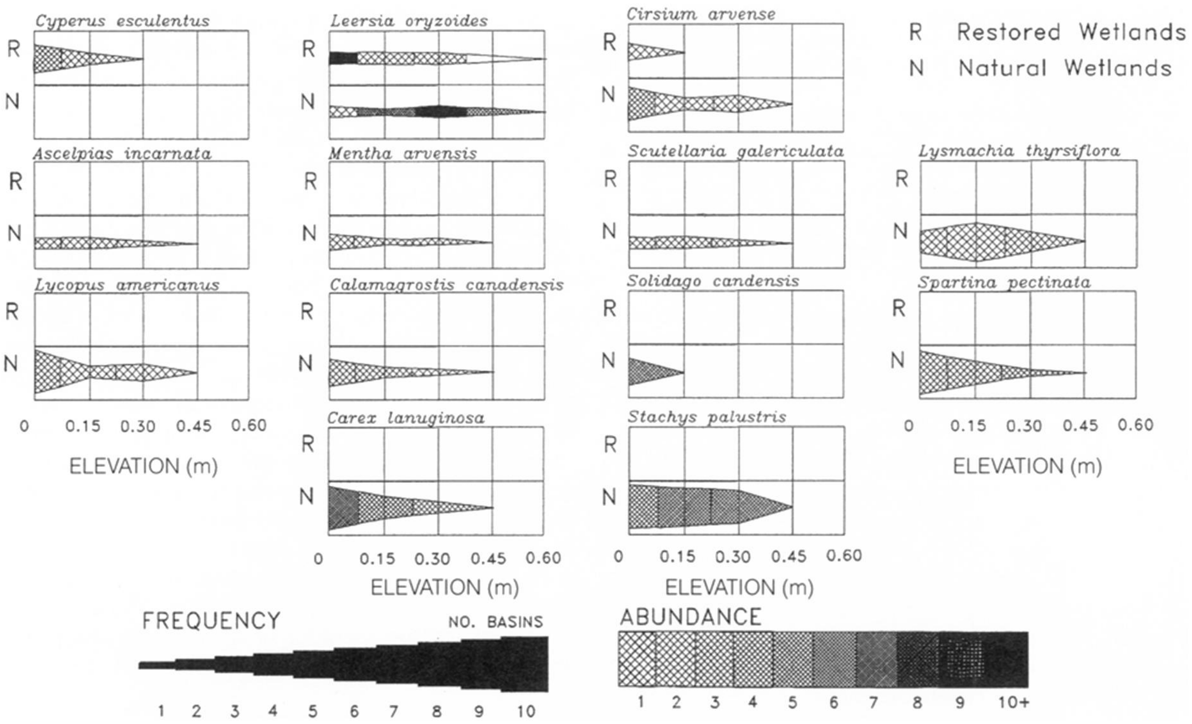

FIG. 2. Frequency and abundance of wet-prairie and sedge meadow plants in the 10 restored and 10 natural wetlands. Only species found in more than two wetlands are shown. Abundance is the sum of cover classes (see *Methods: Species at different elevations* for definition). The elevational gradient depicted ranges from 0 m at the periphery to 0.60 m within the basin.

and floating annual species than did restored wetlands. A greater diversity of submersed aquatics was found in restored wetlands than natural wetlands ($P = 0.002$). The numbers of species of deep emergent perennials, mudflat annuals, and woody plants were similar in natural and restored wetlands.

Nearly one half (45%) of the 106 wetland species observed were found only in natural wetlands. Of the 48 species found only in natural wetlands, 16 (33%) were wet-prairie perennials, 22 (46%) were sedge meadow species, 6 species (13%) were shallow emergent species, and 1 (2%) each was deep emergent, submersed aquatic, floating annuals, and mudflat species. Ten species (9%) were found only in restored wetlands. *Cyperus esculentus*, an introduced perennial, and a cultivated race of *Panicum virgatum* planted to limit soil erosion were two of these species. Two mudflat annuals, *Xanthium strumarium* and *Amaranthus rudis*, were seen only in restored wetlands. The remaining six species were all submersed aquatics.

Leersia oryzoides and *Cirsium arvense* were common wet-prairie/sedge meadow species in both restored and natural wetlands (Fig. 2). *Cyperus esculentus* was present in restored but not in natural wetlands. Although this species is a perennial, it was more common on mudflats than in densely vegetated areas (S. Galatowitsch, *personal observation*). *Sium suave, Glyceria grandis, Iris virginica, Carex atherodes, Carex lacustris*, and *Phragmites australis* were common emergent species of natural wetlands but were not found in restored wetlands (Fig. 3). *Phalaris arundinacea* was considerably more widespread and abundant in natural wetlands than in restored wetlands, as was *Polygonum amphibium*. Mudflat annuals were considerably more abundant in shallow areas of restored wetlands than of natural wetlands. *Bidens cernua, Amaranthus rudis*, and *Echinochloa* spp. were abundant in most restored wetlands (Fig. 4). *Bidens cernua* and *Polygonum pensylvanicum* were found in natural wetlands, but were not common. Of the submersed aquatics, *Potamogeton pectinatus* and *Potamogeton nodosus* were only common in restored wetlands; *Potamogeton foliosus* and *Ceratophyllum demersum* were only sporadic in natural wetlands (Fig. 5). *Potamogeton pectinatus, Potamogeton foliosus*, and *Ceratophyllum demersum* together approached 100% cover in deep (0.6 m) areas in restored marshes. *Utricularia vulgaris* was common in both restored and natural wetlands. This species tended to occur over a larger portion of the basins, often in the understory of emergent vegetation. *Spirodela polyrhiza, Ricciocarpus natans*, and *Riccia fluitans* were more common in the vegetation of natural wetlands. *Lemna minor* was present at high cover in restored and natural wetlands. *Lemna trisulca* was found in the plots of somewhat fewer basins than *Lemna minor*, but with high cover as well.

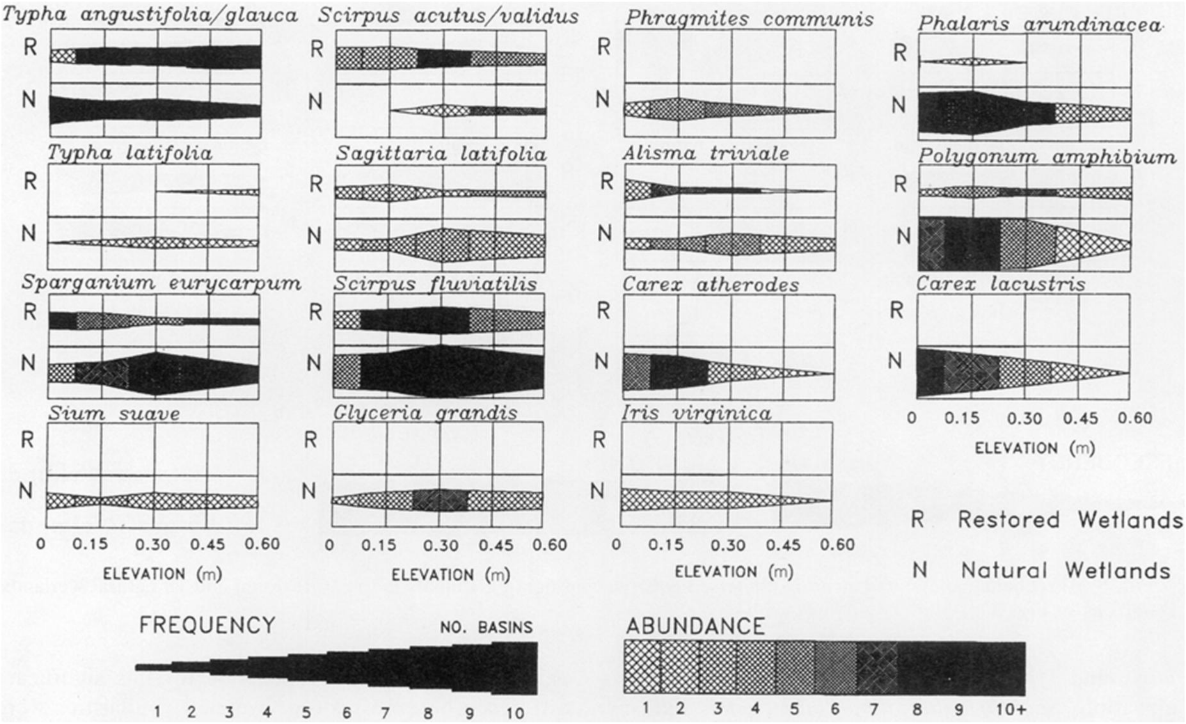

FIG. 3. Frequency and abundance of shallow emergent and deep emergent species in the 10 restored and 10 natural wetlands. Details as in Fig. 2.

Species at different elevations

The vegetation of restored wetlands at the 0-m elevation included, in order of decreasing importance based on frequency and abundance: *Bidens cernua, Lemna minor, Echinochloa* spp., *Amaranthus rudis, Sparganium eurycarpum* and *Leersia oryzoides* (Figs. 2–5). Four of these six species are annuals. In contrast, the 0-m elevation of natural wetlands was dominated exclusively by perennials: *Phalaris arundinacea, Carex lacustris, Carex lanuginosa, Solidago canadensis, Stachys palustris,* and *Typha glauca* (listed in decreasing order of importance, as is true throughout this section). At 0.15 m, *Lemna minor, Scirpus fluviatilis, Bidens cernua, Potamogeton foliosus,* and *Ceratophyllum demersum* predominated in restored wetlands. In natural marshes at the same elevation *Scirpus fluviatilis, Polygonum amphibium, Phalaris arundinacea, Lemna minor, Stachys palustris, Carex lacustris,* and *Lysmachia thyrsiflora* were most common. Similar to the 0.15-m elevation, *Scirpus fluviatilis* and *Lemna minor* were dominants of both restored and natural wetlands at 0.30 m. In addition, *Lemna trisulca, Utricularia vul-*

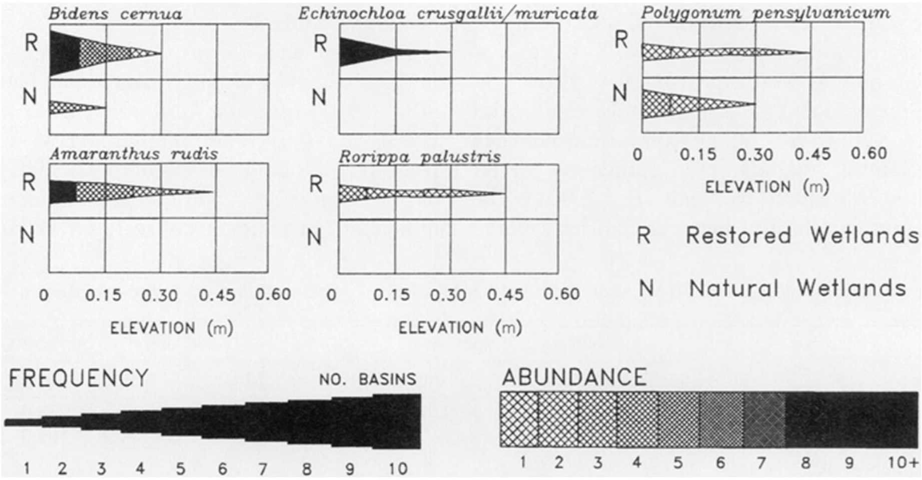

FIG. 4. Frequency and abundance of mudflat annuals in the 10 restored and 10 natural wetlands. Details as in Fig. 2.

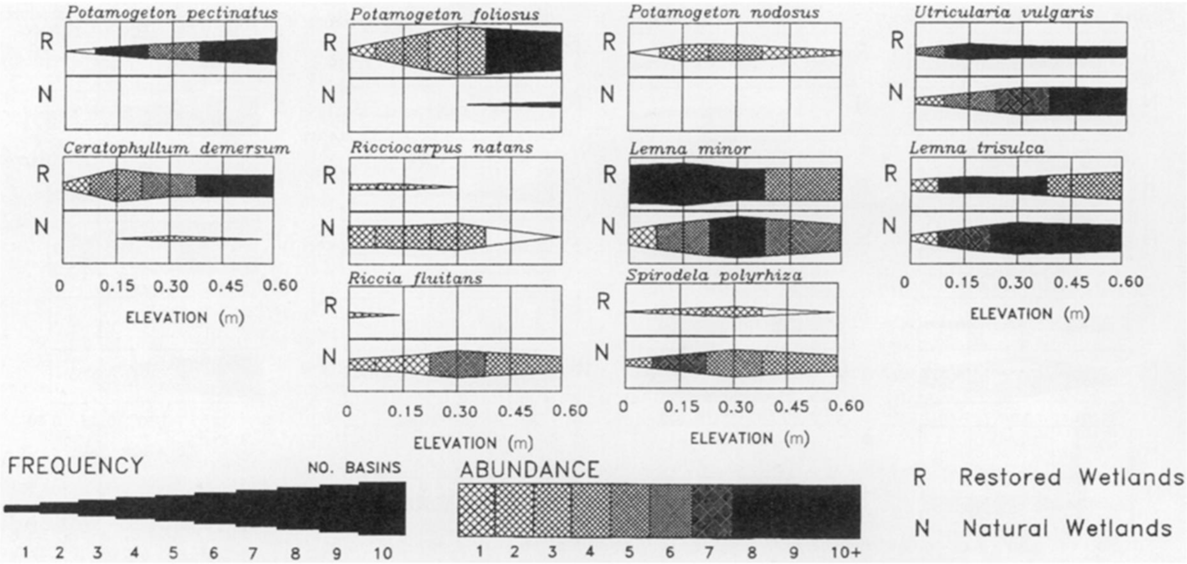

FIG. 5. Frequency and abundance of submersed aquatics and floating annuals in the 10 restored and 10 natural wetlands. Details as in Fig. 2.

garis, and *Typha glauca* were common to both at this elevation. *Sagittaria latifolia*, *Potamogeton foliosus*, and *Ceratophyllum demersum* were other abundant species at this elevation. In natural wetlands, other dominant species included *Sparganium eurycarpum*, *Polygonum amphibium*, *Phalaris arundinacea*, *Stachys palustris*, *Lysmachia thyrsiflora*, *Riccia fluitans*, and *Spriodela polyrhiza*. At 0.6 m, natural wetlands were dominated primarily by the emergents, *Scirpus fluviatilis*, *Sparganium eurycarpum*, and *Typha glauca*, along with *Utricularia vulgaris* and *Lemna trisulca*. In contrast, at this elevation restored wetlands were dominated by the submersed aquatics, *Potamogeton foliosus*, *Potamogeton pectinatus*, *Utricularia vulgaris* and *Ceratophyllum demersum* together with *Lemna trisulca* and *Typha glauca*.

Seed bank survey

Seed bank similarities (Sorenson's Similarity Index, S) among restored wetlands ranged from $S = 0$ to $S = 70$ and among natural wetlands from $S = 27$ to $S = 82$. Between restored and natural wetlands, similarities ranged from $S = 11$ to $S = 50$. Dissimilarities between restored and natural wetlands were significantly greater than for natural or restored wetlands ($P = 0.001$). The consistently high similarities between natural wetland pairs apparently were responsible for this significant difference because restored wetland similarities were highly variable. Natural wetlands had a mean of 15 species in their seed banks; restored wetlands had 8 species (Table 3). Natural wetlands had a mean seed density of 7369 seeds/m^2 while restored wetlands had a mean seed density of 3019 seeds/m^2.

Leersia oryzoides was detected from more sites of both restored and natural wetlands than any other sedge meadow species (Table 4). *Cyperus esculentus*, *Eleocharis* sp., *Scirpus atrovirens*, *Juncus dudleyi*, and *Juncus torreyi* were evident in the seed banks of several restored wetlands. These species were also present in the vegetation. Nine wet-prairie/sedge meadow species were found only in the seed banks of natural wetlands. *Calamagrostis canadensis*, *Lysmachia thyrsiflora*, and *Spartina pectinata* were not detected in the seed bank assay, although they were widespread in the vegetation of natural wetlands.

Typha sp. and *Scirpus acutus/validus* were common in the seed banks of both restored and natural wetlands (Table 4). *Sagittaria latifolia*, *Alisma triviale*, *Sium suave*, and *Polygonum amphibium* were not detected from the seed banks of restored wetlands. A few seeds of *Scirpus fluviatilis* and *Eleocharis macrostachya* germinated from sediments of restored wetlands; although

TABLE 3. Seed density and species richness in the seed banks of the 10 restored and 10 natural wetlands.

	Number of species		Seed density (no. seeds/m^2)	
	Mean	Range	Mean	Range
Restored wetlands	8	3–10	3018.7	500.0–5875.0
Natural wetlands	15	11–20	7368.7	3312.5–12 562.5
Significance of Wilcoxon rank-sum test	$P = 0.001$		$P = 0.003$	

TABLE 4. Species in different guilds in the seed bank samples from the 10 restored and 10 natural wetlands. Seed density was estimated from basins where each species was detected.

Species	Restored basins: No. of basins	Restored basins: Mean seed density (no. seeds/m²)	Natural basins: No. of basins	Natural basins: Mean seed density (no. seeds/m²)
Wet-prairie and sedge meadow species				
Leersia oryzoides	6	956.3	10	1181.3
Eleocharis sp.	2	625.0	4	581.3
Cyperus esculentus	3	375.0	1	125.0
Juncus dudleyi	2	156.3	1	62.5
Juncus torreyi	1	1812.5	1	250.0
Scirpus atrovirens	1	62.5	1	375.0
Solidago canadensis	0	0.0	3	62.5
Asclepias incarnata	0	0.0	2	187.5
Carex sp.	0	0.0	2	187.5
Eupatorium perfoliatum	0	0.0	2	93.8
Stachys palustris	0	0.0	2	93.8
Lycopus americanus	0	0.0	2	93.8
Cirsium arvense	0	0.0	1	125.0
Verbena hastata	0	0.0	1	125.0
Helianthus grosseseratus	0	0.0	1	62.5
Shallow and deep emergent species				
Typha spp.	8	125.0	10	1293.8
Scirpus acutus/validus	5	237.5	8	562.5
Phalaris arundinacea	2	31.3	4	437.5
Eleocharis macrostachya	1	62.5	9	1187.5
Scirpus fluviatilis	1	187.5	3	1812.5
Sparganium eurycarpum	1	125.0	5	125.0
Alisma triviale	0	0.0	7	543.8
Sium suave	0	0.0	5	150.0
Sagittaria latifolia	0	0.0	3	331.3
Polygonum amphibium	0	0.0	1	62.5
Submersed and floating aquatics				
Ricciocarpus natans	4	356.3	10	1006.3
Lemna minor	3	206.3	1	937.5
Potamogeton foliosus	0	0.0	2	62.5
Riccia fluitans	0	0.0	1	187.5
Mudflat annuals				
Echinochloa muricata/crusgallii	6	425.0	6	137.5
Amaranthus rudis	6	656.3	7	181.3
Polygonum pensylvanicum	6	375.0	6	281.3
Bidens cernua	3	331.3	0	0.0
Rorippa palustris	3	206.3	5	262.5
Cyperus aristatus	3	206.3	1	62.5
Polygonum lapathifolium	2	343.8	6	331.3
Eleocharis acicularis	2	125.0	4	468.8
Penthorum sedoides	0	0.0	1	125.0
Ammania robusta	0	0.0	1	125.0
Cyperaceae (unknown genera)	2	2062.5	8	1068.8

Phalaris arundinacea was the only shallow emergent species found in more than one basin. *Iris virginica, Glyceria grandis, Carex lacustris,* and *Carex atherodes* were not detected in the seed bank of natural wetlands although they were common in the vegetation of natural wetlands. *Polygonum amphibium* was rare in the seed banks of natural wetlands although it was common in the vegetation. No species were found in the seed bank that were not observed in the vegetation.

Amaranthus rudis, Polygonum lapathifolium, Polygonum pensylvanicum, Rorripa palustris, Eleocharis acicularis, and *Echinochloa* spp. were found in both restored and natural wetland seed banks (Table 4). *Bidens cernua,* however, was found only in restored wetlands. *Ammania robusta* and *Penthorum sedoides* were found only in seed banks of one natural wetland. Only two seeds of *Potamogeton foliosus* germinated from the sediment collected in restored basins. *Ricciocarpus natans* was frequently detected in restored and natural wetlands, although it was not common in vegetation. *Riccia fluitans* was found in the seed bank of one natural wetland. *Lemna minor* was detected in seed banks of three restored basins and one natural basin.

DISCUSSION

After 3 yr of reflooding, the vegetation of restored wetlands was not similar to that of natural wetlands in a number of ways. First, natural wetlands overall had many more species than restored wetlands. Second, some guilds of species had significantly fewer (e.g., sedge meadow) or more (e.g., submersed aquatics) species in restored than natural wetlands. Third, the distribution and abundance of most species at different elevations was significantly different in natural and restored wetlands. Fourth, the seed banks of restored wetlands contained fewer species and fewer seeds than those of natural wetlands. There were, however, some similarities between the vegetation of restored and natural wetlands. Emergent species in restored wetlands were generally similar to those in natural wetlands, although there were fewer shallow emergent species in restored wetlands. The presence of emergent species is largely what led LaGrange and Dinsmore (1989) to conclude that restored wetlands will revegetate naturally. However, differences among groups of plants to recolonize restored wetlands suggests the efficient-community hypothesis should be rejected.

Why is the vegetation of restored wetlands different from that of natural wetlands? The efficient-community hypothesis assumes that a combination of recruitment from the relict seed banks, from refugial populations, and from propagules dispersed by waterfowl and other means to the restored basins will quickly result in the reestablishment of wetland vegetation. Our results suggest that one or more of the three sources of wetland propagules is not operational for some guilds or, at least, not in the short term. For example, very few sedge meadow species were found in restored wetlands, and only three of these were native sedge meadow species (*Juncus dudleyi, Leersia oryzoides,* and *Verbena hastata*). Many common sedge meadow species in natural wetlands, including *Carex lanuginosa, Stachys palustris,* and *Spartina pectinata,* did not occur in any restored wetlands. Because the wet prairie and sedge meadow zone are only seasonally flooded, they are usually the most efficiently drained parts of a wetland and regularly cultivated. This makes it unlikely that species in these guilds will survive prolonged periods of cultivation. *Carex* species are known to persist primarily by vegetative growth and have very low annual seed production (van der Valk and Davis 1979). Low seed production in *Carex* also reduces the availability of propagules for dispersal.

Wet prairie and sedge meadow species are poorly represented in the seed banks of both natural and restored wetlands, but particularly in restored wetlands. Wienhold and van der Valk (1989) reported that propagules of sedge meadow species persisted <20 yr in the seed bank. Since remnant seed banks will not likely be important for recolonization of sedge meadow species in restored wetlands, the rate and magnitude of dispersal of their propagules will determine how quickly these species will become reestablished. Unfortunately, the probability of many species in these guilds reaching isolated restored wetlands is probably very low. The few fast-growing species, such as *Phalaris arundinacea* or *Leersia oryzoides,* that do seem to be able to become established within a few years after restoration in these zones may eventually preempt the wet prairie and sedge meadow zones. This may make it even more difficult for other species in these guilds to become established should their propagules reach the restored wetland.

The efficient-community hypothesis, however, seems to hold for submersed aquatics. In fact, there were more submersed aquatics in restored wetlands than in natural wetlands. There was only one species of submersed aquatic in the seed banks of natural wetlands and none in the seed banks of restored wetlands. This suggests that seeds or other propagules of submersed species are reaching restored wetlands readily, presumably carried by waterfowl. Waterfowl are known to use restored wetlands as soon as they have standing water (LaGrange and Dinsmore 1989, Sewell and Higgins 1991, Delphey and Dinsmore 1993). Theoretically, submersed propagules should have had an equal chance of reaching restored and natural wetlands in this study because they were adjacent. There are two possible reasons why submersed aquatics are more numerous in restored than natural wetlands. One, the propagules of some submersed aquatic species are more likely to reach restored wetlands than natural wetlands because they are carried by species of waterfowl that prefer the mudflats or open water of restored wetlands. Two, shading by plant canopies (van der Valk and Davis 1978) or fallen litter (van der Valk 1986) may preclude the establishment or growth of many submersed aquatics, such as *Potamogeton* spp., that are not shade tolerant in natural wetlands. Few submersed aquatics, notably *Utricularia vulgaris,* were regularly observed within dense stands of emergent vegetation. If the latter is true, as emergent vegetation becomes more widespread and dense in restored wetlands, submersed aquatics will become less abundant and some species could be eliminated.

There is some additional indirect evidence that dispersal during the first 3 yr is responsible for establishing new species in restored wetlands. A comparison of our seed bank data with that for drained and natural wetlands reported by Wienhold and van der Valk (1989) suggests restored wetlands in our study have more species in their seed banks than is expected. The intensity of seed bank sampling in a wetland by Weinhold and van der Valk (1989) was similar to that in this study. The 3-yr-old restored marshes in this study have seed banks with a mean number of species that is intermediate between drained and natural wetlands. Wienhold and van der Valk (1989) found a mean of 12 species in the seed bank for natural wetlands (the natural wetlands in this study had a mean of 15 species) while wetlands drained between 10 and 70 yr had mean species richnesses between 2 and 5 species. Restored wetlands that had been drained 20–70 yr had a mean

8 species in their seed banks. Galatowitsch (1993) and Galatowitsch and van der Valk (1995) also found that there was an increase in the mean number of species in the vegetation of restored wetlands from 1989 through 1991.

Because there is some similarity between the vegetation of restored and natural wetlands and because there is some evidence that this similarity is increasing with time, a weaker version of the efficient-community hypothesis seems to be more appropriate for restored prairie potholes. In the weak version, dispersal of propagules to hydrologically restored basins is the primary mechanism responsible for the reestablishment of wetland vegetation. Because the dispersability of propagules of different guilds of species varies significantly, the rate of revegetation of different communities in a restored wetland will vary significantly. This implies that the revegetation of some communities will take many years (Godwin 1923), and possibly may never occur because dispersal of propagules to restored wetlands effectively is impossible for restored wetlands that have no surface connections to natural wetlands or other restored wetlands because they are surrounded by farmland. On the basis of a survey of the flora of a number of ponds in the same region of England that varied in age from 25 to 250 yr, Godwin (1923) concluded that land barriers greatly slowed the dispersal of wetland species. Restored prairie wetlands are much more isolated today than prairie potholes were prior to their drainage. So, dispersal may not be as reliable as it was in the past. Large-scale studies of species of small, free-floating aquatic species (lemnids) in Polish aquatic systems also indicate that the dispersal of propagules is essentially random (Wolek 1983). Thus, there is no certainty that species capable of becoming established will ever do so in a particular wetland. Consequently, species in guilds with poor dispersal capabilities may have to be planted or sown in restored prairie pothole wetlands if these restored wetlands are ever to have vegetation that is similar to their pre-drainage vegetation.

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