2001

Invertebrate Egg and Plant Seed Banks in Natural, Resorted, and Drained Wetlands in the Prairie Pothole Region (USA) and Potential Effects of Sedimentation On Recolonization of Hydrophytes and Aquatic Invertebrates

Robert Andrew Gleason
South Dakota State University

INVERTEBRATE EGG AND PLANT SEED BANKS IN NATURAL, RESTORED, AND DRAINED WETLANDS IN THE PRAIRIE POTHOLE REGION (USA) AND POTENTIAL EFFECTS OF SEDIMENTATION ON RECOLONIZATION OF HYDROPHYTES AND AQUATIC INVERTEBRATES

BY

ROBERT ANDREW GLEASON

A dissertation submitted in partial fulfillment of the requirements for the

Doctor of Philosophy

Biological Sciences

Wildlife Science Specialization

South Dakota State University

2001

INVERTEBRATE EGG AND PLANT SEED BANKS IN NATURAL, RESTORED, AND DRAINED WETLANDS IN THE PRAIRIE POTHOLE REGION (USA) AND POTENTIAL EFFECTS OF SEDIMENTATION ON RECOLONIZATION OF HYDROPHYTES AND AQUATIC INVERTEBRATES

This dissertation is approved as a creditable and independent investigation by a candidate for the Doctor of Philosophy degree and is acceptable for meeting the dissertation requirements for this degree. Acceptance of this dissertation does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

Dr. Daniel E. Hubbard — Date
Major Advisor

Dr. Charles G. Scalet — Date
Head, Department of Wildlife and Fisheries Sciences

ACKNOWLEDGMENTS

I thank the U.S. Geological Survey's Northern Prairie Wildlife Research Center (NPWRC), Jamestown, North Dakota, for sponsoring me as a graduate student, and extend a special thanks to Dr. Ned (Chip) H. Euliss, Jr. of NPWRC, for providing funding and the original impetus for this research. I thank committee members, Dr. Walter G. Duffy, Dr. Ned H. Euliss, Jr., Dr. Gary E. Larson, and Dr. James A. Rice for their support and critical review of this dissertation. A special thanks goes to my advisor, Dr. Daniel E. Hubbard, for his guidance and friendship during this research endeavor.

This project would not have been possible without the assistance and cooperation of many state and federal personnel from the U. S. Fish and Wildlife Service (Region 3 and 6), U. S. Department of Agriculture's Natural Resources Conservation Service, Minnesota Department of Natural Resources, South Dakota Department of Game, Fish, and Parks, and Iowa Department of Natural Resources. Additionally, I am indebted to the many land owners in Montana, North Dakota, South Dakota, Minnesota, and Iowa for granting access to wetlands on private lands.

A special thanks goes to the U. S. Department of Agriculture's Agricultural Research Service Northern Plains Insects Laboratory, for providing the geenhouse facilities to conduct my experiments. I an indebted to Dr. Charles W. Holmes of the U. S. Geological Survey's Marine and Coastal Research Laboratory for answering my many questions about isotopic dating techniques. A special thanks goes to Paul Coughlin of the South Dakota Department of Game, Fish, and Parks for participating in a U.S.

Department of Interior State partnership proposal to acquire funding for this project. I also would like to thank Brian Check and Chris Locken for their assistance in collection of 'dirt' samples and for conducting my invertebrate egg bank experiments. Likewise, I extend a special thanks to Kyle Kelsey for assistance with my seedling emergence experiments. Other members of NPWRC that deserve thanks include: Wesley Newton and Deb Buhl for their statistical assistance; David Mushet and Bruce Hanson for coordinating many activities related to this project; and Tom Skelbar and Ann Dahl for providing GIS and mapping assistance.

Lastly, and most importantly, I thank my wife Melissa, for her love, encouragement, and patience while completing this dissertation. And I promise Melissa, I will not pursue any more degrees.

ABSTRACT

INVERTEBRATE EGG AND PLANT SEED BANKS IN NATURAL, RESTORED, AND DRAINED WETLANDS IN THE PRAIRIE POTHOLE REGION (USA) AND POTENTIAL EFFECTS OF SEDIMENTATION ON RECOLONIZATION OF HYDROPHYTES AND AQUATIC INVERTEBRATES

Robert A. Gleason

May 2001

Sediment is the major pollutant of wetlands, lakes, rivers, and estuaries in the United States and it poses unique threats to wetlands of the Prairie Pothole Region (PPR). Sediment may impact the success of wetland restorations because burial of invertebrate and plant propagules may impact hatching and germination success, and hence, may hamper successional changes throughout interannual climate cycles. Sedimentation also reduces the pool depth and volume, further exacerbating the recovery of hydrophyte communities in restored wetlands. I evaluated the potential impacts of sedimentation on prairie wetlands from several perspectives. First, I evaluated the effects of sedimentation on loss of wetland pool depth and volume, and secondly, I examined the effect of sediment load on emergence of plants and invertebrates from seed and invertebrate egg banks. Additionally, I compared the seed and invertebrate egg bank composition of high quality reference wetlands (i.e., having no history of cultivation) to previously farmed

nondrained, restored, and drained seasonal and semipermanent wetlands in the Missouri and Prairie Coteau, and Glaciated Plain physiographic regions of the PPR.

My results demonstrated that previously farmed wetlands of all categories had greater mean (± SE) accretion (0.26 ± 0.02 cm yr^{-1}) and mass accumulation (0.268 ± 0.027 g cm^{-2} yr^{-1}) rates of sediments than non-farmed reference wetlands (0.08 ± 0.03 cm yr^{-1}, 0.068 ± 0.034 g cm^{-2} yr^{-1}). Projected over the next 200 years, I estimated that cultivated and reference wetlands would accrete significant quantities of sediment, resulting in a 57% and 18% loss, respectively, in the number of wetlands capable of attaining water depths ≥ 1 m. Wetland pool depths ≥ 1 m are important for the establishment of vegetative zones during seasonal and interannual wet and dry periods. Also, over the next 200 years, I estimated that 50% and 20% of the wetland volume (203 hectare-meters) would be lost based on my estimated accretion rates for cultivated and reference wetlands, respectively.

Egg bank hatching success in seasonal wetlands was lowest in drained wetlands. Drained and restored semipermanent wetlands in the Glaciated Plain and Missouri Coteau also had poorer hatching success than reference and nondrained wetlands. More restored seasonal wetlands in the Coteau regions attained taxon richness similar to reference and nondrained wetlands than in the Glaciated Plain. Within 5 years after restoration, most restored seasonal wetlands contained viable invertebrate egg banks, but I was unable to detect a significant increase in taxon richness and invertebrate abundance with restoration age. Hatching success and abundance of invertebrate egg banks in restored semipermanent wetlands were lower than in seasonal wetlands.

Trends indicated that for all regions and wetland classes, reference wetlands had greater perennial-native seed density, taxon richness, floristic quality, and fewer annual species than nondrained, restored, and drained wetlands. However, most comparisons of perennial-native response variables were found to be similar among nondrained, restored, and drained wetlands. I found no increase in the floristic quality of seed banks as restored wetlands aged. Sediment load experiments showed burial of seed and egg banks with sediment depths as little as 0.5 cm virtually halted invertebrate and seedling emergence.

My results show that intensive agriculture has negatively impacted seed and invertebrate egg banks in both restored and nondrained wetlands, and that active planting or donor material will be needed to restore certain wetland communities. Results of my burial experiments on seedling emergence corroborated prior research; however, my research also demonstrated that invertebrate emergence is equally impacted by sediment burial. Agricultural activities in the PPR appear to have caused significant loss in wetland volume and depth that have potential to alter the success of wetland restorations. Agricultural conservation strategies need to be implemented to reverse this trend and keep valuable topsoil in place for agricultural production.

TABLE OF CONTENTS

Page

TABLE OF CONTENTS (CONTINUED)

TABLE OF CONTENTS (CONTINUED)

TABLE OF CONTENTS (CONTINUED)

LIST OF TABLES

LIST OF TABLES (CONTINUED)

LIST OF TABLES (CONTINUED)

Table Page

LIST OF TABLES (CONTINUED)

LIST OF FIGURES

LIST OF FIGURES (CONTINUED)

Figure Page

LIST OF FIGURES (CONTINUED)

Figure Page

LIST OF FIGURES (CONTINUED)

LIST OF FIGURES (CONTINUED)

LIST OF FIGURES (CONTINUED)

LIST OF FIGURES (CONTINUED)

LIST OF FIGURES (CONTINUED)

LIST OF FIGURES (CONTINUED)

LIST OF FIGURES (CONTINUED)

LIST OF FIGURES (CONTINUED)

CHAPTER 1

GENERAL INTRODUCTION

The Prairie Pothole Region (PPR) is a major biogeographical region that encompasses 715,000 km^2, and extends from the north central United States to south central Canada (Kantrud et al. 1989). This region is pocketed with millions of shallow wetlands of glacial origin that support diverse and unique assemblages of wetland biota (Kantrud et al. 1989). Superimposed over this region is an intensively farmed landscape. As a consequence of agricultural intensification and cropland expansion, numerous wetlands have been drained and less than 50% of the estimated original 8 million ha of wetlands remain in the PPR (Dahl 1990, Dahl and Johnson 1991). In response to past wetland losses and increased public awareness of wetland functions and their associated values (Brun et al. 1981, Ludden et al. 1983, Hubbard and Linder 1986, Hubbard 1988, Winter 1989, Stevens et al. 1995), numerous wetlands have been restored by international, federal, state, and private agencies to reverse the impacts of wetland drainage (Dornfeld and Warhurst 1988, Interagency Committee 1992). Although tens of thousands of drained wetlands have been restored throughout the PPR, the success of wetland restorations is rarely evaluated.

The goal of most restoration programs is to restore wetland functions and the biological integrity to approximate predrainage conditions. Techniques to restore wetlands typically focus on restoring the hydrologic regime by plugging ditch and tile drains and then relying on natural processes for recolonization of hydrophytes and aquatic invertebrates (i.e., reestablishment from relic seed and egg banks and dispersal of propagules from surrounding wetlands). However, most wetlands targeted for restoration have been drained and farmed for extensive periods which may impede or make untenable the assumed recolonization process of invertebrates and plants (Galatowitsch and van der Valk 1994). Earlier studies examining the response of plant and animal populations to wetland restoration have indicated that both rapidly repopulate restored wetlands (Dornfeld and Warhurst 1988, LaGrange and Dinsmore 1989, Sewell 1989). However, interpretation of these earlier studies is limited because the flora and fauna of restored wetlands were not compared with natural wetlands.

More recent studies that have compared restored wetlands to natural wetlands have indicated that the success of restorations are highly variable. Galatowitsch and van der Valk (1996) found that in recently restored wetlands, wet meadow and sedge meadow zones did not reestablish rapidly and that the number of wet meadow and sedge meadow species was lower in restored than in natural wetlands. In contrast, deep marsh and submersed aquatic zones were comparable between restored and natural wetlands. Reasons for poor recolonization success of certain vegetative zones has been related to impacts of past landuse. For example, relic seed and invertebrate egg banks may be lost because of prolonged drainage, cultivation and/or artificially shortened hydroperiods (Wienhold and van der Valk 1989, Galatowitsch and van der Valk 1994, 1996; Euliss and Mushet 1999).

Another disturbance that may influence reestablishment of invertebrate and plant communities is the impact of anthropogenic sedimentation. Cultivation of wetland catchments has increased sedimentation of wetland basins (Martin and Hartman 1987, Dieter 1991, Gleason 1996, Gleason and Euliss 1996, Luo et al. 1997). Most restored wetlands are designed to achieve historic pool levels, but accelerated sedimentation from cultivation may actually decrease original pool depths. Hence, restored wetlands may be shallower than their natural analogues; such conditions may favor development of monodominant stands of emergent vegetation (e.g., cattails) that contribute little to vegetative diversity and exacerbate problems for farmers because they provide roost sites for depredating blackbirds (Linz et al. 1996). Further, loss of wetland volume from sedimentation may influence water permanence and hydrologic regimes that ultimately determine the hydrophyte and aquatic invertebrate communities that characterize specific wetland classes (Kantrud 1986). Low plant diversity also influences the diversity and composition of invertebrate communities (Krull 1970, Voights 1976). Eroded soils from agricultural fields may also cover viable seed and egg banks and render them unavailable for recolonization of restored wetlands (Euliss and Mushet 1999). *In vitro* experiments have shown that sediment depths as little as 0.25 cm can significantly reduce species richness, emergence, and germination of hydrophytes (Jurik et al. 1994, Wang et al. 1994); however, similar studies have not assessed the effect of sediment load on invertebrate egg banks. Consequently, research is needed to assess the effects of sedimentation on loss of prairie wetland depth and volume and its potential impact on recolonization of hydrophytes and invertebrates. Further, most studies evaluating the success of restored wetlands have focused on wetlands in the southeastern PPR, and evaluations of restored wetlands elsewhere in the PPR are needed.

STUDY AREA, SAMPLING DESIGN, AND OBJECTIVES

My study was developed to complement a larger multiagency research effort coordinated by the U.S. Geological Survey's Northern Prairie Wildlife Research Center (NPWRC) on restored and natural wetlands in the PPR (NPWRC 1997). My research was conducted on the study wetlands selected by NPWRC as part of this multiagency research effort. The study area included portions of Montana, North Dakota, South Dakota, Minnesota, and Iowa. NPWRC's sampling design consisted of stratifying the PPR into three physiographic regions: Missouri Coteau, Prairie Coteau, and Glaciated Plain. A random-systematic sampling design was used to place 9 sampling points in the Missouri Coteau, 3 in the Prairie Coteau, and 12 in the Glaciated Plain (Figure 1). Near each sampling point, seasonal and semipermanent wetlands (wetland water regimes according to Cowardin et al. 1979) were selected from the following categories: (1) restored wetlands < 5 years old and restored wetlands > 5 years old in Conservation Reserve Program (CRP) or similar grasslands (i.e., prior farmed lands planted back to perennial grasses), (2) drained wetlands in CRP type habitats, (3) nondrained wetlands in CRP type habitats, and (4) reference wetlands with no history of cultivation in the wetland basin or the surrounding catchment.

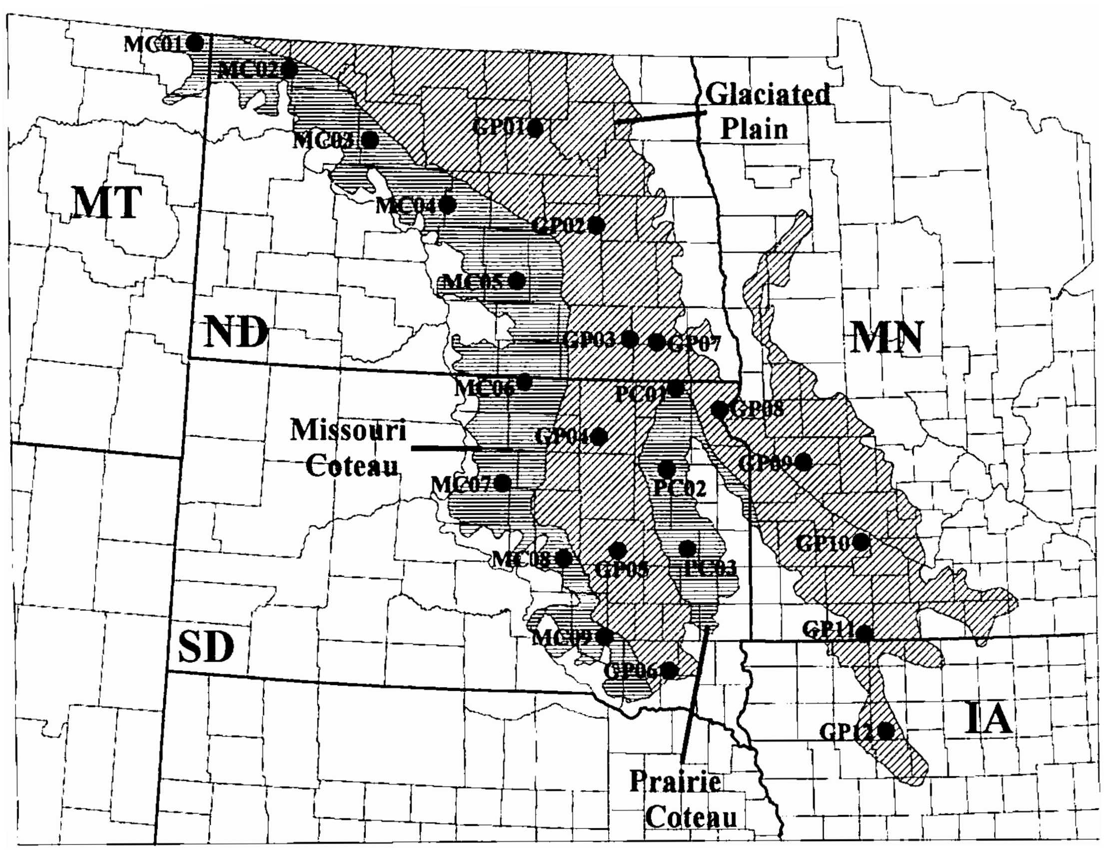

Figure 1. Location of wetland sampling areas in the Glaciated Plain (GP01 - GP12), Missouri Coteau (MC01 - MC09), and Prairie Coteau (PC01 - PC03) physiographic regions in Prairie Pothole Region of the United States.

The extensive survey performed by NPWRC resulted in the sampling of 204 wetlands (Figure 2; Table 1). Detailed information on wetland selection criteria and sampling design are described in the extensive survey Study Plan 168.01 (NPWRC 1997). Specific objectives of my research were to:

(1) examine the effects of sedimentation on loss of prairie wetland depth and volume;

(2) examine invertebrate egg bank composition among reference, nondrained, restored, and drained wetlands and the influence of sedimentation on recolonization potential of aquatic invertebrates in restored wetlands, and

(3) examine seed bank composition among reference, nondrained, restored; and drained wetlands and the influence of sedimentation on recolonization potential of hydrophytes in restored wetlands.

DISSERTATION ORGANIZATION

This dissertation is organized into chapters, with chapters 2-4 representing planned manuscripts. In Chapter 2, I present information on sedimentation rates in reference, nondrained, and restored wetlands and evaluate the potential impacts of sedimentation rates on wetland depth and volume. In Chapter 3, I compare invertebrate egg bank composition among reference, nondrained, restored, and drained wetlands. Additionally, in this chapter, I evaluate the influence of sediment load on emergence of

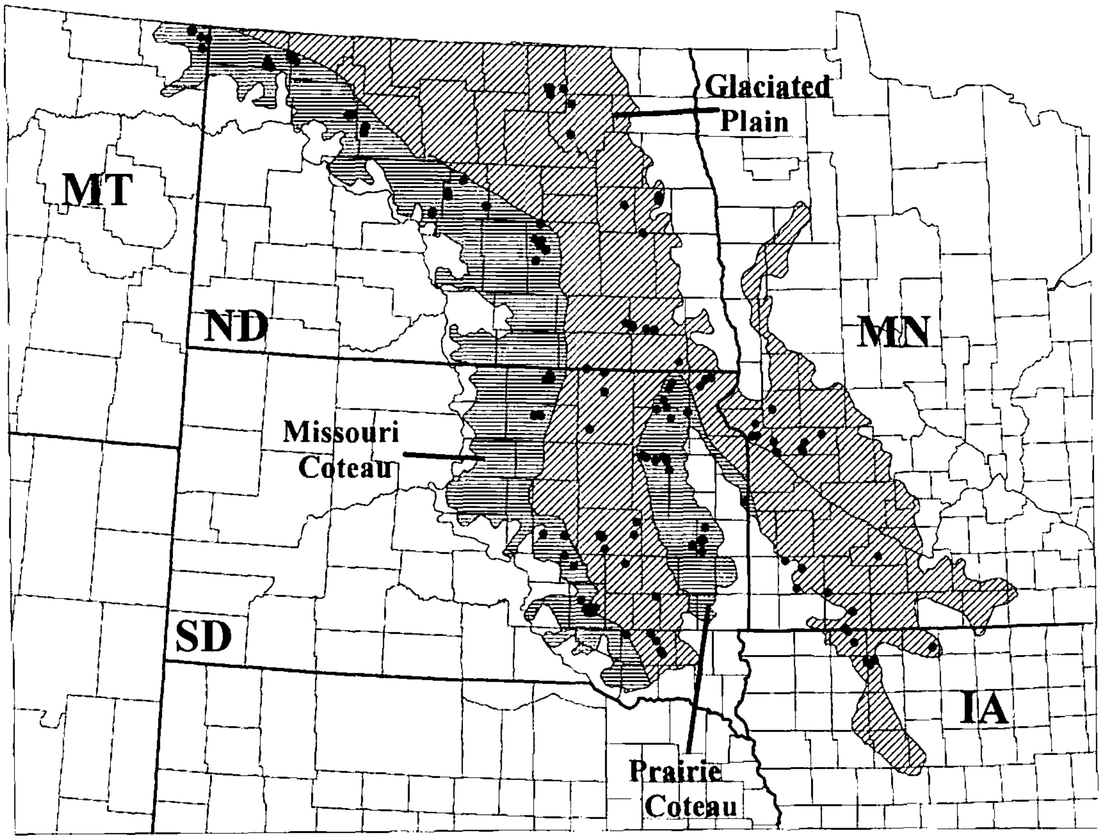

Figure 2. Locations of wetlands sampled during 1997 in the Glaciated Plain, Missouri Coteau, and Prairie Coteau physiographic regions in the Prairie Pothole Region of the United States.

Table 1. Replication of wetland treatments by wetland class and physiographic region sampled during 1997. Wetlands are located in the Glaciated Plain, Missouri Coteau, and Prairie Coteau physiographic regions of the Prairie Pothole Region of the United States.

Wetland class[a]	Physiographic region	Treatments[b] Reference	Nondrained	Restored	Drained
Seasonal	Glaciated Plain	12	12	22	12
	Missouri Coteau	9	9	17	7
	Prairie Coteau	3	3	6	3
Semipermanent	Glaciated Plain	10	9	14	9
	Missouri Coteau	9	8	12	3
	Prairie Coteau	3	3	6	3

[a] Wetland classification according to Cowardin et al. (1979) wetland water regimes.

[b] Reference wetlands have no history of cultivation in their wetland basin or surrounding catchments; nondrained, restored, and drained wetlands have a history of cultivation and are in Conservation Reserve Program (CRP) or similar grasslands (i.e., prior farmed lands planted back to perennial cover).

invertebrates from egg banks. Seed bank composition in reference, nondrained, restored, and drained wetlands and the effects of sediment load on seed bank emergence are evaluated in Chapter 4. A general summary of research findings is presented in Chapter 5.

CHAPTER 2

INFLUENCE OF SEDIMENTATION ON POOL DEPTH AND VOLUME OF PRAIRIE WETLANDS IN THE USA: IMPLICATIONS FOR RESTORATION AND MANAGEMENT

INTRODUCTION

Most wetlands in the Prairie Pothole Region (PPR) of the northern Great Plains occupy topographic depressions in agricultural landscapes and are often the focal points of surface runoff laden with agrochemical residues and eroded soils (Grue et al. 1986, Neely and Baker 1989, Euliss and Mushet 1996). Prior research has indicated that sediment inputs are several-to-many orders of magnitude greater in prairie wetlands surrounded by cropland than in wetlands surrounded by grassland (Adomaitis et al. 1967, Martin and Hartman 1987, Gleason 1996, Gleason and Euliss 1996). The potential for accelerated sedimentation rates to directly or indirectly degrade wetland productivity, wetland functions, and other values of societal interests is great (Gleason and Euliss 1998). Moreover, erosional sediment from anthropogenic sources will effectively shorten the topographic life span of wetlands.

Loss of wetland volume and depth in prairie wetlands to anthropogenic sedimentation has important ecological implications. Natural fluctuation of water levels due to wet/dry cycles is probably the most important cause of vegetative change in prairie wetlands. A conceptual model (van der Valk and Davis 1978) describing how prairie wetland vegetative communities respond to water level fluctuations during wet/dry cycles includes 4 phases: dry marsh, regenerating marsh, degenerating marsh, and lake marsh. When water returns following a dry marsh phase (i.e., regenerating marsh phase), development of emergent vegetation and species composition is influenced by individual tolerance of macrophytes to depth and hydroperiod. If wetlands are shallowly flooded and conditions remain stable, emergent vegetation will eventually dominate wetland basins. During this phase, wetlands will frequently develop monodominant stands of tall, robust emergents (e.g., *Typha* spp.) that contribute little to biotic diversity (Kantrud 1986). The flooding-out of tall, robust emergent vegetation commonly associated with the degenerating and lake marsh phase of prairie wetlands (van der Valk and Davis 1978) is often dependent on water depth. Though not well defined in the literature, about 1 m of water is generally believed to be adequate to flood-out most tall robust emergents such as cattails (Beule 1979, Weller 1987). Consequently, anthropogenic sedimentation may make wetlands too shallow to attain water depths adequate to flood-out tall robust emergents.

As a consequence of agricultural development, numerous wetlands have been drained for agricultural conversion, and less than 50% of the estimated 8 million ha of original wetlands remain in the PPR (Dahl 1990, Dahl and Johnson 1991). To mitigate the extreme loss of wetlands due to agricultural drainage, numerous wetlands have been restored in the PPR (National Research Council 1992). The aforementioned ecological significance of water depth should be considered when restoring wetlands. For example, most wetlands are restored to historic pool elevations by plugging ditches or surface drains to restore hydrology. However, anthropogenic sedimentation may have decreased original pool depth and volume. To restore wetland volume and depth to pre-drainage conditions, depth and volume loss need to be quantified and incorporated in management plans (Gleason and Euliss 1998).

Anthropogenic sedimentation results in loss of wetland volume which in turn impacts water retention and storage values of economic importance (i.e., flood attenuation), and other hydrological functions (e.g., ground water recharge) associated with prairie wetlands. Studies have related wetland drainage and land-use change to increased flooding frequency of the Red River Valley of North Dakota (Brun et al. 1981) and Mississippi River Valley (Miller and Nudds 1996). However, studies have not considered the effect of lost storage capacity in existing wetlands to anthropogenic sedimentation.

The objectives of my study were to (1) relate land-use to sedimentation rates in prairie wetlands, (2) evaluate the influence of sedimentation rates on loss of wetland pool depth and volume, and (3) examine the relation between catchment characteristics and sedimentation rates in wetlands. To address these objectives, I compared sedimentation rates, using isotopic dating techniques (i.e., ^{137}Cs and ^{210}Pb), in nonfarmed reference wetlands to previously farmed nondrained and restored wetlands. Using this information, I projected over a larger sample population of wetlands temporal loss of wetland volume and depth using sedimentation rates under nonfarmed (reference) and farmed scenarios.

Additionally, I used the presence of invertebrate remains (e.g., resting eggs and shells) to determine post-glacial sediment depth. The relation between sedimentation rate in wetlands and surrounding catchment characteristics was examined to identify indicators of sedimentation impacts.

METHODS AND MATERIALS

Collection and Processing of Sediment Cores

I collected sediment cores from 58 wetlands located throughout the PPR of Montana, North Dakota, South Dakota, Minnesota, and Iowa (Figure 3). These 58 wetlands were a subsample of the 204 wetlands selected by the U.S. Geological Survey's Northern Prairie Wildlife Research Center (NPWRC) in an effort to evaluate restored wetlands throughout the PPR of the United States (Figure 2). The subsample of wetlands that I collected sediments from included 17 seasonal and 13 semipermanent restored wetlands, 7 seasonal and 7 semipermanent nondrained wetlands, and 6 seasonal and 8 semipermanent reference wetlands (Figure 3). Wetlands selected were in the Missouri Coteau and Glaciated Plain physiographic regions.

During 1998 (June-July), I collected 1 sediment core from each of the 58 wetlands (Figure 3) using a 10.8 cm (I.D.) corer. I collected cores at the mid-elevation of the shallow-marsh zone in locations where sediment accumulation would be expected to be severe (Richardson et al. 1994). Selection of coring location was based on visual observation of the wetland and catchment basin topography (e.g., collected in the

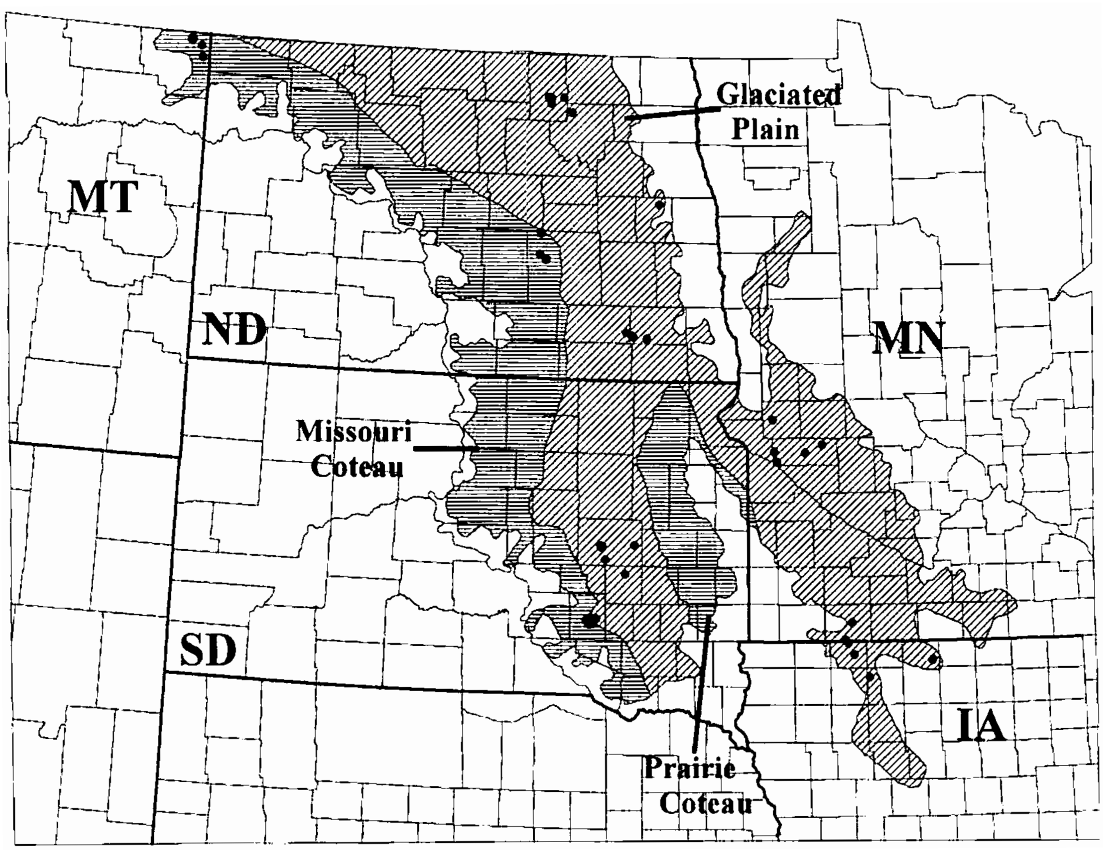

Figure 3. Locations of reference (n = 14), nondrained (n = 14), and restored (n = 30) wetlands in the Prairie Pothole Region of the United States, sampled during 1998 for sedimentary analysis.

shallow-marsh zone at the base of steep concave slopes). During field collection, distance to the sediment surface on the outside and inside of the corer barrel was recorded to determine core compaction. Average depth of cores collected was 58.6 cm (range 30 - 80 cm) and average compaction was 4.8% (range 0 - 24%). Sediment cores were kept in an upright position during transport to the laboratory, then were stored in a freezer (< 0°C). Sediment cores were sectioned into 5-cm intervals and quartered. When quartering samples the outer surface of each interval was shaved off to remove any possible contaminants (e.g., invertebrate remains) transported from upper strata during coring. Textural class and color of the outer surface that was shaved off was recorded to provide information on core stratigraphy. Textural class was determined using the 'feel method' and color was determined using the Munsell soil color system (Brady 1984).

Determination of Sedimentation Rates and Post-Glacial Overburden

Invertebrate Remains: The presence of invertebrate remains (e.g., resting eggs and shells) was used to determine post-glacial sediment depth (i.e., post-glacial overburden). I assumed that the depth at which no invertebrate remains were detected would define the sediment overburden that has accrued since glaciation. All 58 cores were examined for invertebrate remains. Laboratory procedures consisted of removing a 20-30 cc sample from each 5-cm section for analysis. Each sample was placed in a solution of mild soap and water buffered with sodium bicarbonate. Samples were allowed to set for several days in this solution to facilitate dis-aggregation of sediments.

Samples were then washed through nested sieves (150 μm mesh, 63 μm mesh). Sieved samples were scanned at a 10-63X magnification using a stereomicroscope and the presence or absence of invertebrate remains was recorded.

Isotope Dating Techniques: The isotopes ^{210}Pb and ^{137}Cs were used to determine sedimentation rates (Holmes 1998) in 19 of the 58 cores. Wetlands selected for analyses included only cores that showed minimal disturbance (e.g., from tillage) as indicated by core stratigraphy. The wetlands selected included 3 seasonal and 4 semipermanent reference wetlands, 1 seasonal and 4 semipermanent nondrained wetlands, and 3 seasonal and 4 semipermanent restored wetlands (Figure 4).

Cesium-137 and ^{210}Pb dating techniques are good for dating the sedimentary dynamics over the past 100 years (Holmes 1998). Cesium-137 is a product of nuclear testing and has a half-life of 30.3 years. Atmospheric fallout of ^{137}Cs began in the early 1950's with detectable levels in soils occurring in 1954 and peak quantities in 1963-1964 (Ritchie and McHenry 1990). In general, the vertical distribution of ^{137}Cs in the sediment profile can be related to yearly fallout peaks. The 1954 and 1963 peaks are often the most readily identified peaks in the sediment profile that can be used to date sediments (Ritchie and McHenry 1990). In this study, I considered the maximum depth that ^{137}Cs activity was detected as the 1954 deposition, and accretion rates (cm yr^{-1}) were calculated from 1954 to the sampling date.

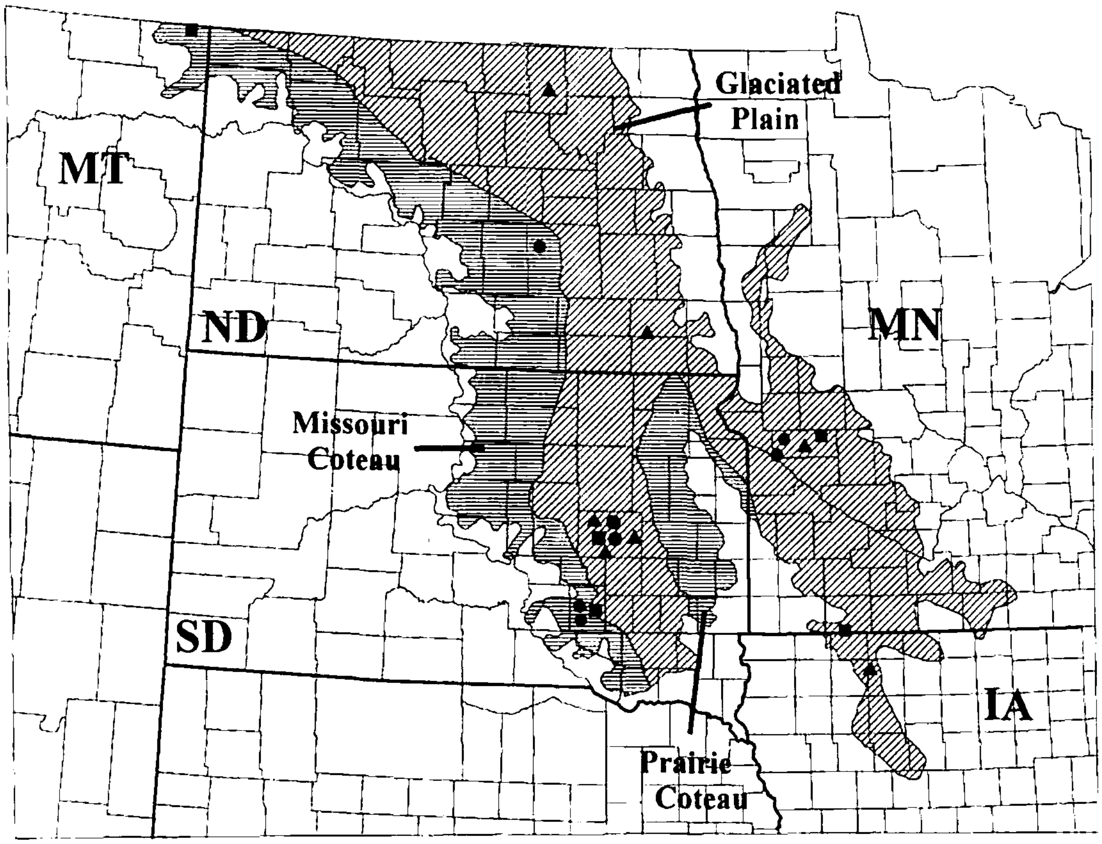

Figure 4. Locations of reference (circles; n = 7), nondrained (squares; n = 5), and restored (triangles; n = 7) wetlands in the Prairie Pothole Region of the United States, sampled during 1998 for isotopic dating.

Lead-210 is naturally occurring in the atmosphere and has a half-life of 22.3 years. Lead-210 is a member of the uranium decay series and is the daughter of ^{222}Rn. Radon-222, a daughter of ^{226}Ra, diffuses from the earth's crust into the atmosphere where it decays to ^{210}Pb. The ^{210}Pb is then entrapped in rainfall and is returned to earth. Atmospheric residence time of ^{210}Pb is about 10 days and the concentration of ^{210}Pb in rainwater is believed to have remained constant over time (Delaune et al. 1989, Holmes 1998). The activity of ^{210}Pb returned to earth (i.e., unsupported ^{210}Pb), is greater than that of background activity in the soil (i.e., supported ^{210}Pb produced by the decay of ^{226}Ra in the sediment column). The age of sediments is determined by calculating the decrease in ^{210}Pb activity in the sediment profile which is a function of time (Holmes 1998).

Portions of the 19 cores were sent to the U.S. Geological Survey's Center for Marine and Coastal Research Laboratory for determination of ^{210}Pb and ^{137}Cs activity. Cesium-137 and ^{210}Pb activity were determined using a germanium detector and multichannel analyzer. Details of analytical methods used by the Laboratory for determination of isotopic activity are presented in Appendix A. For each core section, bulk density was determined as total dry weight (dried at 110°C) per unit volume and total organic matter was determined by weight-loss-on-ignition (temperature at 450°C). Unsupported ^{210}Pb activities and ^{137}Cs activities for each depth interval were provided from the Laboratory in disintegrations-per-minute-per-gram of soil (dpm g^{-1}). For each core, I modeled the decrease in unsupported ^{210}Pb activity with depth using curve fitting procedures (SigmaPlot 2000). Age of each interval was then determined from predicted values of unsupported ^{210}Pb using the following equation from Holmes (1998):

$$Age = \ln(A_0 / A_h) * 1/0.03114$$

where A_0 is the unsupported activity of ^{210}Pb at the surface (present), A_h is the ^{210}Pb activity at depth h, and 0.03114 is the decay constant for ^{210}Pb. Vertical accretion rates (cm yr^{-1}) were calculated by dividing depth (cm) of interval h by interval age. Cesium-137 and ^{210}Pb based accretion rates were adjusted for compaction that occurred during field collection. Average compaction was low (1.0%) for these 19 cores with little variation among treatments (range 1.0% to 1.2%). Additionally, bulk density (g cm^{-3}) and % loss-on-ignition data were used to calculate total, organic, and inorganic mass accumulation rates (g cm^{-2} yr^{-1}).

Wetland and Catchment Morphometry Information

During 1997, a topographic field survey was made of all wetlands sampled by NPWRC (Figure 2). Wetland basins and their surrounding catchments were surveyed using a total station (Nikon model 750). Using the program ForeSight version 1.3 (Tripod Data Systems, Inc., Corvallis, Oregon), I calculated potential maximum water depth (m) and volume (ha m) of reference (n=36), nondrained (n=35), and restored wetlands (n=63) sampled in the Missouri Coteau and Glaciated Plain physiographic regions. Maximum potential water depth was calculated as the vertical difference (m) between the lowest elevation in the wetland basin to the lowest surface outlet elevation of the catchment. Likewise, potential wetland volume was calculated as the maximum pool level possible as limited by the lowest outlet elevation. Catchment area (ha), wetland area (ha), and average % slope and slope length (m) of catchments were determined for the 19 wetlands selected for isotopic dating. Catchment area was delimited by the catchment divide and wetland area was delimited by wetland hydrophytes (e.g., wet-meadow edge).

I estimated soil loss from catchments surrounding the 19 wetlands selected for isotopic dating. To predict catchment soil loss, I used the U.S. Department of Agriculture's (USDA) Revised Universal Soil Loss Equation, RUSLE. The RUSLE is defined as (Wischmeier and Smith 1978, Renard et al. 1997):

$$A = RKLSCP$$

where A is the estimated soil loss per unit area caused by rainfall, R is the climatic erosivity factor, K is the soil erodibility factor, L and S are the slope length and steepness factors, C is the cover and management factor, and P is the supporting practice factor. Revised Universal Loss Equation values for R, K, and C factors were provided by USDA field office personnel in counties where wetlands were sampled. Cover-management values (C) for nondrained and restored treatments were based on cropping and tillage practices prior to grassland restoration. Supporting practice values (P) were assumed to be = 1 in all catchments, and LS values were estimated using topographic survey data (i.e., average % slope and length).

Statistical Analysis

I used analysis of variance (ANOVA) to assess the influence of wetland *treatment* (i.e., reference, nondrained, and restored), wetland class (i.e., seasonal and semipermanent), and physiographic region (Missouri Coteau and Glaciated Plain) main effects and their interactions (Region X Wetland-class X Treatment) on post-glacial sediment depth (i.e., analysis of invertebrate remains). In this analysis, I used a block design where each sampling area was treated as a block (e.g., GP01-GP12; Figure 1). For the 19 wetlands selected for isotopic dating, I only assessed the influence of wetland treatment and wetland-class main effects and their interactions (Treatment X Wetland-class) on accretion and accumulation rates, and catchment characteristics; physiographic region and sampling area effects were not included because criteria used to select the 19 wetlands resulted in incomplete replication among physiographic region and sampling areas (Figure 4). I used simple linear regression to model the relationship between catchment soil loss and sedimentation rates. I conducted ANOVAs using the mixed models procedure (PROC MIXED) and regression using the linear regression model procedure (PROC REG) of SAS (SAS Institute, Inc. 1989, 1997). Fisher's protected least significant difference test was used to separate means following significant ($P \leq 0.05$) main effects and interactions in the ANOVAs (Milliken and Johnson 1984).

RESULTS AND DISCUSSION

Use of Invertebrate Remains to Determine Post-Glacial Overburden

Common invertebrate remains found in sediment cores were molluscans, ostracods, and the resting eggs of cladocerans (i.e., ephippia). Maximum depth that invertebrate remains occurred did not significantly ($P > 0.05$) differ among main effects or their interactions (Table 2). The use of invertebrate remains to determine post-glacial overburdens was dependent on meeting 2 assumptions: (1) that cores would be collected to a depth adequate to reach parent-glacial material, and (2) that the maximum depth invertebrate remains occurred would represent the start of post-glacial sedimentation. Examination of the distribution of invertebrate remains in the sediment profiles indicated that I sometimes did not meet the first assumption and also, that the validity of the second assumption is questionable.

Invertebrate remains in the sediment profiles followed 3 basic patterns. In the first pattern, invertebrate remains occurred in every section of the sediment profile (Figure 5). This continuous distribution of invertebrate remains indicate that I did not collect cores to a depth adequate to reach parent-glacial material. In the second pattern, invertebrate remains occurred in a discrete and continuous upper portion of the core (Figure 6). I assumed that this discrete portion containing invertebrate remains represented post-glacial overburden. However, the third pattern was characterized by a discontinuous distribution of invertebrate remains in the profile with the presence or absence changing with depth (Figure 7). This third pattern implies that I may not have

Table 2. Least squares means (± SE) of maximum depth (cm) that invertebrate remains were found in soil profiles of seasonal and semipermanent wetlands in the Glaciated Plain and Missouri Coteau physiographic regions of the United States Prairie Pothole Region. Mixed-model ANOVA (Region X Wetland-class X Treatment) results indicated no significant ($P < 0.05$) main effects or interactions.

		Treatments[a]								
		Reference			Nondrained			Restored		
Region	Wetland-class	Mean	SE	n	Mean	SE	n	Mean	SE	n
Glaciated Plain	Seasonal	39.1	(11.2)	4	21.2	(10.1)	5	27.9	(7.4)	11
	Semipermanent	29.6	(10.1)	5	34.3	(11.2)	4	35.8	(8.0)	9
Missouri Coteau	Seasonal	15.9	(15.8)	2	35.9	(15.8)	2	25.0	(10.3)	6
	Semipermanent	45.0	(13.2)	3	38.3	(13.2)	3	28.3	(12.0)	4

[a] Mixed-model ANOVA probabilities for main effects and interactions: region X wetland-class X treatment = ($F_{2, 37} = 1.48$, $P = 0.2398$).

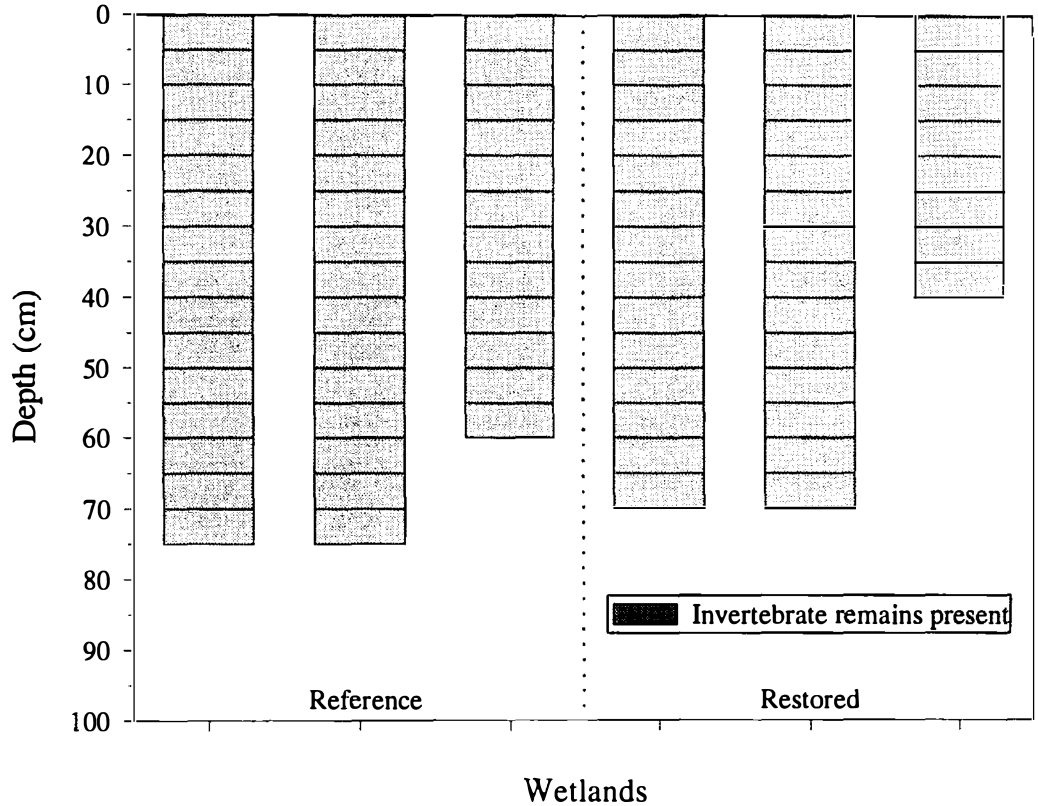

Figure 5. Reference and restored wetlands sampled during 1998 in the Prairie Pothole Region of the United States with a continuous distribution of invertebrate remains in soil profiles.

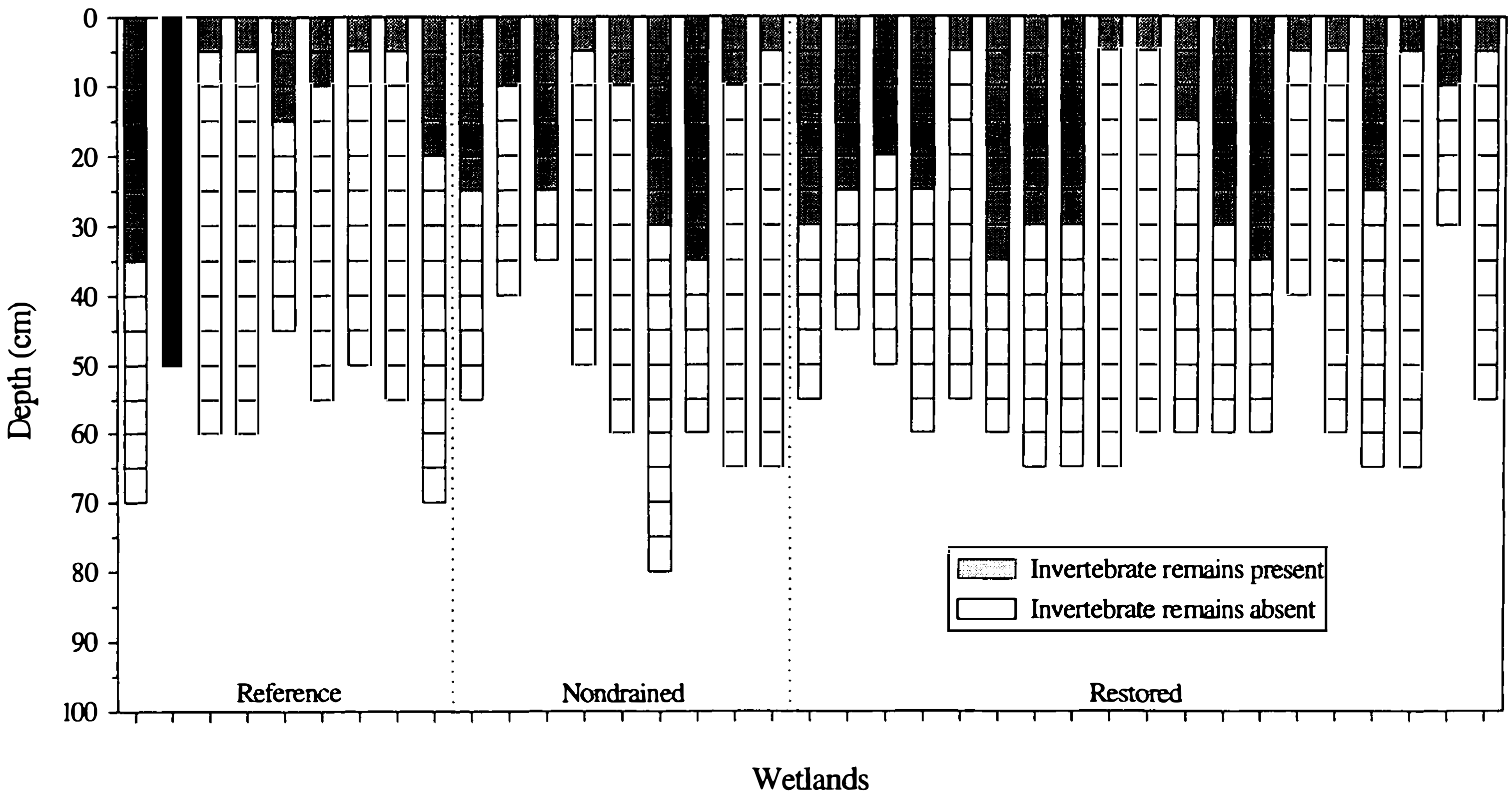

Figure 6. Reference, nondrained, and restored wetlands sampled during 1998 in the Prairie Pothole Region of the United States with a discrete distribution of invertebrate remains in soil profiles.

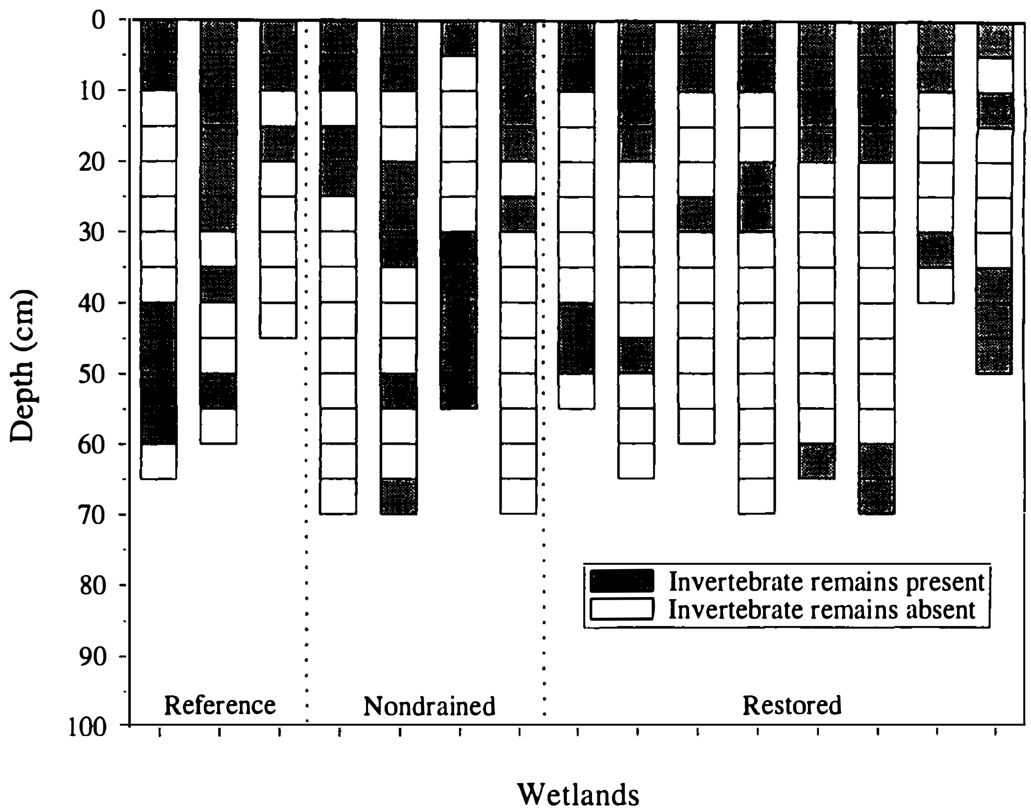

Figure 7. Reference, nondrained, and restored wetlands sampled during 1998 in the Prairie Pothole Region of the United States with a discontinuous distribution of invertebrate remains in soil profiles.

gone deep enough, even in cores where I had a discrete distribution of invertebrate remains (i.e., the second pattern). As I have no other supporting information, I cannot assume that the maximum depth that invertebrate remains occur is representative of the time since last glaciation.

Of the many plausible explanations for discontinuities of invertebrate remains in the sediment profile, only a few can be eliminated with the invertebrate and sediment dating evidence that I collected. The discontinuous pattern of invertebrate remains in soil profiles was not unique to restored wetlands, and therefore the absence of invertebrates cannot be related to agricultural drainage (e.g., Figure 7). Further, in most cases, discontinuities in soil profiles occurred over a hundred years before present (see below, Figure 8), which is before most wetlands were drained or intensively farmed. Most likely, the presence and absence of invertebrate remains in the sedimentary sequence is related to climatic wet and dry cycles. Studies in the PPR have related the absence of invertebrates in the sedimentary sequence to drier periods (Cvancara et al. 1971, Malo 1988). Within the past several thousand years, the Northern Great Plains has experienced severe and frequent droughts, some persisting for centuries (Bryson and Murray 1977, Van Stempvoort et al. 1993, Laird et al. 1996). Many of these droughts were of greater intensity than that of the 1930s (Laird et al. 1996). Over the long term, the presence or absence of invertebrates may represent stable periods of extremes in climate. For example, the periodic absence of invertebrates in the sediment profile may represent a climatically stable time period of extreme drought that lasted for several centuries.

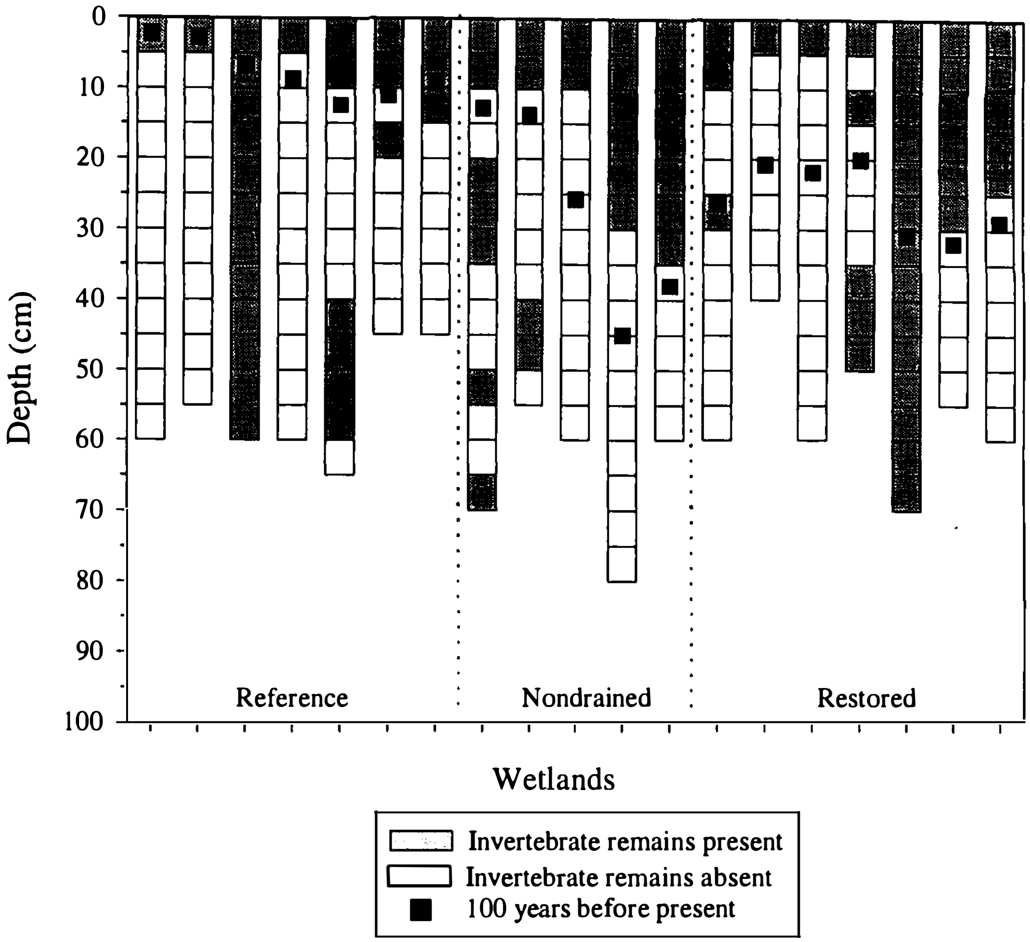

Figure 8. Distribution of invertebrate remains in soil profiles of reference, nondrained, and restored wetlands sampled during 1998 in the Prairie Pothole Region of the United States. The 100 year before present date was based on ^{210}Pb dating.

Similar arguments can be made that the absence of invertebrates represents a mass wasting of soils due to upland or bank erosion which is more frequent during wet periods. Fossorial animals that colonize dry wetlands or ungulates that concentrate on remaining ponds during drought, also may have influenced the observed invertebrate distributions. Given the many plausible explanations for the absence or presence of invertebrate remains, and the great variability observed in distributions of invertebrate remains, it is doubtful that invertebrate remains alone could be used to determine post-glacial overburden. In addition to collecting deeper cores, other dating techniques (i.e., carbon-14), sediment chemistry and structure (e.g., carbon, particle size), and fossil (i.e., diatom assemblages, pollen) evidence would be necessary to determine if the maximum depth that invertebrate remains occur represents the start of post-glacial sedimentation.

Sedimentation: Accretion and Accumulation Rates

Estimates of accretion rates based on ^{137}Cs dating, ranged from 0.06 to 0.30 cm yr^{-1} in reference wetlands and from 0.06 to 0.64 cm yr^{-1} in wetlands with a history of cultivation (i.e., restored and nondrained wetlands) (Table 3). Mean accretion rates estimated by ^{137}Cs dating were significantly greater in nondrained (0.40 cm yr^{-1}) and restored (0.40 cm yr^{-1}) wetlands than in reference (0.17 cm yr^{-1}) wetlands (Table 3). Accretion rates determined using ^{210}Pb dating were generally lower than those determined by ^{137}Cs dating and ranged from 0.02 to 0.12 cm yr^{-1} in reference wetlands and from 0.13 to 0.45 cm yr^{-1} in wetlands with a cultivated history (Figure 9, Table 3). Statistical

Table 3. Least squares means (± SE) of vertical accretion rates in reference (n = 7), nondrained (n = 5), and restored (n = 7) wetlands sampled during 1998 in the Prairie Pothole Region of the United States. Means (± SE) within columns with an *asterisk* (*) are significantly ($P < 0.05$) different from reference wetlands.

	^{137}Cs dating (cm yr^{-1})[a]				^{210}Pb dating (cm yr^{-1})[b]			
Treatment	Mean	SE	Min	Max	Mean	SE	Min	Max
Reference	0.17	(0.06)	0.06	0.30	0.08	(0.02)	0.02	0.12
Nondrained	0.40	(0.09)*	0.06	0.53	0.34	(0.04)*	0.13	0.45
Restored	0.40	(0.06)*	0.17	0.64	0.25	(0.02)*	0.20	0.32

[a-b] Mixed-model ANOVA probabilities for treatment effects: a = ($F_{2,13} = 4.65$, $P = 0.030$); b = ($F_{2,13} = 21.45$, $P < 0.001$).

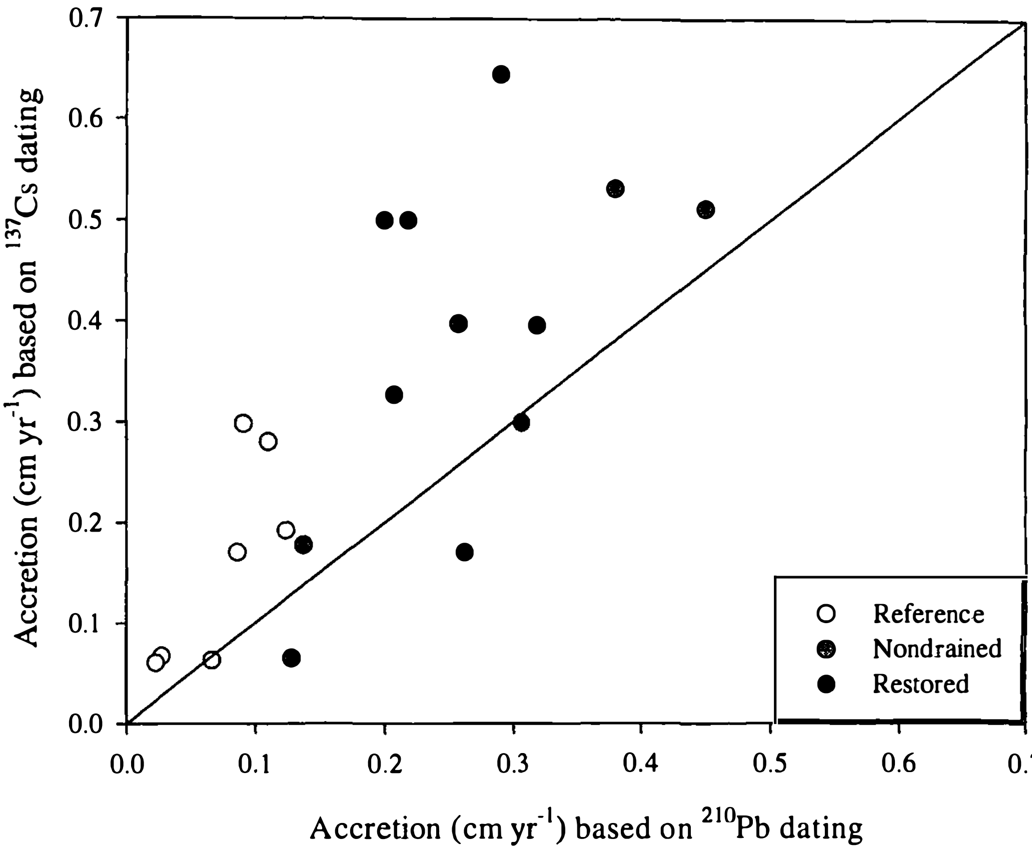

Figure 9. Accretion rates based on ^{137}Cs and ^{210}Pb dating techniques in reference (n = 7), nondrained (n = 5), and restored (n = 7) wetlands sampled during 1998 in the Prairie Pothole Region of the United States.

analysis of accretion rates based on ^{210}Pb dating showed a significant treatment-by-wetland-class interaction effect. Examination of accretion rate among treatments by wetland class (i.e., interaction effect), indicated that nondrained and restored wetlands had significantly greater accretion rates than did reference wetlands regardless of wetland class (Table 4). Thus, overall treatment effects adequately describe the trend of greater accretion rates in nondrained (0.34 cm yr^{-1}) and restored (0.25 cm yr^{-1}) wetlands than in reference (0.08 cm yr^{-1}) wetlands (Table 3). Differences between nondrained and restored wetlands were dependent on wetland class, with greater accretion in nondrained seasonal wetlands (0.45 cm yr^{-1}) than in restored seasonal wetlands (0.22 cm yr^{-1}); however, because nondrained seasonal wetlands lacked replication ($n = 1$), this difference is tenuous (Table 4).

Similar to accretion rates, accumulation rates (g cm^{-2} yr^{-1}) were generally greater for ^{137}Cs estimates than for ^{210}Pb estimates (Figure 10). Based on ^{137}Cs dating, total and inorganic accumulation rates were significantly greater in restored than in reference wetlands, whereas nondrained rates were statistically similar to other treatments (Table 5). Total and inorganic accumulation rates calculated using ^{210}Pb were significantly greater in nondrained and restored wetlands than in reference wetlands (Table 5).

Organic accumulation rates based on ^{137}Cs in nondrained (0.047 g cm^{-2} yr^{-1}), restored (0.061 g cm^{-2} yr^{-1}) and reference (0.020 g cm^{-2} yr^{-1}) wetlands were not statistically different (Table 5); whereas, based on ^{210}Pb dating, organic accumulation rates were

Table 4. Least squares means (± SE) of vertical accretion rates by wetland class in reference, nondrained, and restored wetlands sampled during 1998 in the Prairie Pothole Region of the United States. Accretion rates were estimated using ^{210}Pb dating techniques. Means (± SE) within columns with a common letter are not significantly ($P > 0.05$) different.

	Accretion (cm yr^{-1})[a]					
	Seasonal			Semipermanent		
Treatment	Mean	SE	n	Mean	SE	n
Reference	0.11	(0.04)a	3	0.05	(0.03)a	4
Nondrained	0.45	(0.06)b	1	0.23	(0.03)b	4
Restored	0.22	(0.04)c	3	0.28	(0.03)b	4

a Mixed-model ANOVA probability for treatment X wetland-class interaction effects, $F_{2,13} = 5.34$, $P = 0.0203$.

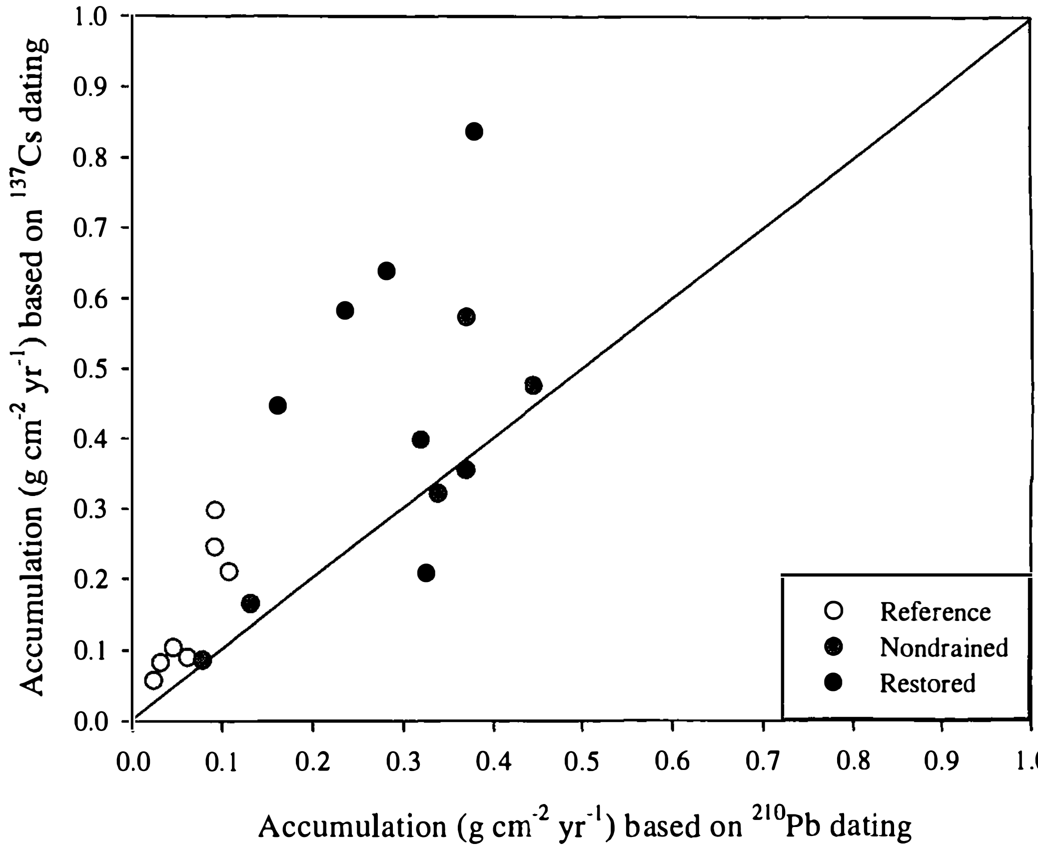

Figure 10. Accumulation rates based on ^{137}Cs and ^{210}Pb dating techniques in reference (n = 7), nondrained (n = 5), and restored (n = 7) wetlands sampled during 1998 in the Prairie Pothole Region of the United States.

Table 5. Least squares means (± SE) of total, inorganic, and organic mass accumulation rates in reference (n = 7), nondrained (n = 5), and restored wetlands (n = 7) sampled during 1998 in the Prairie Pothole Region of the United States. Accumulation rates were determined using ^{137}Cs and ^{210}Pb dating techniques. Means (± SE) within columns with a common letter are not significantly ($P > 0.05$) different.

	^{137}Cs dating (g cm^{-2} yr^{-1})			^{210}Pb dating (g cm^{-2} yr^{-1})		
	Total[a]	Inorganic[b]	Organic[c]	Total[d]	Inorganic[e]	Organic[f]
Treatment	Mean SE	Mean SE	Mean SE	Mean SE	Mean SE	Mean SE
Reference	0.159 (0.070)a	0.138 (0.066)a	0.020 (0.018)a	0.068 (0.037)a	0.058 (0.033)a	0.010 (0.004)a
Nondrained	0.324 (0.102)ab	0.277 (0.096)ab	0.047 (0.026)a	0.298 (0.054)b	0.261 (0.049)b	0.037 (0.006)b
Restored	0.485 (0.070)b	0.451 (0.066)b	0.061 (0.018)a	0.290 (0.037)b	0.267 (0.033)b	0.022 (0.004)b

[a-f] Mixed-model ANOVA probabilities for treatment main effects: a = ($F_{2,13}$ = 5.39, P = 0.020); b = ($F_{2,13}$ = 5.69, P = 0.017); c = ($F_{2,13}$ = 1.32, P = 0.301); d = ($F_{2,13}$ = 11.13, P = 0.002); e = ($F_{2,13}$ = 11.43, P = 0.001); f = ($F_{2,13}$ = 7.84, P = 0.0006).

significantly higher in nondrained (0.037 g cm^{-2} yr^{-1}) and restored (0.022 g cm^{-2} yr^{-1}) wetlands than in reference (0.010 g cm^{-2} yr^{-1}) wetlands (Table 5).

Overall, few differences were found between nondrained and restored wetland sedimentation rates. Given this, I estimated sedimentation rates for these 2 treatments combined (hereafter called cultivated wetlands). Average accretion, and total and inorganic mass accumulation estimates based on ^{137}Cs and ^{210}Pb dating, and organic accumulation based on ^{210}Pb dating were significantly greater in cultivated wetlands than in reference wetlands (Table 6). Organic mass accumulations estimated from ^{137}Cs dating were elevated in cultivated treatments relative to reference wetlands, but this difference was not significant (Table 6).

In most cases, sedimentation rates (i.e., accretion and accumulation) determined from ^{210}Pb dating were less than those obtained from ^{137}Cs dating (Figures 9, 10). This suggests either more rapid filling (i.e., accretion or accumulation) within the past 44 years (i.e., since 1954) or downward movement of ^{137}Cs in the sediment profile. Because ^{137}Cs is strongly adsorbed to cation exchanges sites, movement in the sediment profile due to chemical and hydrologic processes is limited (Ritchie and McHenry 1990). Though limited, minor movement of ^{137}Cs from one depth interval to the next can result in a difference of 0.11 cm yr^{-1}. Isotopic activity determinations at a finer scale (e.g., 1-2 cm intervals) may have resulted in better concordance among dating techniques. Physical processes, such as tillage, can cause major redistribution of ^{137}Cs, and restored and nondrained wetlands both have a history of cultivation. This might explain why dating

Table 6. Least squares means (± SE) of accretion rates, and total, inorganic, and organic mass accumulation rates in reference (n = 7) and cultivated wetlands (n = 12) sampled during 1998 in the Prairie Pothole Region of the United States. Accretion and accumulation rates were determined using ^{137}Cs and ^{210}Pb dating techniques. For each dating technique, means (± SE) within columns with an asterisk (*) indicate a significant (P < 0.05) difference between reference and cultivated wetlands.

		Accretion ($cm\ yr^{-1}$)	Mass accumulation ($g\ cm^{-2}\ yr^{-1}$)		
			Total	Inorganic	Organic
Dating technique	Treatment	Mean SE	Mean SE	Mean SE	Mean SE
^{210}Pb	Reference	0.08 (0.03)^{a}	0.068 (0.037)^{b}	0.058 (0.033)^{c}	0.010 (0.005)^{d}
	Cultivated	0.27 (0.02)*	0.282 (0.030)*	0.256 (0.027)*	0.025 (0.004)*
^{137}Cs	Reference	0.17 (0.06)^{e}	0.159 (0.073)^{f}	0.138 (0.069)^{g}	0.021 (0.019)^{h}
	Cultivated	0.38 (0.05)*	0.416 (0.059)*	0.379 (0.056)*	0.050 (0.015)

$^{a-h}$ Mixed-model ANOVA probabilities for treatment effects: a = ($F_{1,15}$ = 22.13, P = 0.0003); b = ($F_{1,15}$ = 20.38, P = 0.0004); c = ($F_{1,15}$ = 21.43, P = 0.0003); d = ($F_{1,15}$ = 7.00, P = 0.0183); e = ($F_{1,15}$ = 7.14, P = 0.0175); f = ($F_{1,15}$ = 7.46, P = 0.0154); g = ($F_{1,15}$ = 7.33, P = 0.0162); h = ($F_{1,15}$ = 1.47, P = 0.2434).

technique concordance was better in reference wetlands than in nondrained and restored wetlands (Figures 9, 10). Physical mixing of sediments can also influence distribution of ^{210}Pb; however, sedimentation rates calculated from ^{210}Pb are interpolated over a larger portion of the sediment profile and are less likely influenced by mixing in the upper plow layer.

The dating techniques I used to estimate sedimentation rates do not reflect the most recent activities within the catchment, rather they integrate land-use and climatic effects that have occurred within the past 40 to 80 years. Hence, estimates of sedimentation rates in nondrained and restored wetlands are more reflective of their cultivated history rather than their recent grassland history (i.e., catchments restored to nonnative grasses). The mitigating effects of the recent grassland planting on sedimentation rates in my study wetlands cannot be addressed given the resolution of the dating techniques I used. However, Dryer et al. (1996) measured sedimentation rates in restored and cropland prairie wetlands from 1993 to 1995 using a feldspar clay technique that provides annual estimates of accretion. They found accretion rates to be 0.34 cm yr^{-1} in cropland wetlands and 0.13 cm yr^{-1} in restored wetlands. Though Dryer et al. (1996) were unable to separate these accretion rates statistically, these estimates are similar to what I found in my study wetlands. Their estimate of 0.34 cm yr^{-1} in cropland wetlands is similar to my 0.34 to 0.40 cm yr^{-1} (depending on dating technique) estimate for nondrained and restored wetlands (Table 3). Their estimate of 0.13 cm yr^{-1} in restored wetlands was similar to the 0.08 to 0.17 cm yr^{-1} in my reference wetlands (Table 3). The study by Dryer et al. (1996) tends to support my contention that estimates of accretion in my nondrained and restored wetlands are more representative of a cultivated history, and also suggests that restoring catchments to grassland cover can reduce sedimentation of wetlands.

Influence of Catchment Characteristics on Sedimentation Rates

Erosion of upland soils and the concomitant delivery and deposition of upland soils into wetlands is dependent on erodibility and size of the catchments surrounding wetlands. Average wetland area, catchment area, and ratio of catchment to wetland area did not significantly differ among treatments (Table 7), suggesting that differences in sedimentation rates among treatments were not due to differences in area of erodible surfaces surrounding wetlands. When treated independently of land-use effects, the overall erodibility of catchments may vary by soil type and relief, and local precipitation that provides erosive energy to detach and transport soils. To estimate overall erodibility of catchments independent of land-use, I assumed that the cover-management factor (C) in the RUSLE ($A = RKLSCP$) was = 0.003 for all catchments. Prediction of soil loss, independent of land-use effects, showed soil loss (A = Mg ha^{-1} yr^{-1} or A = 10^{6} g ha^{-1} yr^{-1}) from catchments to be similar among nondrained, restored, and reference wetlands (Table 7). This implies that differences in sedimentation rates among treatments were due to differences in land-use rather than differences in erodibility of catchments. Further, this suggests that physiographic region and sample location effects (e.g., as implied/described

Table 7. Least squares means (± SE) of wetland and catchment areas, ratio of catchment to wetland area, and predicted soil loss from catchments in reference (n = 7), nondrained (n = 5), and restored (n = 7) wetlands surveyed during 1998 in the Prairie Pothole Region of the United States. Means (± SE) within columns were not significantly ($P > 0.05$) different.

				Predicted soil loss from catchment (Mg ha^{-1} yr^{-1})[a]	
	Wetland[b] area (ha)	Catchment[c] area (ha)	Catchment/[d] wetland area ratio	minus C[e] factor	plus C[f] factor
Treatment	Mean SE	Mean SE	Mean SE	Mean SE	Mean SE
Reference	2.8 (0.6)	6.9 (1.9)	2.3 (0.4)	0.07 (0.02)	0.08 (3.06)
Nondrained	2.1 (0.9)	5.7 (2.8)	2.6 (0.5)	0.08 (0.02)	10.62 (4.47)
Restored	2.6 (0.6)	5.7 (1.9)	2.4 (0.4)	0.06 (0.02)	4.69 (3.06)

a Soil loss was predicted using the Revised Universal Soil Loss Equation, $A = RKLSCP$ (Wischmeier and Smith 1978.): where A = computed soil loss, R = rainfall erosivity factor, K= soil erodibility factor, C = cropping factor. The supporting practice (P) factor was assumed to be = 1 for all soil loss estimates. Minus C soil loss estimates do not include the cropping factor (i.e., assumed to be 0.003 for all treatments). Plus C soil loss estimates include the cropping factor associated with each wetland within treatments.

b-f Mixed-model ANOVA probabilities for treatment effects: b = ($F_{2, 13}$ = 0.20, P = 0.822); c = ($F_{2, 13}$ = 0.12, P = 0.891); d = ($F_{2, 13}$ = 0.09, P = 0.916); e = ($F_{2, 13}$ = 0.44, P = 0.881); f = ($F_{2, 13}$ = 1.95, P = 0.182).

by R, K, L, and S, factors) not completely controlled for by the study design (Figure 4) were similar among treatments.

When including the C factor associated with land-use (i.e., treatment effects), annual average soil erosion was greater in nondrained and restored wetland catchments than in reference catchments (Table 7). Multiplying estimated soil loss (Mg ha^{-1} yr^{-1}) by total upland catchment area (ha) provides an estimate of catchment soil loss (Mg yr^{-1}) potentially entering wetlands. Eighteen of 19 catchment soil loss estimates were < 35 Mg yr^{-1}, the remaining estimate was 494 Mg yr^{-1}; this wetland had a large catchment area with extremely steep slopes. Estimates of catchment soil loss (when excluding the high estimate of 494 Mg yr^{-1}) were better correlated with ^{210}Pb based accretion ($r = 0.67$; $P = 0.002$) and accumulation ($r = 0.79$; $P < 0.0001$) rates than with ^{137}Cs based accretion ($r = 0.43$; $P = 0.08$) and accumulation ($r = 0.47$; $P = 0.05$) rates. Using catchment soil loss (Mg yr^{-1}) as a predictor (x) of ^{210}Pb based sedimentation rates, the regression function for accretion rate (cm yr^{-1}) = $0.0777 + 0.0261x - 0.0007x^2$ ($F_{2, 15} = 14.92$, $P = 0.0003$, $R^2 = 0.67$), and for accumulation rate (g cm^{-2} yr^{-1}) = $0.0630 + 0.0292x - 0.0007x^2$ ($F_{2, 15} = 26.87$, $P < 0.0001$, $R^2 = 0.78$) (Figure 11).

The curvilinear relationship depicted in Figure 11 indicates that catchment soil loss estimates predicted by the RUSLE do not equate perfectly with sediment accumulation in wetlands. Examination of catchment characteristics showed that differences in percent slope and slope lengths among wetlands were the cause of the curvilinear relationship. The 3 wetlands with the highest per-catchment erosion estimates had long slope lengths

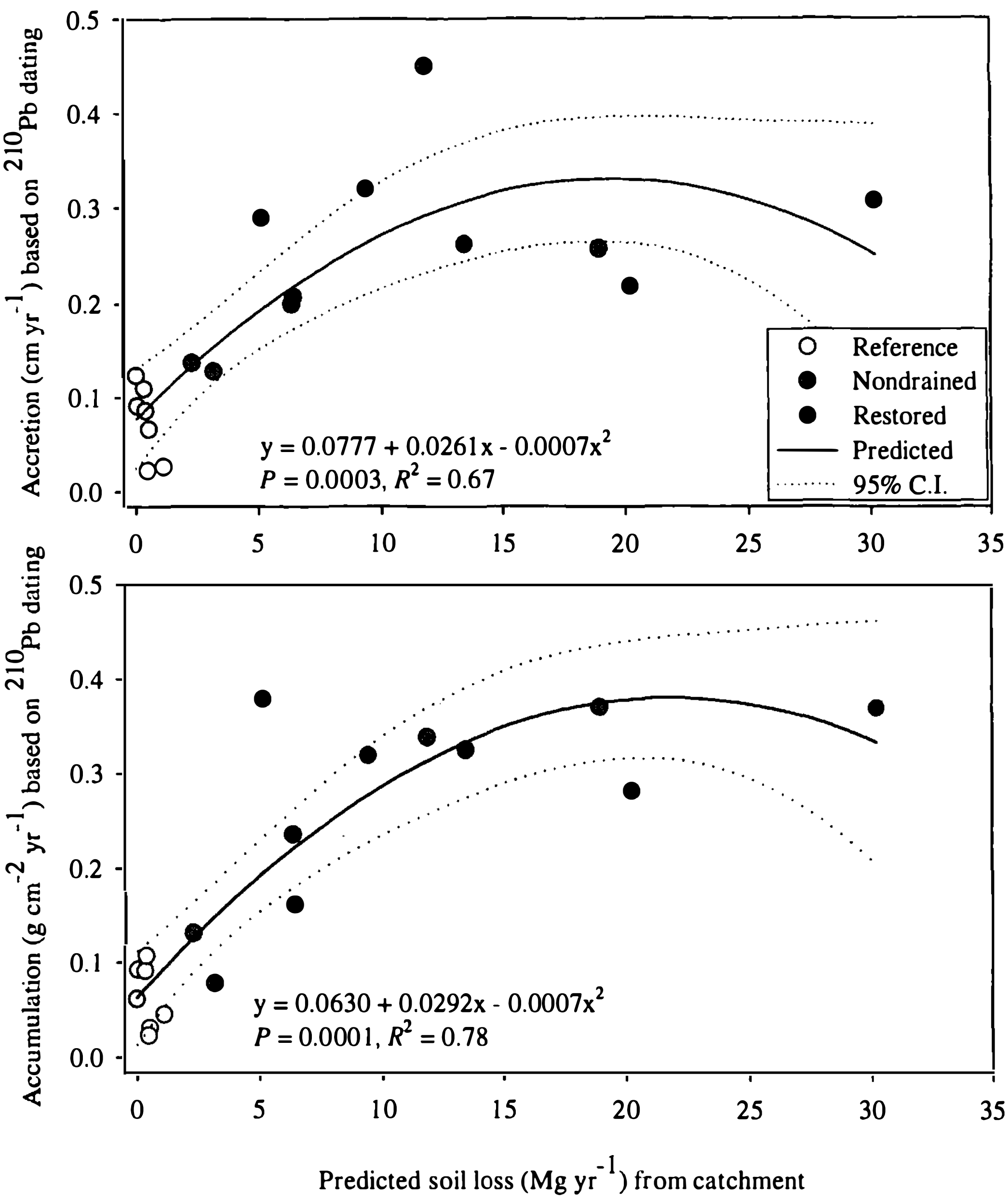

Figure 11. Relationship between predicted soil loss from catchments and sedimentation rates in reference (n = 7), nondrained (n = 5), and restored (n = 7) wetlands sampled during 1998 in the Prairie Pothole Region of the United States. Catchment soil loss estimates were predicted using the revised universal soil loss equation (Wischmeier and Smith 1978) and sedimentation rates in wetlands were based on ^{210}Pb dating.

with moderate relief, whereas wetlands with lower catchment soil loss estimates tended to have short slopes with higher relief (Figure 12). Consequently, wetlands with larger catchments and slope lengths had greater mass movement of soils within their catchments, but low relief reduced the transport and delivery of eroded soils into wetland basins.

The RUSLE was developed to assess on-site soil loss, but not off-site sediment accumulation (Mutchler et al. 1994). Similar to my findings, other studies have also found that sediment accumulations do not necessarily coincide with major erosional areas (Novotny and Chesters 1989). Based on my small sample size, per-catchment soil loss as predicted by the RUSLE did provide an indicator of sediment impacts to wetlands; however, predicting sediment yield or sedimentation rates from per-catchment soil loss estimates is tenuous.

Effects of Sedimentation on Wetland Pool Depth and Volume

To examine the potential effects of accelerated sedimentation on pool depth and volume, I projected forward over a 200-year period the effect of reference (0.08 cm yr^{-1}) and cultivated wetland (0.27 cm yr^{-1}) (Table 6) accretion rate estimates on pool depth and volume of 134 wetlands. Accretion rates were based on ^{210}Pb dating. To incorporate ecological significance into projections of sedimentation effects on wetland pool depth, I only included wetlands that had pool depths ≥ 1 m (77 of 134) because 1 m of water is generally believed to be adequate to flood-out tall robust emergents such as cattails

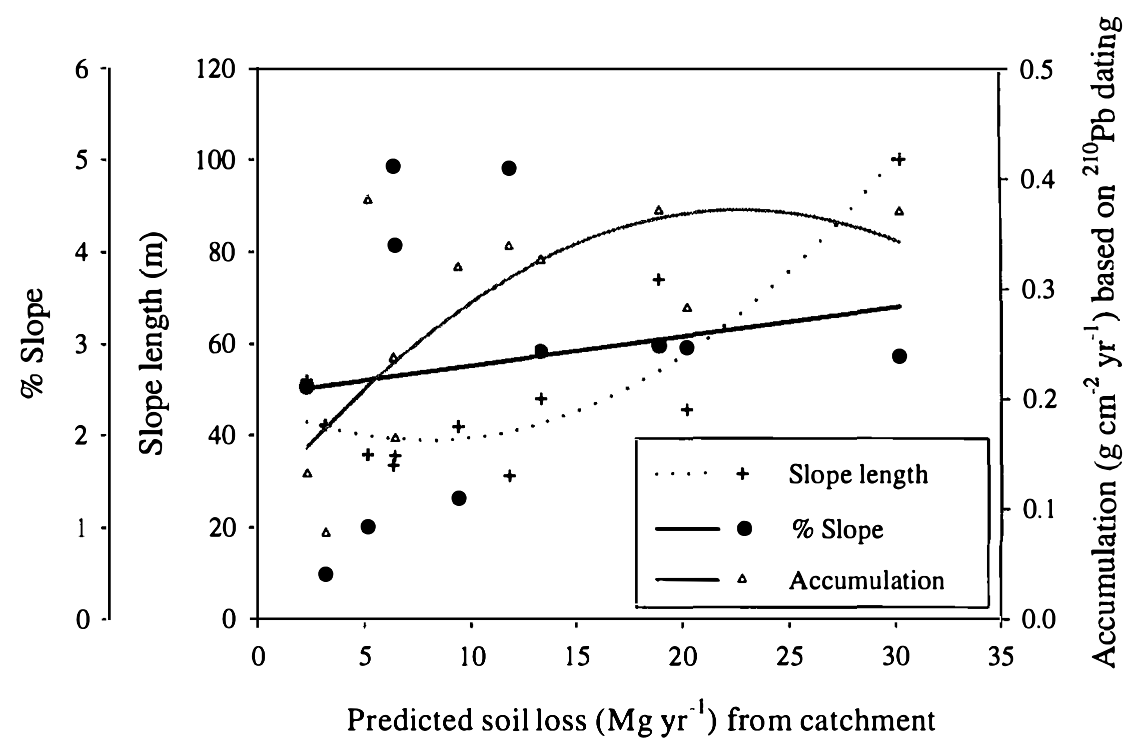

Figure 12. Relationship of catchment soil loss to accumulation rates in cultivated wetlands (n = 12), and average percent slope and slope length of catchments. Wetlands were sampled during 1998 in the Prairie Pothole Region of the United States. Catchment soil loss estimates were calculated using the universal soil loss equation (Wischmeier and Smith 1978) and accumulation rates were estimated using ^{210}Pb dating.

(Beule 1979, Weller 1987). A quadratic function was found to describe the relationship between maximum pool depth (m) and volume, where volume (ha m) = 0.3958 - 0.9369depth + 1.1603depth^2 ($F_{2,131}$, $P < 0.0001$, $R^2 = 0.67$) (Figure 13). Using this quadratic relationship, I used loss of depth estimates over time to estimate corresponding volumetric loss in each of the 134 wetlands.

Projected over the first 100 years, and assuming a cultivated wetland accretion rate, 35.1% of the 77 wetlands would no longer attain water depths of ≥1 m; whereas over the same time frame, a reference wetland accretion rate would result in a 10.4% loss (Figure 14). Projected over the full 200 years, cultivated and reference wetland accretion rates would result in a 57.1% and 18.2% loss, respectively, in the number of wetlands capable of attaining water depths of ≥1 m (Figure 14). Total volume or water storage capacity of the 134 wetlands was estimated to be 203 ha m. Based on a cultivated wetland accretion rate, 49.8% of this volume would be lost within 200 years, whereas based on reference a wetland accretion rate, 20.0% of the total volume would be lost (Figure 15).

SUMMARY AND MANAGEMENT IMPLICATIONS

My research demonstrated the potential future impact of accelerated sedimentation on loss of wetland pool depth and volume. Wetland volume and depth loss projections also suggest that past agricultural land-use activities have already led to a significant loss in wetland depth and volume. Several studies in the PPR have related

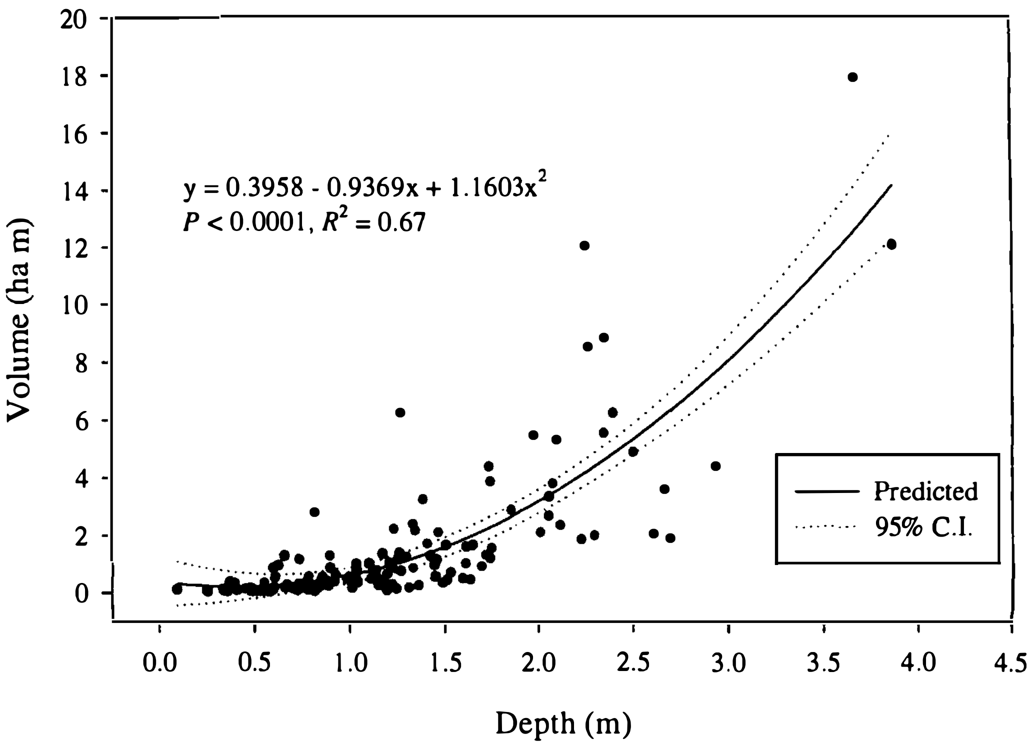

Figure 13. Relation between maximum wetland pool depth and maximum potential volume. Based on a 134 wetlands surveyed during 1998 in the Prairie Pothole Region of the United States.

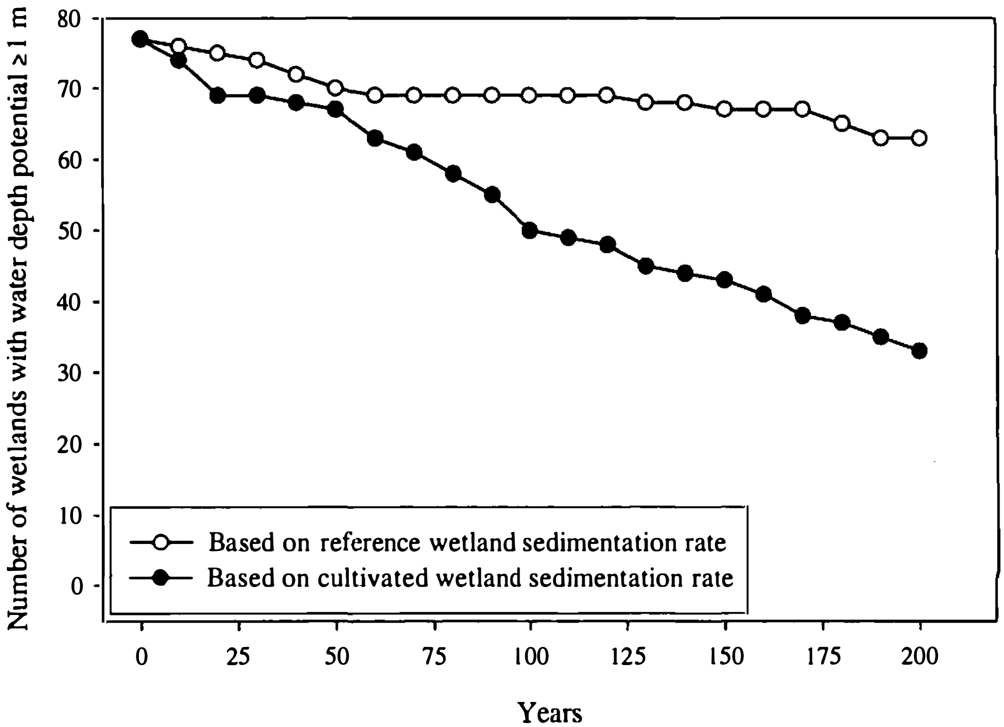

Figure 14. Projected influence of reference and cultivated wetland sedimentation rates on loss of wetland depth in 77 wetlands surveyed during 1998 in the Prairie Pothole Region of the United States.

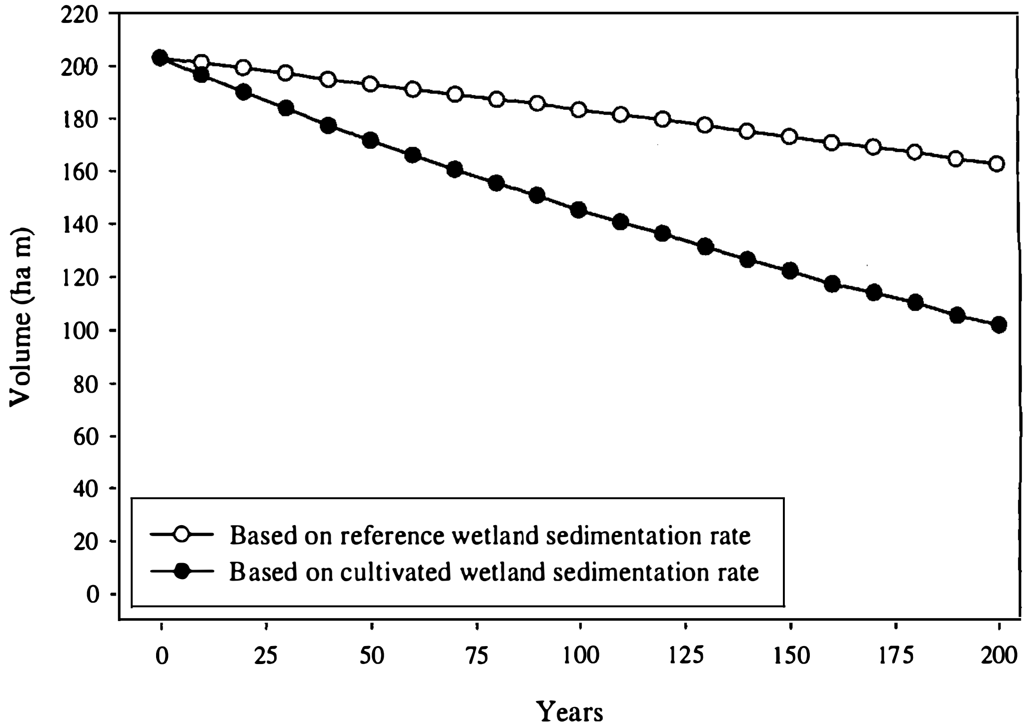

Figure 15. Projected influence of reference and cultivated wetland sedimentation rates on loss of volume in 134 wetlands surveyed during 1998 in the Prairie Pothole Region of the United States.

artificial drainage of wetlands and land-use to increased flooding (Brun et al. 1981, Miller and Nudds 1996). Although not considered by these previous studies, significant losses in water storage capacity of wetlands due to accelerated sedimentation may have exacerbated flooding problems. Projected over a small population of wetlands, my results suggest that 30 - 50% of the volume (ca. 100 ha m) would be lost within 100-200 years. Presumably, losing 30-50% of the water storage capacity in all remaining agricultural wetlands would substantially increase the risk of flooding.

My projections of sedimentation effects on loss of wetland volume and depth assumed that erosion rates and surface outlet elevations remain constant over time. However, erosion rates would be expected to change as catchments are eroded. Further, when water does flow out of surface outlets, this enhances erosion and lowers elevations of surface outlets which effectively reduces water holding capacity and decreases maximum pool depths. Given that agricultural practices increase surface runoff and water-level fluctuations, water outflow events that erode and reduce surface outlet elevations would be expected to occur more frequently in agricultural wetlands than in grassland wetlands (Euliss and Mushet 1996). Consequently, loss of wetland volume in conjunction with factors that lower surface outlet elevations may result in more rapid loss of wetland water storage capacity than suggested by my projections.

My research highlights the need to determine the amount of sediment accrued in drained basins targeted for restoration. Ideally, sediments would be excavated to the depth necessary to restore the wetland depression back to pre-agricultural conditions.

Given cost and time constraints, resource managers generally do not have easy access to techniques to quantify the amount of sediment that needs to be excavated. The relationship I found between RUSLE estimates and sedimentation rates shows promise as a tool to determine the extent of sediment accumulations. However, more research is needed from a larger reference domain to better define the relationship between sediment delivery, catchment soil loss, and sediment accumulation in wetlands.

The RUSLE was developed to estimate long-term average annual soil loss (Risse et al. 1993), and thus would not account for a single or multiple catastrophic sedimentation events; such events have completely filled wetlands with sediments during single catastrophic events (personal observation). Substantial sediment accumulations are often readily recognized in the field as alluvial fans entering wetlands or by examination of soil profiles that often reveal buried soil horizons and inconsistent stratigraphy (e.g., buried A or O soil horizons). Catastrophic sedimentation events largely go unnoticed in the prairies. However, buried A horizons were found in 17% of the 158 drained, nondrained and restored wetlands surveyed by NPWRC during 1997. Average burial depth was 35 cm and ranged from 12 to 98 cm (NPWRC unpublished data). Given this, soil profiles of drained wetlands targeted for restorations should be examined to determine if major sedimentation events have significantly reduced wetland pool depth and volume. Restoration of historic pool depths and volumes of silted in wetlands can be accomplished by excavation of sediments or increasing water depths with water control structures. Excavating wetlands or using water control structures to increase depth may have the same effect on targeted wetlands functions. Future research should evaluate the ecological implications and economic feasibility of these 2 restoration techniques.

Agricultural programs such as the Conservation Reserve Program (CRP) offer great potential to protect wetlands from agricultural sedimentation. Though substantial amounts of land have been planted to perennial cover as part of the CRP, studies have not been conducted to evaluate which cover type or diversity of cover best reduces erosion and sedimentation of wetlands. Further, studies have not considered the hydrological effects of different cover types. In a study by van der Kamp et al. (1999), wetlands with farmed catchments converted to smooth bromegrass (*Bromus inermis*) dried out within a few years, and remained dry even in years of high precipitation, whereas wetlands in neighboring cultivated areas retained water. Van der Kamp et al. (1999) speculated that smooth bromegrass reduced runoff of snowmelt and enhanced infiltration capacity of soil. Certainly, research is needed to better describe the influence of catchment cover types on hydrologic processes.

The potential for agricultural soil erosion to degrade prairie wetlands is great and the ultimate impact of accelerated sedimentation is the complete loss of wetland pool depth, at which time all natural wetland functions and associated societal values have been lost. Agricultural programs such as CRP protect wetlands, but application of such programs are temporal and are limited by fiscal budgets. Agricultural research in recent years has been instrumental in development of management practices that reduce soil erosion, greenhouse emissions, and water quality impacts (Neely and Baker 1989, Kern and Johnson 1993, Fawcett et al. 1994), but the benefits of these conservation practices to preserve wetlands in an agricultural landscape have not been evaluated. Future research needs to integrate both agricultural and wetland interests in order to evaluate and implement management strategies that sustain both agriculture and wetlands.

CHAPTER 3

AQUATIC INVERTEBRATE EGG BANK COMPOSITION IN RESTORED, NATURAL, AND DRAINED PRAIRIE WETLANDS AND POTENTIAL EFFECTS OF SEDIMENT LOAD ON INVERTEBRATE EMERGENCE.

INTRODUCTION

Numerous wetlands have been restored in the Prairie Pothole Region (PPR) to mitigate for past wetland losses (Galatowitsch and van der Valk 1994). Restoration of these wetlands typically consists of plugging ditch or tile drains and relying on natural processes for recolonization of aquatic invertebrates. Insects with aerial dispersal capabilities have been shown to rapidly recolonize restored wetlands (LaGrange and Dinsmore 1989, Sewell 1989, Delphey 1991, Hemesath 1991, VanRees-Siewert 1993). However, some studies indicated that less mobile and passively dispersed invertebrates (e.g., Amphipoda, Conchostraca, Ostracoda) were poorly represented in restored wetlands (Delphey 1991, VanRees-Siewert 1993). Passive dispersers are reliant on wind or animals for dispersal to wetlands (Euliss et al. 1999). Many passive dispersers have devised various strategies to persist and recolonize reflooded wetlands, including production of resting eggs and cysts, diapause, and aestivation (Wiggins 1980, Euliss et al. 1999). Some of these eggs remain viable in dry wetland soils for many years (Pennak 1989) and may play an important role in recolonization of restored wetlands.

The role of remnant invertebrate egg banks in repopulating restored wetlands has not been evaluated. However, most remaining wetlands, as well as drained basins targeted for restoration have been degraded by intensive agriculture, a factor which may negatively impact invertebrate egg banks. Studies have shown that invertebrate egg banks are negatively impacted by agricultural cultivation and artificial drainage (Euliss and Mushet 1999, 2001). Further, cultivation of wetland catchments has increased sedimentation of wetlands (Martin and Hartman 1987, Dieter 1991, Gleason and Euliss 1998). Sedimentation buries seed banks and reduces plant emergence (Jurik et al. 1994, Wang et al. 1994), and presumably sedimentation would have a similar effect on emergence of invertebrates from egg banks.

The objectives of my study were to (1) compare invertebrate egg bank composition among reference, nondrained, restored, and drained wetlands, (2) evaluate the influence of restoration age on invertebrate egg bank composition, and (3) examine the effect of sediment load on emergence of invertebrates from egg banks.

MATERIALS AND METHODS

Field Collection and Laboratory Processing of Experimental Material

During June to September 1997, I collected soil samples (i.e., invertebrate egg bank samples) from 201 wetlands in a 5 state region of the PPR (Figure 2). Wetlands selected for study included seasonal and semipermanent drained, restored, and nondrained wetlands in Conservation Reserve Program type habitats (i.e., once farmed lands planted back to perennial grassland) and reference wetlands with no history of cultivation in the wetland basin or catchment (Table 8). I collected soils samples along 4 randomly established transects that radiated from the center of each wetland. Along each transect, I collected 3 cores to a depth of 5 cm in the wet-meadow and shallow-marsh zone using a 7.5 cm diameter corer. Samples were stored in a freezer (< 0°C) until needed for laboratory experiments. In the laboratory, soil samples from each wetland (12 cores from shallow marsh and 12 cores from wet meadow) were composited, mixed, and sieved to remove litter, roots, and tubers. One subsample (380 cm^3) from each composite sample (n = 201) was spread evenly over the surface of a plastic flat (19.5 X 19.5 X 6 cm). This resulted in a soil depth of ca. 1 cm.

Aquarium Experiments

Aquarium experiments were performed in an environmentally controlled experimental room at the U.S. Geological Survey's Northern Prairie Wildlife Research Center, Jamestown, ND. Incubation experiments were conducted in 1998. Four experimental runs were necessary to incubate soils from all the wetland replicates. Each experimental run was restricted by wetland class and physiographic region (Table 8). Separate runs were necessary because the number of wetland replicates exceeded the number of aquaria available in the experimental room. Experimental runs were performed in the following order: (1) Glaciated Plain seasonal wetlands, (2) Missouri and Prairie Coteau seasonal wetlands, (3) Glaciated Plain semipermanent wetlands, and (4)

Table 8. Replication of wetland treatments by wetland class and physiographic region sampled for invertebrate egg banks, June-September 1997. Wetlands are located in the Glaciated Plain, Missouri Coteau, and Prairie Coteau physiographic regions of the Prairie Pothole Region of the United States.

Wetland class	Physiographic region	Treatments			
		Reference[a]	Nondrained	Restored	Drained
Seasonal	Glaciated Plain	12 (8)	12	21	12
	Missouri Coteau	9 (4)	9	16	7
	Prairie Coteau	3 (3)	3	6	3
Semipermanent	Glaciated Plain	10 (9)	9	14	9
	Missouri Coteau	9 (7)	8	11	3
	Prairie Coteau	3 (1)	3	6	3

[a] Numbers in parentheses indicate number of wetlands used to determine the effects of sediment load on emergence of invertebrates.

Missouri and Prairie Coteau semipermanent wetlands. Separate runs limit statistical comparisons among physiographic regions and wetland classes; however, it allowed for unbiased comparisons of wetlands of the same class within physiographic region.

During each experimental run, flats containing wetlands soils were randomly assigned to aquaria. Samples were incubated for 6 weeks in 37.8 L glass aquaria containing well water adjusted to the approximate mean specific conductance typical of seasonal (700 μS) and semipermanent (1400 μS) wetlands being evaluated. Temperatures were maintained at 10°C for the first 3 weeks and then raised to 20°C for the remainder of the experiment. The light regime was maintained at 12 h light:12 h dark and aquaria were aerated during experiments. Aquaria temperatures were checked daily and distilled water was added to maintain water levels and salt concentrations. Procedures used for incubating invertebrates from soil egg bank samples, including maintenance of light, water chemistry, and temperature regimes follow those described by Euliss and Mushet (1999).

During the first experimental run, attempts were made to directly observe invertebrates as they hatched in the aquaria and to remove them from the aquaria as soon as they could be identified. However, during the first experimental trial, it was found that this procedure was unreliable because very small cladocerans could not be readily observed through the aquarium glass. To reduce the risk of overlooking small immature invertebrates during subsequent trials, aquaria were harvested every 2 weeks by siphoning the water from the aquaria through a 0.1 mm screen to concentrate invertebrates. The siphoned water was then returned to the aquaria. All harvested invertebrates were enumerated and identified using keys by Pennak (1989).

Sediment Load Experiments

During each of the 4 experimental runs, a subsample of reference wetlands (Table 8) were used to determine the effects of sediment load on emergence of invertebrates. To determine the effect of sediment load on emergence of invertebrates, an additional 3 subsamples of soil from each reference wetland were placed in flats and overlain with 0.5 cm, 1 cm, and 2 cm of sterilized upland soil. To prevent mixing of wetland soils and sediments, wetland soils were placed in a freezer for 5-10 minutes prior to covering with upland soils. Additional flats containing only upland soils were also prepared and subjected to aquarium conditions to verify that they were free of viable eggs. Upland soil used to overlay wetland soils had a silty-clay-loam texture and was sieved through 0.017 mm mesh to concentrate particle sizes similar to erosional sediment. Upland soil was provided by U.S. Department of Agriculture's Northern Grain Insects Research Laboratory, Brookings, SD and was determined to be free of agrochemical residues.

Statistical Analysis

I used analysis of variance (ANOVA) to assess the influence of wetland treatment (i.e., drained, restored, nondrained, and reference) on abundance and taxon richness of invertebrates incubated from egg banks. Analyses were performed separately for each wetland-class-physiographic-region combination and I used a block design where sampling area was treated as a block (i.e., GP01-GP12; Figure 1). I conducted ANOVAs using the mixed model procedure (PROC MIXED) of SAS (SAS Institute, Inc 1997). Prior to analysis, transformations [ln(count + 1)] were performed on the data to stabilize variances (Steel and Torrie 1980). Fisher's protected least significant difference tests (LSD) were used to assess individual differences when main effects were significant (Milliken and Johnson 1984).

RESULTS

Hatching Success and Taxon Richness

Anostracans, conchostracans, copepods, ostracods, and 4 families of cladocerans (Daphnidae, Macrothricidae, Chydoridae, and Bosminidae) were the only invertebrate taxa successfully incubated during aquarium experiments. Invertebrates successfully hatched from 74% of the 201 wetlands sampled for invertebrate egg banks. In all physiographic regions, hatching success (% percent of wetlands that hatched one or more invertebrates) for seasonal treatments was lower in drained wetlands than in other treatments (Figure 16a-c). Hatching success in semipermanent wetlands in the Glaciated

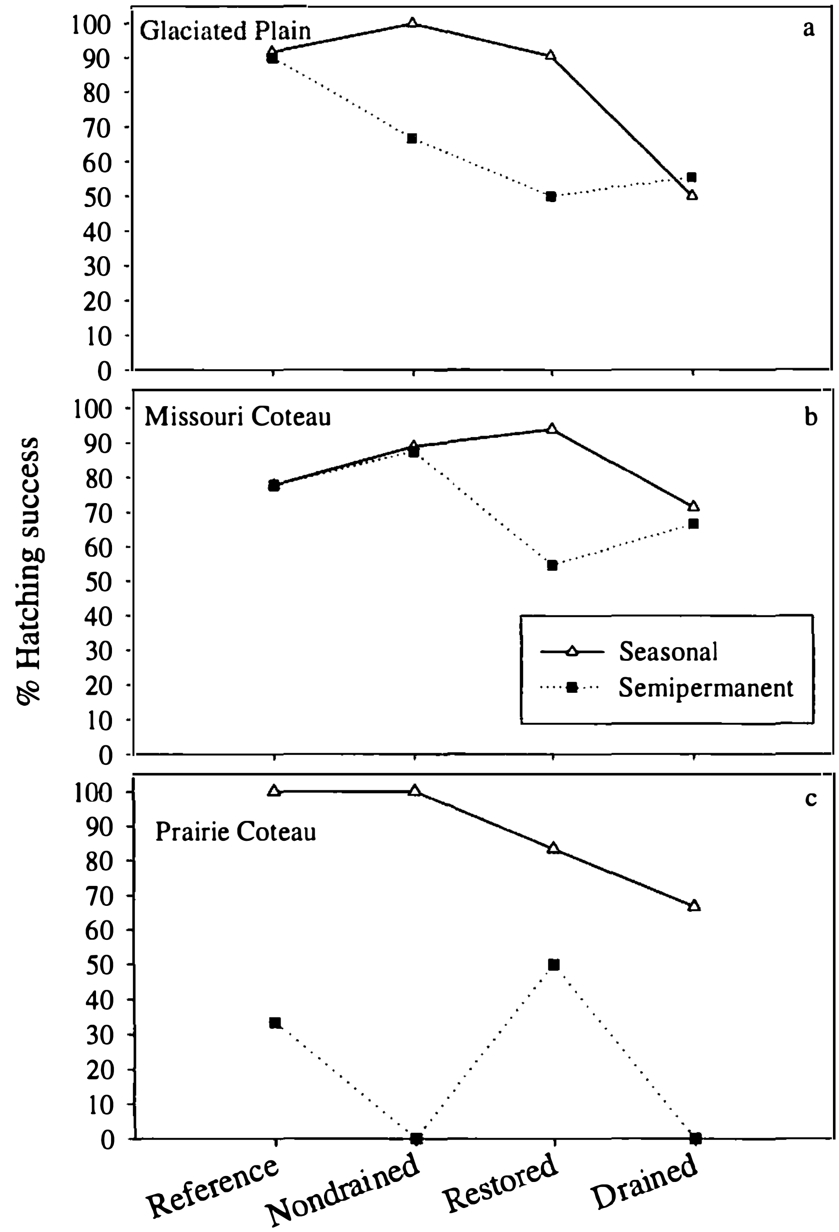

Figure 16. Percent of seasonal and semipermanent reference, nondrained, restored, and drained wetlands that successfully hatched invertebrates during soil egg bank incubation experiments. Egg bank samples were collected June-September 1997. Wetlands are located in the Glaciated Plain (a), Missouri Coteau (b), and Prairie Coteau (c) physiographic regions of the Prairie Pothole Region of the United States. Replication of treatments by region and wetland class are shown in Table 8.

Plain and Missouri Coteau regions was generally lower in restored and drained wetlands than in nondrained and reference wetlands (Figure 16a, b). Hatching success was lower and more variable in semipermanent wetlands than in seasonal wetlands (Figure 16a-c).

I found few significant differences in taxon richness among wetland treatments. Only Glaciated Plain seasonal wetlands showed a significant ($F_{3,31} = 3.32$, $P = 0.033$) response with lower taxon richness in drained wetlands than in other wetland treatments (Figure 17a). Taxon richness in restored and drained Glaciated Plain semipermanent wetlands was lower than in reference and restored wetlands, but this was not statistically significant ($F_{3,23} = 2.51$, $P = 0.084$) (Figure 17b). Taxon richness did not significantly differ among treatments for Missouri Coteau seasonal ($F_{3,22} = 0.42$, $P = 0.74$) and semipermanent ($F_{3,15} = 1.02$, $P = 0.41$) wetlands or Prairie Coteau seasonal ($F_{3,6} = 3.87$, $P = 0.074$) and semipermanent ($F_{3,6} = 1.03$, $P = 0.45$) wetlands (Figure 17c-f).

Invertebrate Abundance

Mean counts of invertebrates incubated from egg banks were significantly ($F_{3,31} = 7.57$, $P = 0.0006$) lower in drained Glaciated Plain seasonal wetlands than in other wetland treatments (Figure 18a). Drained and restored Glaciated Plain semipermanent wetlands had lower mean counts than reference and restored wetlands, but this was not statistically significant ($F_{3,23} = 2.45$, $P = 0.088$) (Figure 18b). Mean counts did not

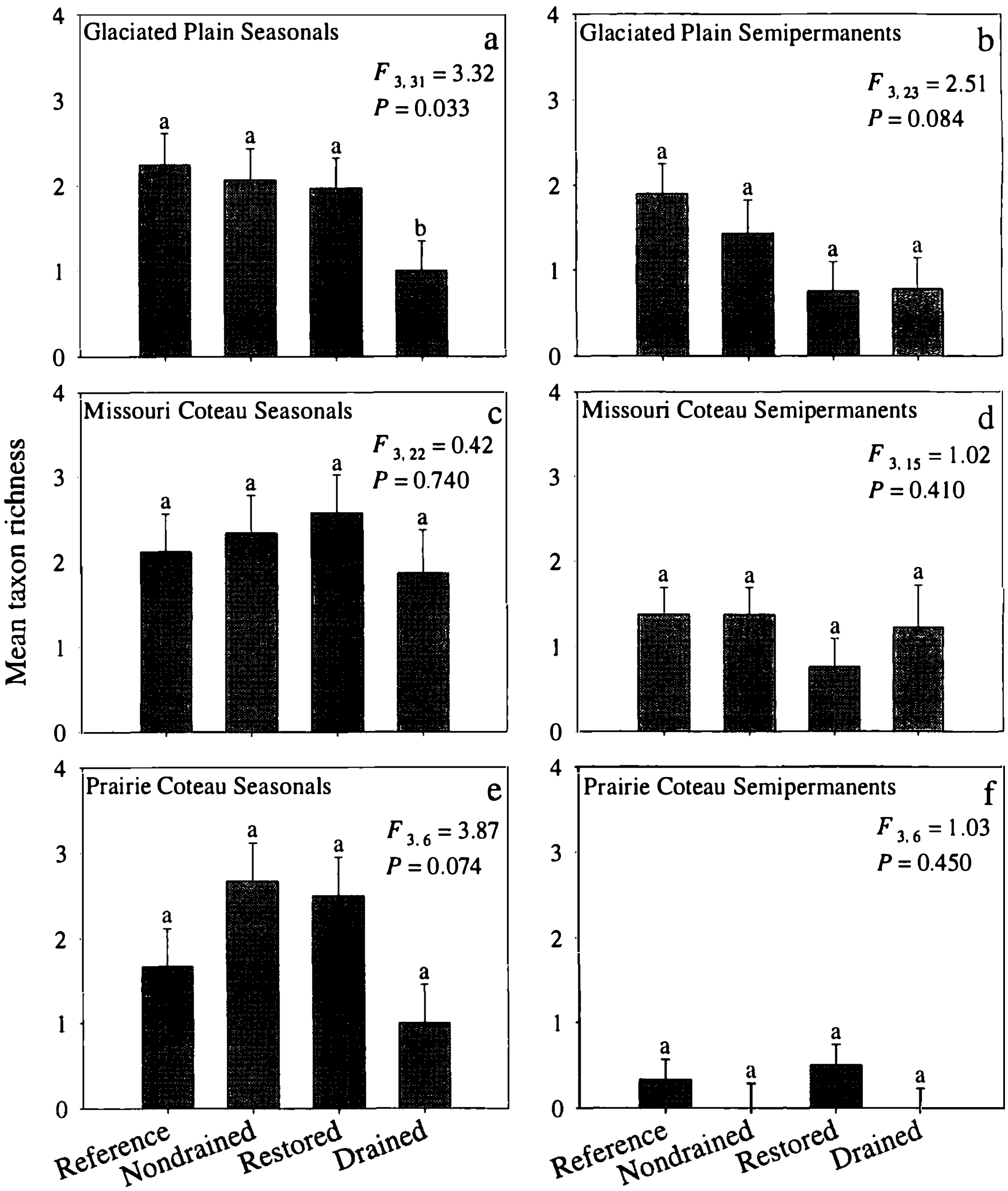

Figure 17. Mean (+ SE) taxon richness of invertebrates incubated from soils collected in seasonal and semipermanent reference, nondrained, restored, and drained wetlands. Egg bank samples were collected June-September 1997. Wetlands are located in the Glaciated Plain (a-b), Missouri Coteau (c-d), and Prairie Coteau (e-f) physiographic regions of the Prairie Pothole Region of the United States. Bars within each graph (a-f) with a common letter are not significantly ($P > 0.05$) different. Replication of treatments by region and wetland class are shown in Table 8.

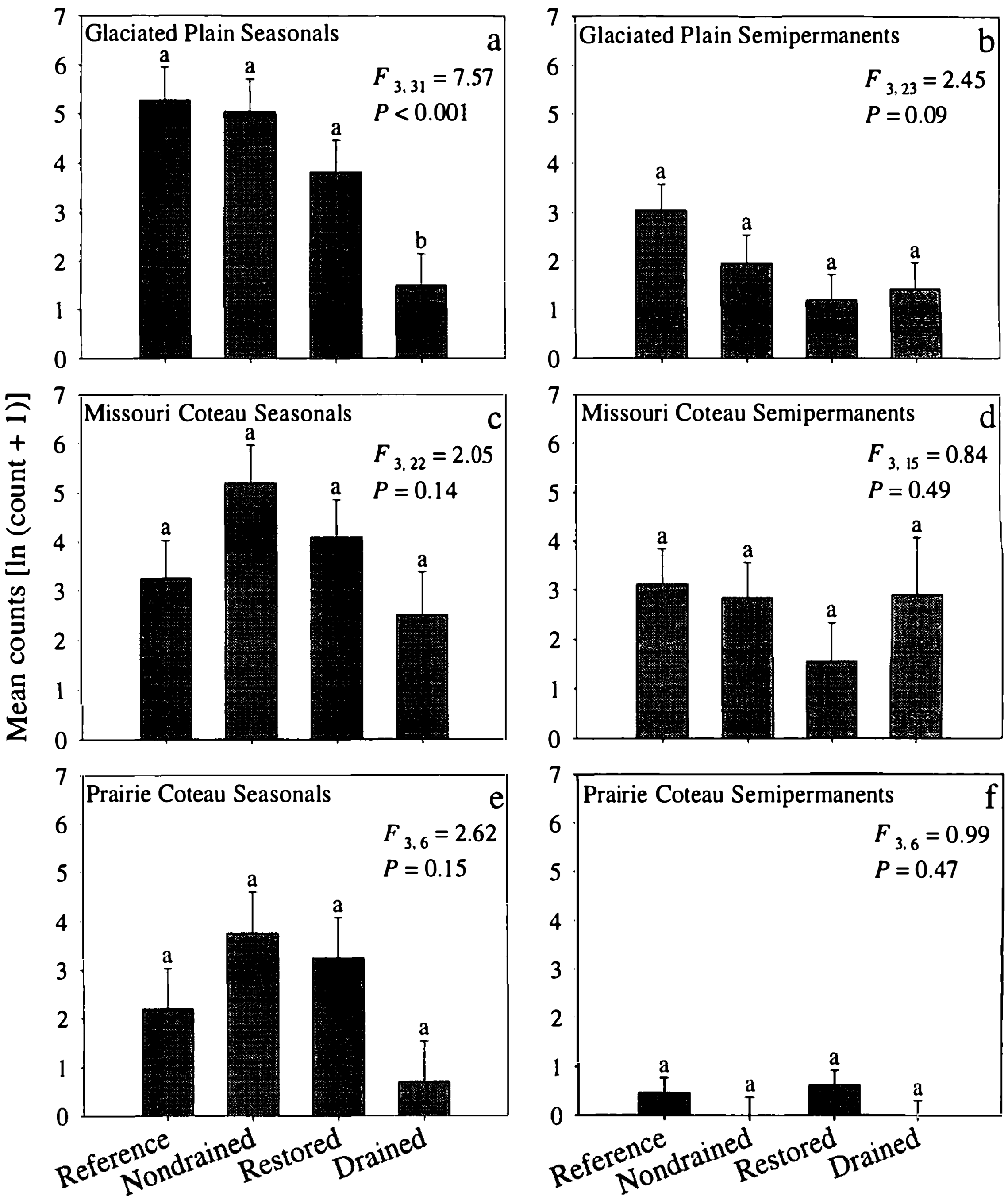

Figure 18. Mean counts (+ SE) of invertebrates incubated from soils collected in seasonal and semipermanent reference, nondrained, restored, and drained wetlands. Egg bank samples were collected June-September 1997. Wetlands are located in the Glaciated Plain (a-b), Missouri Coteau (c-d), and Prairie Coteau (e-f) physiographic regions of the Prairie Pothole Region of the United States. Bars within each graph (a-f) with a common letter are not significantly ($P > 0.05$) different. Replication of treatments by region and wetland class are shown in Table 8.

significantly differ among treatments for Missouri Coteau seasonal ($F_{3, 22} = 2.05$, $P = 0.14$) and semipermanent ($F_{3, 15} = 0.84$, $P = 0.49$) wetlands or Prairie Coteau seasonal ($F_{3, 6} = 2.62$, $P = 0.15$) and semipermanent ($F_{3, 6} = 0.99$, $P = 0.47$) wetlands (Figure 18c-f).

Of the 8 taxa successfully incubated during aquarium experiments, only ostracods and chydorids were found to differ among treatments (Figure 19a-d). Mean counts of chydorids in Glaciated Plain seasonal wetlands were highest ($F_{3, 31} = 4.58$, $P = 0.009$) in reference wetlands, followed in descending order by nondrained, restored, and drained wetlands (Figure 19a). Chydorid abundance in Missouri Coteau seasonal wetlands was greater ($F_{3, 22} = 4.36$, $P = 0.015$) in nondrained than in reference and drained wetlands, but similar to restored wetlands (Figure 19b). Abundance of ostracods in Glaciated Plain seasonal wetlands was significantly ($F_{3, 31} = 4.43$, $P = 0.010$) lower in drained wetlands than in other treatments (Figure 19c), and ostracod abundance in Prairie Coteau seasonal wetlands was greater ($F_{3, 6} = 5.98$, $P = 0.031$) in nondrained wetlands than in other treatments (Figure 19d). Mean counts of other invertebrate taxa did not significantly ($P > 0.05$) differ among treatments (Table 9).

Effects of Restoration Age on Invertebrate Egg Banks

Taxon richness and abundance of invertebrates did not show a significant relationship with restoration age (Figures 20, 21). Relative to restored seasonal wetlands in the Glaciated Plain (Figure 20a), more restored seasonal wetlands in the Coteau regions had taxon richness values similar to average taxon richness in reference and

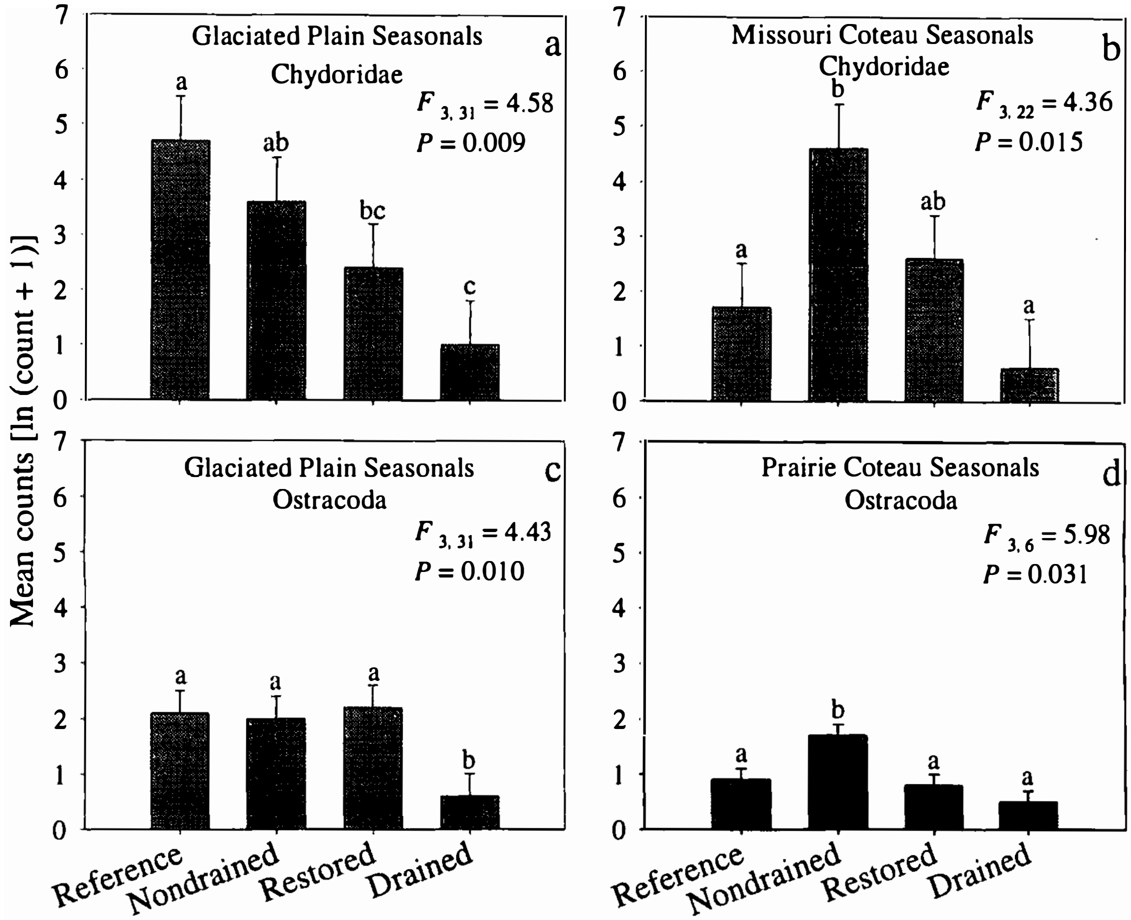

Figure 19. Mean counts (+ SE) of invertebrate taxa incubated from soils collected in seasonal and semipermanent reference, nondrained, restored, and drained wetlands. Egg bank samples were collected June-September 1997. Wetlands are located in the Glaciated Plain (a, c), Missouri Coteau (b), and Prairie Coteau (d) physiographic regions of the Prairie Pothole Region of the United States. Bars within each graph with a common letter are not significantly ($P > 0.05$) different. Replication of treatments by region and wetland class are shown in Table 8.

Table 9. Mean (± SE) counts of invertebrate taxa incubated from soils collected in seasonal and semipermanent reference, nondrained, restored, and drained wetlands. Egg bank samples were collected June-September 1997. Wetlands are located in the Glaciated Plain, Missouri Coteau, and Prairie Coteau physiographic regions of the Prairie Pothole Region of the United States.

Region and Wetland Class	Taxa	Reference Mean SE	Nondrained Mean SE	Restored Mean SE	Drained Mean SE
Glaciated Plain Seasonals		(n = 12)[a]	(n = 12)	(n = 21)	(n = 12)
	Chydoridae	596.9 (166.6)	279.6 (138.8)	212.1 (90.5)	33.6 (23.6)
	Daphnidae	11.5 (9.5)	144.7 (77.7)	54.8 (32.1)	103.8 (73.0)
	Ostracoda	13.8 (4.9)	14.2 (6.8)	48.5 (23.9)	12.3 (11.9)
	Copepoda	0.1 (0.1)	0.2 (0.1)	0.2 (0.1)	0.2 (0.2)
	Macrothricidae	0.9 (0.9)	–	–	–
	Conchostraca	–	–	0.2 (0.2)	–
	Anostraca	–	–	–	0.1 (0.1)
Missouri Coteau Seasonals		(n = 9)	(n = 9)	(n = 16)	(n = 7)
	Chydoridae	94.0 (68.7)	721.0 (281.7)	104.9 (41.4)	2.9 (2.5)
	Daphnidae	33.6 (28.4)	228.1 (141.5)	21.0 (12.2)	51.6 (46.9)
	Ostracoda	5.8 (2.6)	10.6 (3.2)	34.0 (23.4)	1.3 (0.6)
	Macrothricidae	54.4 (54.4)	–	3.7 (2.8)	46.9 (34.7)
	Copepoda	3.8 (3.7)	1.0 (0.7)	3.9 (3.0)	–
	Anostraca	–	0.1 (0.1)	–	–
Prairie Coteau Seasonals		(n = 3)	(n = 3)	(n = 6)	(n = 3)
	Chydoridae	39.0 (39.0)	26.3 (13.2)	26.3 (25.5)	–
	Daphnidae	0.3 (0.3)	10.3 (10.3)	82.8 (68.7)	0.7 (0.7)
	Ostracoda	1.7 (0.7)	4.3 (0.3)	2.3 (1.6)	0.7 (0.3)
	Copepoda	–	1.0 (0.6)	0.2 (0.2)	–
	Bosminidae	–	–	3.8 (3.8)	–
	Macrothricidae	–	–	0.2 (0.2)	–

Table 9. (continued)

Region and Wetland Class	Taxa	Reference Mean (SE)	Nondrained Mean (SE)	Restored Mean (SE)	Drained Mean (SE)
Glaciated Plain Semipermanents		(n = 10)	(n = 9)	(n = 14)	(n = 9)
	Chydoridae	34.2 (19.2)	5.0 (3.9)	12.7 (8.7)	3.3 (2.5)
	Daphnidae	19.9 (17.4)	24.1 (15.9)	1.6 (1.5)	19.6 (19.6)
	Ostracoda	4.2 (2.6)	2.7 (1.1)	1.4 (0.6)	1.8 (1.8)
	Copepoda	0.2 (0.1)	1.3 (1.3)	–	–
	Anostraca	–	–	–	0.7 (0.6)
Missouri Coteau Semipermanents		(n = 9)	(n = 8)	(n = 14)	(n = 3)
	Chydoridae	80.1 (48.7)	17.9 (8.2)	21.7 (12.1)	50.0 (50.0)
	Daphnidae	91.1 (91.0)	0.4 (0.3)	2.8 (1.9)	0.3 (0.3)
	Ostracoda	2.6 (2.0)	11.3 (10.1)	9.6 (8.8)	28.0 (16.8)
	Macrothricidae	–	9.6 (9.6)	–	–
Prairie Coteau Semipermanents		(n = 3)	(n = 3)	(n = 6)	(n = 3)
	Ostracoda	1.0 (1.0)	–	0.8 (0.8)	–
	Daphnidae	–	–	0.5 (0.5)	–

[a] n = number of wetland treatment replicates within each region.

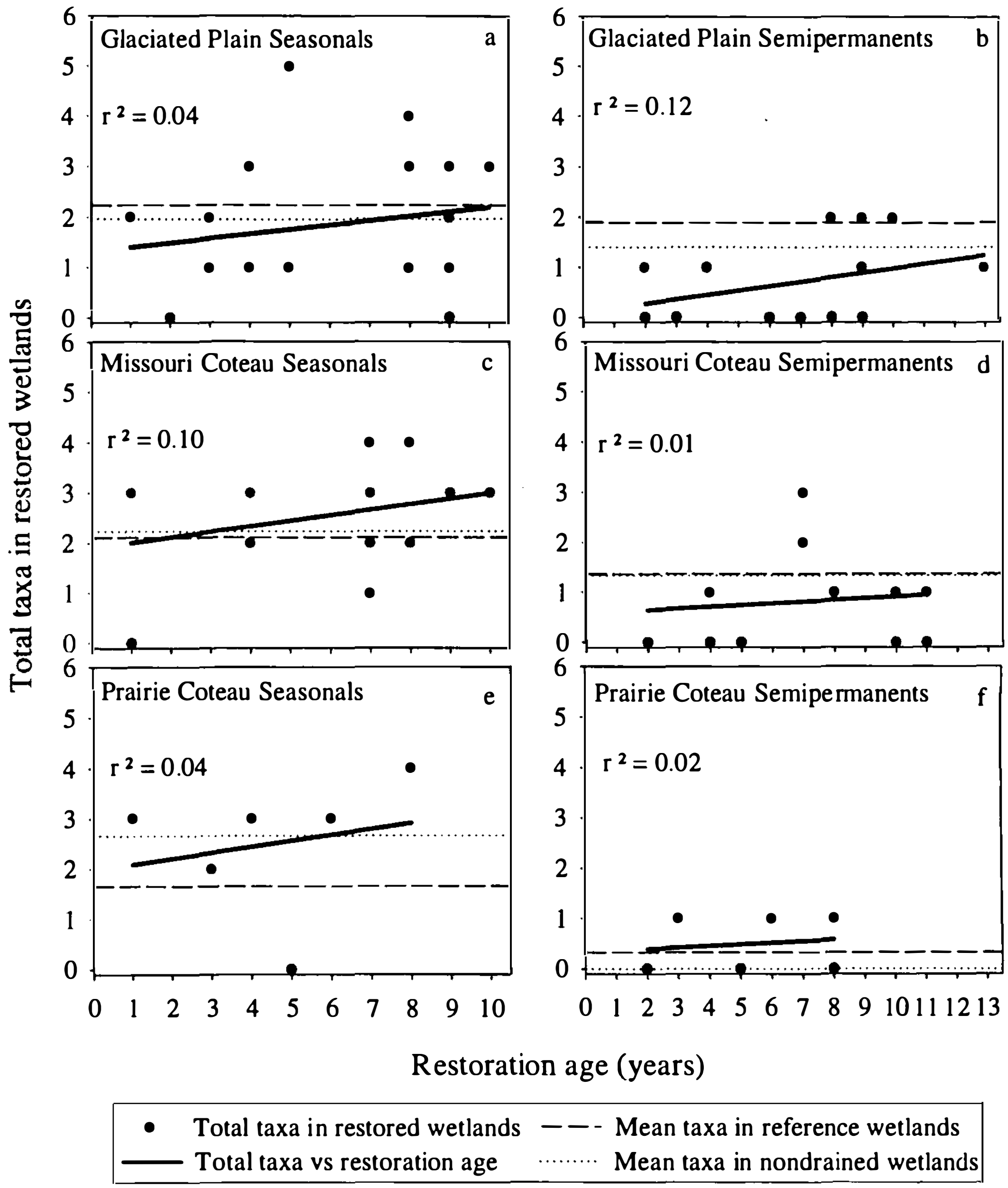

Figure 20. Relationship between restoration age (years) and total number of taxa incubated from soils collected in restored seasonal and semipermanent wetlands. Egg bank samples were collected June-September 1997. Wetlands are located in the Glaciated Plain (a-b), Missouri Coteau (c-d), and Prairie Coteau (e-f) physiographic regions of the Prairie Pothole Region of the United States. Horizontal lines are the mean number of taxa for reference and nondrained treatments.

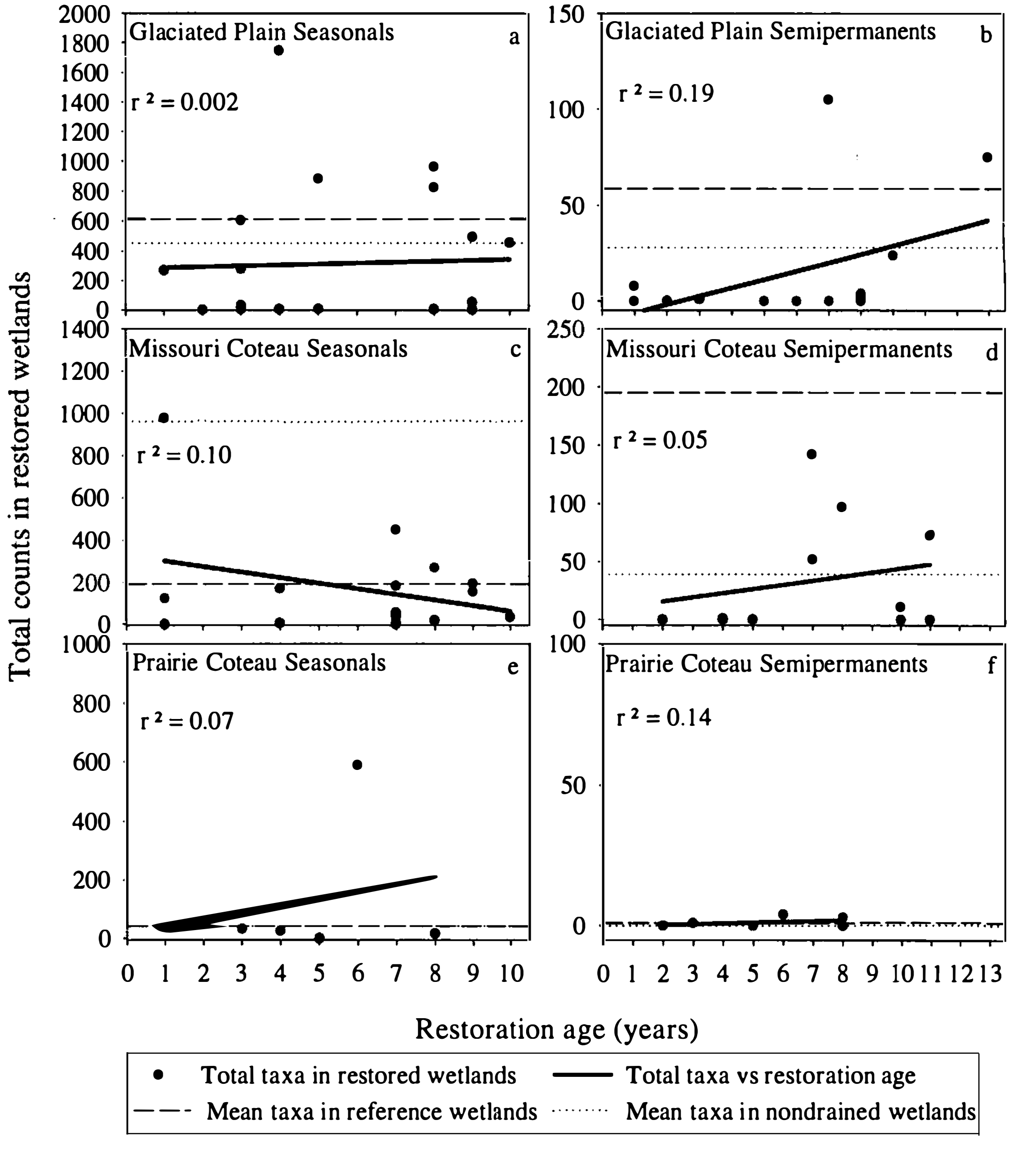

Figure 21. Relationship between restoration age (years) and total invertebrates incubated from soils collected in restored seasonal and semipermanent wetlands. Egg bank samples were collected June-September 1997. Wetlands are located in the Glaciated Plain (a-b), Missouri Coteau (c-d), and Prairie Coteau (e-f) physiographic regions of the Prairie Pothole Region of the United States. Horizontal lines are the mean number of taxa for reference and nondrained treatments.

nondrained wetlands (Figure 20c, e). Overall, very few restored semipermanent wetlands attained taxon richness values similar to reference and nondrained wetlands (Figure 20b, d, f).

Hatching success in restored seasonal and semipermanent wetlands appeared to increase and be less variable 4-5 years after restoration (Figures 22, 23). Similar to earlier findings (Figure 16), hatching success was generally greater in seasonal than in semipermanent restored wetlands regardless of restoration age (Figure 22). Relative to semipermanent wetlands, more restored seasonal wetlands had hatching success values similar to reference and nondrained wetlands (Figures 22, 23).

Effects of Sediment Load on Aquatic Invertebrate Emergence

Covering wetland soils with a sediment depth of 0.5 cm almost completely eliminated emergence of aquatic invertebrates from soil egg banks (Table 10). A total of 9,838 invertebrates emerged from the 0 cm sediment depth treatment (i.e., reference), 10 from the 0.5 cm treatment, 21 from the 1 cm treatment, and 4 from the 2 cm treatment (Table 10). Of the 32 wetland soil samples covered with sediment, 84%, 84%, and 94% failed to hatch invertebrates when covered with 0.5 cm, 1 cm, and 2 cm of sediment, respectively (Table 10). Examination of sediment load effects at the taxon level, indicated that 0.5 cm of sediment effectively reduced emergence of all taxa (Figure 24). No invertebrates emerged from control flats containing upland soils.

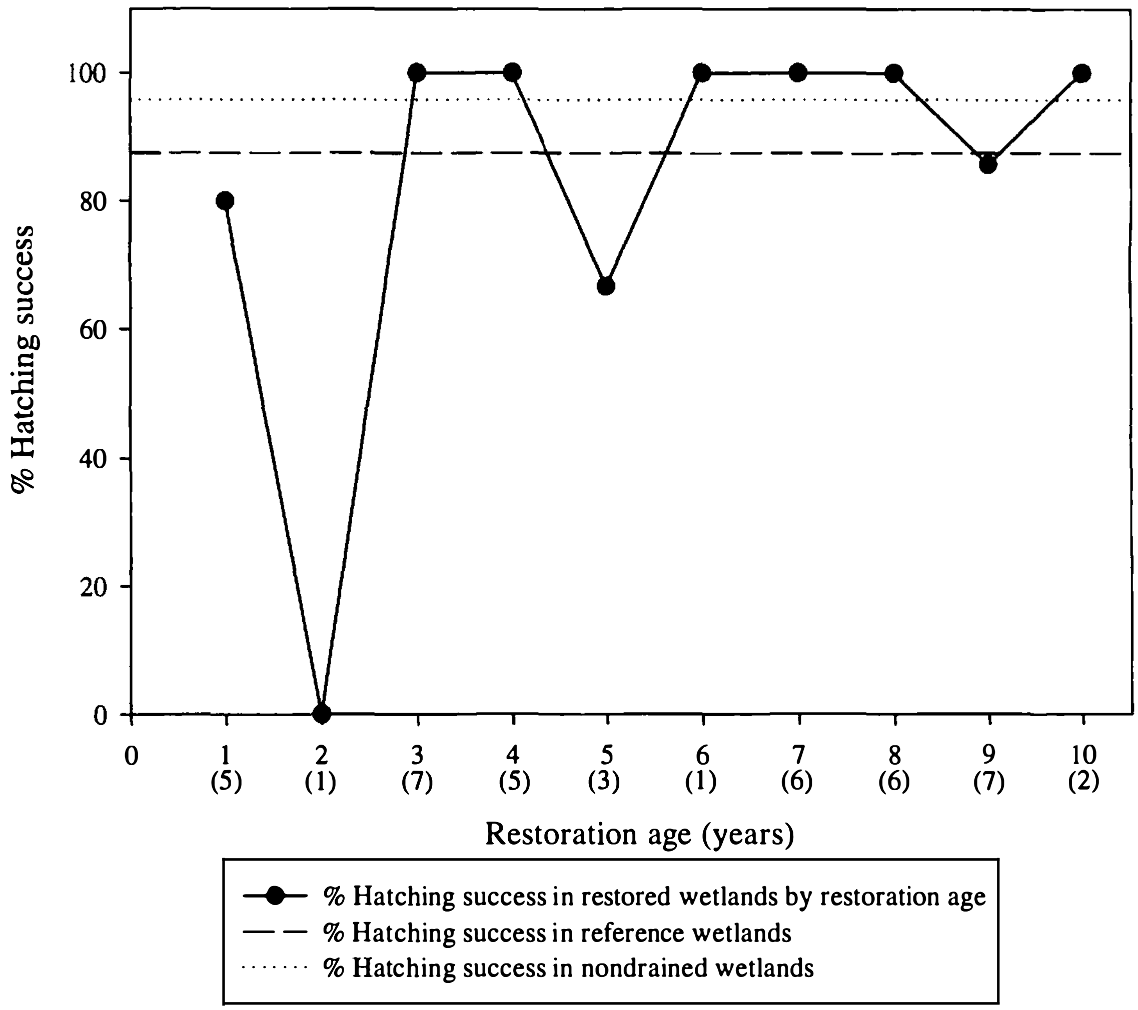

Figure 22. Relationship between restoration age (years) and percent of restored seasonal wetlands that successfully hatched invertebrates during soil egg bank incubation experiments. Egg bank samples were collected June-September 1997. Wetlands are located in the Glaciated Plain, Missouri Coteau, and Prairie Coteau physiographic regions of the Prairie Pothole Region of the United States. Numbers in parentheses indicate number of restored wetland replicates in each age class. Horizontal lines show average % hatching success for reference (n = 24) and nondrained wetlands (n = 24).

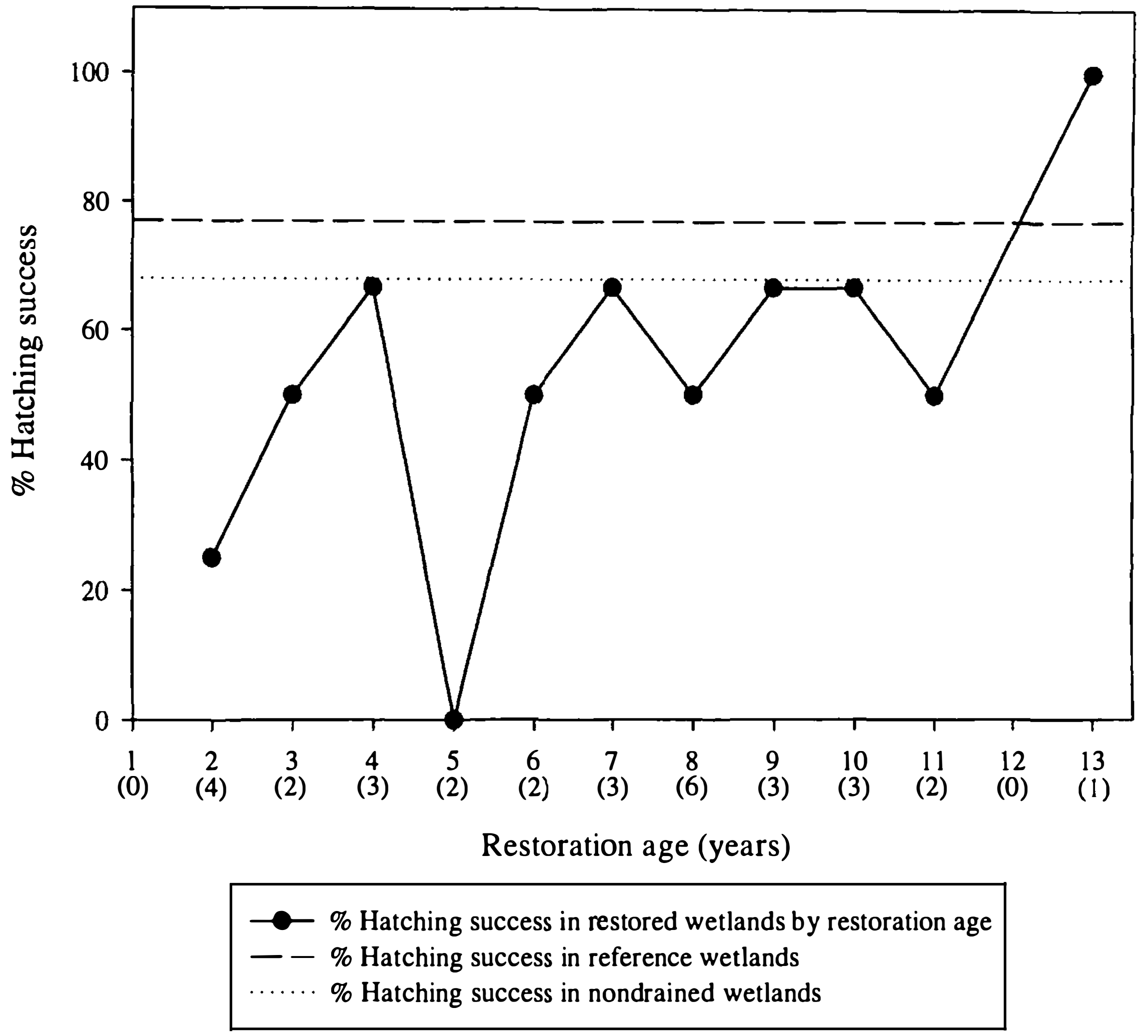

Figure 23. Relationship between restoration age (years) and percent of restored semipermanent wetlands that successfully hatched invertebrates during soil egg bank incubation experiments. Egg bank samples were collected June-September 1997. Wetlands are located in the Glaciated Plain, Missouri Coteau, and Prairie Coteau physiographic regions of the Prairie Pothole Region of the United States. Numbers in parentheses indicate number of restored wetland replicates in each age class. Horizontal lines show average % hatching success for reference (n = 22) and nondrained wetlands (n = 20).

Table 10. Effects of sediment depth on total number of invertebrates incubated from the soil egg banks of 32 reference wetlands. Egg bank samples were collected June-September 1997. Wetlands are located in the Glaciated Plain, Missouri Coteau, and Prairie Coteau physiographic regions of the Prairie Pothole Region of the United States.

Physiographic region	Wetland class	Wetland number	Sediment depth (cm) 0	0.5	1	2
Glaciated Plain	seasonal	GP02175	17	0	0	0
		GP04139	1025	0	0	0
		GP05095	1877	1	1	0
		GP08045	466	0	0	0
		GP09035	986	0	0	0
		GP10026	201	3	0	0
		GP11006	508	2	0	0
		GP12008	1046	0	2	0
Missouri Coteau	seasonal	MC01200	276	0	1	3
		MC04171	1114	0	0	0
		MC05144	38	3	16	0
		MC08102	9	0	0	0
Prairie Coteau	seasonal	PC01057	1	0	0	1
		PC02067	2	0	0	1
		PC03087	120	0	0	0
Glaciated Plain	semipermanent	GP02176	64	0	0	0
		GP02178	1	0	0	0
		GP05096	10	0	0	0
		GP06122	20	0	0	0
		GP08046	16	0	0	0
		GP09036	8	0	0	0
		GP10027	177	0	0	0
		GP11010	184	0	1	0
		GP12005	105	0	0	0
Missouri Coteau	semipermanent	MC01206	407	0	0	0
		MC02191	1073	0	0	0
		MC03186	2	0	0	0
		MC04172	4	0	0	0
		MC05145	19	1	0	0
		MC08101	50	0	0	0
		MC09116	9	0	0	0
Prairie Coteau	semipermanent	PC01056	3	0	0	0
Total			9838	10	21	4
Mean ± SE			307.4 ± 83.2	0.3 ± 0.1	0.7 ± 0.5	0.1 ± 0.1

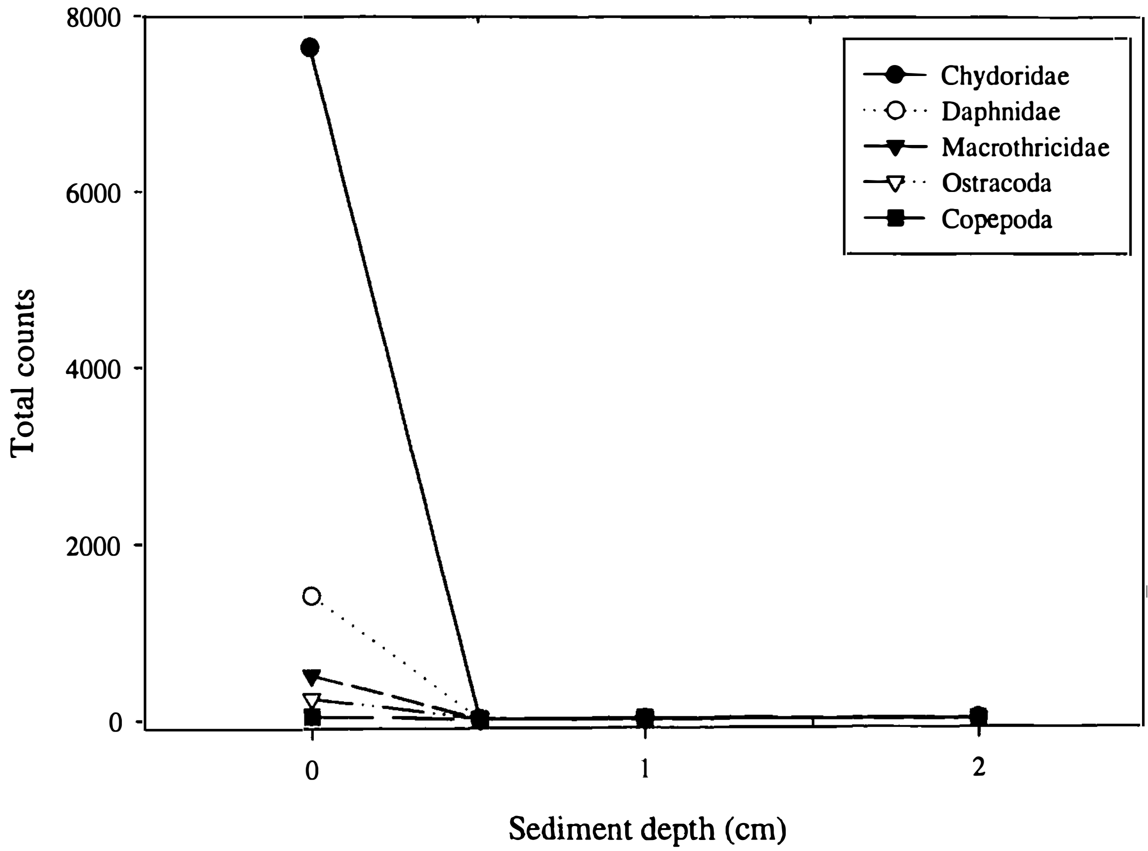

Figure 24. Effects of sediment depth on emergence of invertebrate taxa from soil egg banks.

DISCUSSION

Hatching success in seasonal wetlands in all regions was shown to be lower in drained wetlands than in other seasonal wetland treatments (Figure 16). Likewise, drained and restored semipermanent wetlands in the Glaciated Plain and Missouri Coteau, and drained seasonal wetlands in the Prairie Coteau were found to have lower hatching success than reference and nondrained wetlands (Figure 16). Lower hatching success in drained wetlands and restored wetlands was probably related to drainage and cultivation impacts; research has shown that prolonged drainage and cultivation negatively impact invertebrate egg banks (Euliss and Mushet 1999, 2001).

Although I observed differences in hatching success, I found few statistically significant differences in taxon richness and abundance of invertebrates among treatments (Figures 17, 18). Of the few invertebrate egg bank differences I detected, most occurred among wetland treatments in the Glaciated Plains. Taxon richness and invertebrate abundance in Glaciated Plain seasonal wetlands were lower in drained wetlands than in other wetland treatments (Figures 17a, 18a). Though not statistically significant, overall trends indicated that both reference and nondrained seasonal and semipermanent wetlands in the Glaciated plains had higher taxon richness and invertebrate abundance than did restored and drained wetlands (Figures 17, 18). Similar trends were noted for chydorids in Glaciated Plain seasonal wetlands (Figure 19). Conversely, wetlands in the Missouri and Prairie Coteau showed no consistent trends in taxon richness and invertebrate abundance among wetland treatments.

Differences in agricultural land-use and wetland drainage among physiographic regions might explain why differences among treatments were more prevalent in Glaciated Plain wetlands. Wetlands in the Glaciated Plain typically have been drained more efficiently, and drained and farmed for a longer duration than wetlands in the Coteau regions. As noted earlier, cultivation and prolonged drainage negatively impacts invertebrate egg banks (Euliss and Mushet 1999, 2001). Further, wetland drainage has been more intense in the Glaciated Plain, thereby decreasing the number of wetlands in the landscape that may serve as invertebrate sources to repopulate wetlands. Altogether, agricultural impacts have been more severe in the Glaciated Plains than in the Coteau regions; negative impacts from previous agricultural land use on remnant invertebrate egg banks in restored and drained wetlands, and large losses of wetlands in the landscape may have reduced the availability of invertebrates to recolonize restored wetlands.

I was unable to detect a significant relationship between restoration age and taxon richness or invertebrate abundance (Figures 20, 21). The low within-age-class sample sizes and high variability may have limited my ability to evaluate the relationship between restoration age and invertebrate egg bank composition. Overall trends did indicate that more seasonal wetlands in the Coteau regions attained taxon richness values similar to reference and nondrained wetlands than did seasonal wetlands in the Glaciated Plains (Figure 20). This result is likely related to the longer history of agricultural activity in the Glaciated Plain physiographic region. My research indicated that within several years after restoration, most seasonal wetlands attained hatching success values similar to reference and nondrained wetlands (Figure 22); however, hatching success in most restored semipermanent wetlands was lower than in reference and nondrained wetlands (Figure 23).

Seasonal wetlands frequently had higher hatching success, taxon richness and invertebrate abundance than did semipermanent wetlands. Some of these difference may be because I kept semipermanent wetland egg banks samples in cold storage longer than the seasonal wetlands egg banks samples. A more plausible explanation, is that taxa incubated from egg bank samples are better adapted to seasonal wetlands; hence, production of drought resistant eggs should occur more frequently in seasonal than in semipermanent wetlands (Wiggins 1980, Pennak 1989).

My study clearly demonstrated the negative impact of sediment load on emergence of invertebrates. The lowest sediment load depth of 0.5 cm essentially halted invertebrate emergence (Table 10) and no individual taxon appeared to be resilient to the effects of sediment load (Figure 24). Edge effects may have played some role in emergence of invertebrates from other sediment load treatments. It is likely that factors known to regulate or cue hatching of invertebrate eggs (e.g., salinity, temperature, oxygen, osmotic pressure, and photoperiod) may have varied from the center to the edge of trays containing soils. Consequently, conditions along tray edges (e.g., enhanced illumination and oxygen diffusion) may have been more favorable for invertebrate emergence. This might explain why increasing sediment depth from 0.5 to 1 cm and 2 cm did not completely eliminate invertebrate emergence.

SUMMARY AND MANAGEMENT IMPLICATIONS

Taxon richness and abundance of invertebrate egg banks in restored wetlands were found to be highly variable both within and between restoration age classes. My results indicated that within 5 years after restoration most restored wetlands contained viable invertebrate egg banks. Invertebrate abundance and taxon richness was not found to significantly increase with restoration age. However, there was some indication that taxon richness in seasonal Glaciated Plain wetlands was recovering more slowly than in wetlands in the Coteau Regions. Based on my results, I cannot conclude that invertebrate egg banks are adequately recovering in restored wetlands through natural processes. Inoculation of restored wetlands with remnant wetlands soils may result in faster recolonization of wetlands by invertebrates (Brown et al. 1997) and future research should evaluate the benefits of such inoculations on the recolonization and development of invertebrate egg banks in restored prairie wetlands.

Some restored wetlands are equipped with water control structures, and manipulation of water levels may offer potential to stimulate production of invertebrate propagules. For example, manipulation of hydroperiods might be used to trigger development of invertebrate communities that produce resting eggs. Some restored wetlands in the southern PPR receive water collected from tile lines outside of their catchments and often have artificially lengthened hydroperiods (Galatowitsch and van der Valk 1994). Such wetlands may benefit the most from water level manipulations that trigger production of invertebrate resting eggs. Management efforts in such systems should focus on techniques that mimic seasonal and interannual variations in hydroperiods.

Studies have shown that cultivation of wetland catchments has increased sedimentation of wetland basins (Martin and Hartman 1987, Dieter 1991, Luo et al. 1997). Also, sediment loads impact emergence of hydrophytes from soil seed banks (Jurik et al. 1994, Wang et al. 1994). Likewise, my study clearly demonstrated the impact of sediment load on emergence of invertebrates from egg banks. Hence, the potential for wetlands to be degraded by agricultural practices in the PPR is great. During severe drought most prairie wetlands are completely dry and many are cultivated. When wetlands reflood, initial recolonization by invertebrates comes from invertebrate egg banks. Cultivation of dry wetlands in conjunction with sediment inputs that cover invertebrate egg banks may greatly impact recovery of invertebrate populations during wet periods of the interannual climate cycle.

Invertebrates are important in nutrient cycling (Merritt et al. 1984) and in providing required nutrition for many species of wetland dependent wildlife such as waterfowl (Swanson et al. 1985). Studies are needed to identify minimally acceptable sediment loads (< 0.5 cm) to maximize emergence of invertebrates from egg banks. In addition to controlled laboratory experiments, research on the broad spectrum of agricultural land-use practices (e.g., from no-till to conventional agricultural practices) are needed to elucidate relationships between intensity of cultivation and sedimentation on egg bank maintenance and viability. Knowledge gained from such studies will provide insight into which agricultural practices should be promoted to enhance invertebrate productivity and sustain wetlands on agricultural lands.

CHAPTER 4

SEED BANK COMPOSITION IN RESTORED, NATURAL, AND DRAINED PRAIRIE WETLANDS AND POTENTIAL EFFECTS OF SEDIMENT LOAD ON SEEDLING EMERGENCE

INTRODUCTION

Restoring wetland ecosystems in the Prairie Pothole Region (PPR) generally focuses on restoring the hydrology and relying on natural processes for revegetation. Natural recovery of vegetation will result from remnant seed banks, refugial populations, or by dispersal of propagules into wetlands from surrounding sources (Galatowitsch and van der Valk 1994). Persistent seed banks in natural wetlands have been shown to maintain plant diversity during cyclical changes in plant communities associated with interannual wet/dry cycles that frequent the prairies (van der Valk and Davis 1978, van der Valk 1981). Qualitative models also have been developed that describe vegetative succession during wet/dry cycles in conjunction with seed bank species life histories (van der Valk and Davis 1978, van der Valk 1981). However, relying on seed banks for revegetation of recently restored wetlands has been shown to be highly variable because of prior land-use impacts on remnant seed banks (Galatowitsch and van der Valk 1994, 1996).

Most drained wetlands targeted for restoration in the prairies have been cultivated. Nondrained wetlands in agricultural fields are also frequently cultivated when they go dry

(Stewart and Kantrud 1973, Cowardin et al. 1981). Both prolonged drainage and cultivation have been shown to decrease species diversity and abundance of seed banks (Erlandson 1987, Wienhold and van der Valk 1989). Cultivation of catchments surrounding wetlands has increased upland erosion and delivery of sediment laden runoff and associated agrochemicals and fertilizers to wetlands (Martin and Hartman 1987, Neely and Baker 1989, Dieter 1991). The covering of seed banks with sediment has been shown to greatly decrease seedling recruitment from seed banks (Jurik et al. 1991, Wang et al. 1991, Dittmar and Neely 1999).

It is generally assumed that the greater the intensity of the disturbance, the less likely a wetland will recover following restoration (National Research Council 1992). The intensity and magnitude of agricultural disturbances believed to influence recovery of restored wetlands varies throughout the PPR. For example, in the northwest portion of the PPR, agricultural production consists mostly of small grains that transitions into row crop production in the southeast. In general, row crop production represents more of a disturbance than does small grain production. Further, in the southeast portion, fewer wetlands remain in the landscape that might provide a source of propagules for recently restored wetlands and wetlands have been farmed and drained for a longer duration than in the northwest. Landscape diversity and wetland densities also differ among the 3 major physiographic regions in the PPR: Glaciated Plain, Missouri Coteau, and Prairie Coteau (Figure 1). The Missouri and Prairie Coteau are characterized as having high densities of wetlands and tracts of native grasslands containing high quality wetlands. In contrast, agricultural conversion of grassland and wetland drainage has been more complete in the Glaciated Plain. Thus, there are fewer high quality wetlands remaining in the Glaciated Plain than in the Coteau regions.

Most research evaluating restored wetlands has been conducted on wetlands in the southern PPR, and there is little information on restored wetlands in other areas and physiographic regions of the PPR. Most evaluations have focused on comparisons of vegetation of restored wetlands to high quality natural wetlands without a history of cultivation or drainage. Given that restored wetlands have been impacted by both drainage and land-use, comparing seed bank composition in restored wetlands to that of drained and nondrained wetlands with similar agricultural histories will help elucidate drainage and agricultural impacts on wetland seed banks. The objectives of my study were to (1) compare seed bank composition among reference, nondrained, restored, and drained wetlands, (2) evaluate the influence of restoration age on seed bank composition, and (3) examine the effects of sediment load on emergence of seedlings from seed banks.

MATERIALS AND METHODS

Seed Bank Survey

During 1997, I collected seed bank samples from 201 wetlands in a 5 state region of the PPR (Figure 2). Wetlands selected for study included seasonal and semipermanent drained, restored, and nondrained wetlands in Conservation Reserve Program type habitats (i.e., once farmed lands planted back to perennial cover) and reference wetlands with no history of cultivation in the wetland basin or catchment (Table 8). I collected seed bank samples along 4 randomly established transects that radiated from the wetland center. Along each transect, I collected 3 cores to a depth of 5 cm in the wet-meadow and shallow-marsh zones using a 7.5-cm diameter corer. Seed bank samples were stored in a cold room (< 4°C) until needed for greenhouse experiments.

Seed bank samples from each wetland (12 cores from shallow marsh and 12 cores from wet meadow) were composited, mixed, and sieved to remove litter, roots, and tubers. One subsample (380 cm^3) from each composite sample (n = 201) was spread evenly over the surface of a plastic flat (19.5 X 19.5 X 6 cm) containing 3 cm (depth) of steam-sterilized sand. To determine the effect of sediment load on emergence of hydrophytes an additional 3 flats were prepared for each of 36 reference wetlands and overlain with 0.5 cm, 1 cm, and 2 cm of steam-sterilized upland soils. Additional flats containing only upland soils and sterilized sand were also prepared and subjected to greenhouse conditions to verify that they were free of viable seeds. Upland soil used to overlay wetland soils had a silty-clay-loam texture and was sieved through 0.017 mm mesh to concentrate particle sizes similar to erosional sediment. Upland soil was provided by U.S. Department of Agriculture's Northern Grain Insects Research Laboratory, Brookings, SD and was determined to be free of agrochemical residues.

Two runs were necessary to complete the seed bank survey. Greenhouse experiments on seasonal wetland seed banks were performed from May to July 1998, and semipermanent seed banks from August to October 1998. Flats were placed on a greenhouse bench in a completely randomized block design with each block representing sampling locations (e.g., GP01-GP12; Figure 1). Soils were maintained in a saturated state to simulate the drawdown phase of wetlands and thereby to stimulate germination of mudflat annuals and perennial emergents. Greenhouse temperature and photoperiod were incrementally increased during the experiment to simulate environmental conditions from May-July (i.e., temperature range 15-30°C; light range of 13-15 h). These environmental conditions provided a range of alternating temperatures and photoperiods that are critical factors in seed germination (Galinato and van der Valk 1986, Baskin and Baskin 1989, Hartleb et al. 1993). Seedlings were counted and removed as they reached an identifiable stage. At the end of each 3-month run, all unknown seedlings were transferred to pots and grown to an identifiable stage. Seedling emergence experiments were conducted in an environmentally controlled greenhouse at the U.S. Department of Agriculture's Northern Grain Insects Research Laboratory, Brookings, SD.

I identified and classified plants according to their life history (annual or biennial, perennial, native, or introduced) using standard floras for the region (Great Plains Flora Association 1986, Larson 1993). To assess floristic quality of seed banks, I assigned coefficients of conservatism (C-values range 0 to 10) to each native plant species and calculated a mean C for each wetland. Coefficients of conservatism are an index of a species' ability to persist in a disturbed area, with 0 assigned to native species that persist in highly disturbed habitats, and 10 assigned to species restricted to the most natural undisturbed habitats. Additionally, I calculated a floristic quality index (FQI) for each wetland by multiplying mean C by the square-root of the total number of native species. Procedures for calculating mean C and FQI, and coefficients for each species are described by the Northern Great Plains Floristic Quality Assessment Panel (2001).

Statistical Analysis

I used analysis of variance (ANOVA) to assess the influence of wetland treatment (i.e., drained, restored, nondrained, and reference) on mean C and FQI, and seed bank density and taxon richness by life-history group (i.e., annual-native, annual-introduced, perennial-native, and perennial-introduced). Analyses were performed separately for each wetland-class-physiographic-region combination and I used a blocked design where sampling area was treated as a block (i.e., GP01-GP12; Figure 1). I conducted ANOVAs using the mixed model procedure (PROC MIXED) of SAS (SAS Institute, Inc 1997). Prior to analysis of seed bank densities, transformations $[(y + 0.5)^{0.5}]$ were performed on the data to stabilize variances (Steel and Torrie 1980). Fisher's protected least significant difference tests (LSD) were used to assess individual differences when main effects were significant (Milliken and Johnson 1984). Seed densities are expressed as the number of germinated seeds per m^2 in a layer of soil 5 cm thick.

To evaluate species composition among wetlands treatments within regions, I used detrended correspondence analysis (DCA) to ordinate plant species according to presence and absence. I then overlaid species ordinations with the following information associated with each wetland: treatment, mean C, mean FQI, percent native species and perennial species, and numbers of annual, perennial, native and introduced species. I then generated joint plots to determine which combination of information best described treatment groupings. All ordination analyses were performed using PC-ORD Version 4 (McCune and Mefford 1999).

RESULTS

I identified 62 plant taxa that emerged from wetland seed banks (Table 11). Seventy-three percent of the taxa were classified as low-prairie and wet-meadow species and 27% shallow-marsh and deep-marsh species. Taxa included: 25 perennial-native, 5 perennial-introduced, 23 annual-native, and 5 annual-introduced taxa (Table 12). Unidentified forbs and grasses, *Rumex* spp, and in part *Typha* spp., were not assigned to life history groups (Table 12). These taxa with incomplete life history information were not included in statistical analyses (i.e., ANOVAs) of seed bank density, taxon richness, mean C, and FQI among wetland treatments. However, frequency of occurrence and seed bank density of each of these taxa are presented graphically for comparison among wetland treatments by region. No seeds germinated from control sand and upland soil flats.

Table 11. Life history and wetland zones associated with plant species that emerged from the seed banks of seasonal and semipermanent wetlands in the Prairie Pothole Region of the United States. Seed bank samples were collected June-September 1997.

Zone Species	Coefficient of [a] conservatism	Plant life history	
Wet-prairie species			
Ambrosia artemisiifolia	0	Native	Annual
Ambrosia psilostachya	2	Native	Perennial
Artemisia ludoviciana	3	Native	Perennial
Conyza canadensis	0	Native	Annual
Coreopsis tinctoria	3	Native	Annual
Dichanthelium oligosanthes	6	Native	Perennial
Medicago sp.	*	Introduced	Perennial
Melilotus spp.	*	Introduced	Annual
Oxalis stricta	0	Native	Perennial
Panicum capillare	0	Native	Annual
Setaria glauca	*	Introduced	Annual
Setaria viridis	*	Introduced	Annual
Wet-meadow species			
Agrostis hyemalis	1	Native	Perennial
Ammannia coccinea	2	Native	Annual
Ammannia robusta	2	Native	Annual
Artemisia absinthium	*	Introduced	Perennial
Aster brachyactis	0	Native	Annual
Aster simplex	3	Native	Perennial
Bidens cernua	3	Native	Annual
Carex spp.	(5)	Native	Perennial
Cyperus aristatus	2	Native	Annual
Cyperus erythrorhizos	2	Native	Annual
Cyperus odoratus	2	Native	Annual
Cirsium arvense	*	Introduced	Perennial
Echinochloa crusgalli	*	Introduced	Annual
Echinochloa muricata	0	Native	Annual
Eleocharis obtusa	2	Native	Annual
Epilobium spp.	(3)	Native	Perennial
Hordeum jubatum	0	Native	Perennial
Juncus bufonius	1	Native	Annual
Juncus torreyi	2	Native	Perennial
Juncus dudleyi	4	Native	Perennial
Juncus interior	5	Native	Perennial
Lactuca serriola	*	Introduced	Annual
Mentha arvensis	3	Native	Perennial
Phleum pratense	*	Introduced	Perennial
Plantago major	*	Introduced	Perennial
Poa palustris	4	Native	Perennial
Polygonum lapathifolium	1	Native	Annual

Table 11. Continued.

Zone Species	Coefficient of conservatism[a]	Plant life history	
Wet-meadow species (continued)			
Polygonum pensylvanicum	0	Native	Annual
Potentilla norvegica / rivalis	(1)	Native	Annual
Rorippa palustris	2	Native	Annual
Rumex spp.	*	Introduced/Native	Annual/Perennial
Scirpus saximontanus	7	Native	Annual
Shallow-marsh species			
Alisma plantago-aquatica	2	Native	Perennial
Alopecurus aequalis	2	Native	Perennial
Bacopa rotundifolia	3	Native	Perennial
Beckmannia syzigachne	1	Native	Annual
Chenopodium rubrum	2	Native	Annual
Cyperus acuminatus	2	Native	Annual
Eleocharis acicularis	3	Native	Perennial
Eleocharis spp.	(4)	Native	Perennial
Leptochloa fascicularis	0	Native	Annual
Ranunculus cymbalaria	3	Native	Perennial
Ranunculus sceleratus	3	Native	Perennial
Sagittaria cuneata	6	Native	Perennial
Scirpus pungens	4	Native	Perennial
Sparganium eurycarpum	4	Native	Perennial
Deep marsh species			
Scirpus acutus / validus	3	Native	Perennial
Typha spp.	*	Introduced/Native	Perennial
Unknown			
Forb unidentified	*	*	*
Grass unidentified	*	*	*

[a] Parentheses indicate that coefficients of conservatism are based on the most frequently occurring species within the genus. Coefficients of conservatism are not assigned to introduced species (*) or to genera (i.e., *Typha* spp, *Rumex* spp.) that contained both introduced and native species.

Table 12. Total number of plant taxa by life history and wetland zone associated with plants that emerged from the seed banks of seasonal and semipermanent wetlands in the Prairie Pothole Region of the United States. Seed bank samples were collected June-September 1997.

Plant life history	Wet-prairie and wet-meadow taxa	Shallow-marsh and deep-marsh taxa
Perennial		
Perennial-native	14	11
Perennial-introduced	5	0
Perennial-unknown[a]	0	1
Annual		
Annual-native	19	4
Annual-introduced	5	0
Annual/perennial-introduced/native[b]	1	0
Life history unknown		
Unidentified grasses and forbs	?	?

[a] This taxon = *Typha* spp. which includes native and introduced species.
[b] This taxon = *Rumex* spp. which includes all plant types listed.

Seasonal Wetlands

Seed Density by Plant Type

I found few significant ($P < 0.05$) differences in seed bank density of plant life history types among seasonal wetland treatments in the Glaciated Plain, Missouri Coteau, and Prairie Coteau regions (Table 13). Seed density of perennial-native plants was significantly greater in Missouri Coteau reference wetlands than in the other wetland treatments, whereas density of annual-natives was generally lower in reference and drained wetlands than nondrained, and restored wetlands (Table 13). Reference wetlands in the Glaciated Plain and Prairie Coteau also had higher perennial-native and lower annual-native seed bank densities than other treatments, but these differences were not statistically significant. In all 3 regions, seed banks in reference wetlands were dominated by native-perennials. In contrast, annual-natives often composed a greater proportion of the seed banks in nondrained, restored, and drained wetlands (Table 13). Seed bank density of other plant life history types in the 3 regions did not significantly differ among treatments (Table 13).

Taxon Richness by Plant Type

Across all regions, reference wetlands had greater numbers of perennial-native taxa, and in most cases, fewer annual-native and introduced taxa than nondrained, restored, and drained wetlands (Table 14). Mean taxon richness of perennial-natives was significantly greater in Glaciated Plain and Missouri Coteau reference wetlands than

Table 13. Transformed [(seeds + 0.5)$^{0.5}$] least-squares means (± SE) seed bank density (no. seeds/m^2) of perennial and annual introduced and native plant taxa that emerged from the seed banks of seasonal reference, nondrained, restored > 5 year, restored < 5 year, and drained wetlands. Seed bank samples were collected June-September 1997. Wetlands are located in the Glaciated Plain, Missouri Coteau, and Prairie Coteau physiographic regions of the Prairie Pothole Region of the United States. Where significant treatment effects were detected (*P* - values in bold type), means (± SE) within rows with a common letter are not significantly (*P* > 0.05) different.

	Seasonal wetland treatments						
	Reference	Nondrained	Restored > 5 years	Restored < 5 years	Drained	ANOVA	
Region Plant type	Mean seed density	Mean seed density	Mean seed density	Mean seed density	Mean seed density	*F*	*P*
Glaciated Plain						df = 4, 41	
Perennial-native	13.7 (2.2)	9.2 (2.2)	12.4 (2.4)	5.7 (2.3)	9.1 (2.2)	1.89	0.1306
Perennial-introduced	0.7 (0.6)	0.7 (0.6)	0.7 (0.6)	2.2 (0.6)	1.6 (0.6)	1.58	0.1984
Annual-native	8.6 (3.0)	11.3 (3.0)	6.0 (3.2)	12.9 (3.1)	13.3 (3.0)	1.73	0.1625
Annual-introduced	0.6 (0.6)	1.6 (0.6)	1.8 (0.6)	2.0 (0.6)	1.8 (0.6)	1.43	0.2423
Total	17.3 (3.1)	16.7(3.1)	14.8 (3.3)	17.0 (3.2)	18.0 (3.0)	0.24	0.9154
n[a]	12	12	11	10	12		
Missouri Coteau						df = 4, 29	
Perennial-native	17.4 (2.0)a	12.5 (1.9)b	7.5 (1.8)c	7.6 (2.5)bc	7.5 (2.2)bc	6.92	**0.0005**
Perennial-introduced	1.2 (0.4)	0.7 (0.4)	1.5 (0.4)	1.6 (0.6)	0.7 (0.5)	0.73	0.5812
Annual-native	5.6 (2.6)b	10.0 (2.6)ab	13.9 (2.4)a	11.1 (3.3)ab	3.9 (2.9)b	3.44	**0.0203**
Annual-introduced	0.8 (0.6)	1.7 (0.6)	0.8 (0.5)	2.1 (0.8)	2.3 (0.7)	1.56	0.2127
Total	18.8 (2.6)	17.2 (2.5)	17.0 (2.4)	15.9 (3.2)	9.5 (2.8)	2.43	0.0704
n	9	9	11	5	7		
Prairie Coteau						df = 4, 8	
Perennial-native	23.8 (5.0)	7.2 (5.0)	6.6 (5.0)	4.3 (5.0)	10.1 (5.0)	3.38	0.0670
Perennial-introduced	0.7 (1.5)	2.2 (1.5)	2.9 (1.5)	2.2 (1.5)	3.7 (1.5)	0.53	0.7197
Annual-native	3.9 (3.7)	7.5 (3.7)	4.4 (3.7)	11.3 (3.7)	4.9 (3.7)	0.71	0.6087
Annual-introduced	0.7 (0.7)	0.7 (0.7)	0.7 (0.7)	2.2 (0.7)	0.7 (0.7)	1.00	0.4609
Total	24.4 (5.6)	12.9 (5.6)	8.5 (5.6)	12.8 (5.6)	12.3 (5.6)	1.48	0.2949
n	3	3	3	3	3		

a n = number of wetland treatment replicates within each region.

Table 14. Total numbers and least-squares means (± SE) taxon richness of perennial and annual introduced and native plant taxa that emerged from the seed banks of seasonal reference, nondrained, restored > 5 year, restored < 5 year, and drained wetlands. Seed bank samples were collected June-September 1997. Wetlands are located in the Glaciated Plain, Missouri Coteau, and Prairie Coteau physiographic regions of the Prairie Pothole Region of the United States. Where significant treatment effects were detected (*P* - values in bold type), means (± SE) within rows with a common letter are not significantly ($P > 0.05$) different.

	Seasonal wetland treatments											
	Reference		Nondrained		Restored > 5 years		Restored < 5 years		Drained		ANOVA	
Region / Plant type	No. taxa	Mean richness	No. taxa	Mean richness	No. taxa	Mean richness	No. taxa	Mean richness	No. taxa	Mean richness	*F*	*P*
Glaciated Plain											df = 4, 41	
Perennial-native	13	2.8 (0.4)a	9	1.5 (0.4)bc	8	2.0 (0.4)ab	6	0.8 (0.4)c	10	1.3 (0.4)bc	4.18	**0.0062**
Perennial-introduced	0	0.0 (0.1)	0	0.0 (0.1)	0	0.0 (0.1)	2	0.2 (0.1)	3	0.3 (0.1)	1.52	0.2134
Annual-native	5	1.1 (0.4)	10	1.9 (0.4)	10	1.3 (0.5)	14	2.2 (0.5)	10	2.1 (0.4)	1.62	0.1885
Annual-introduced	0	0.0 (0.1)	2	0.2 (0.1)	1	0.3 (0.1)	3	0.3 (0.1)	2	0.3 (0.1)	1.31	0.2808
Total	18	5.3 (0.7)	21	4.7 (0.7)	19	4.6 (0.8)	25	4.2 (0.7)	25	4.9 (0.7)	0.39	0.8148
n[a]	12		12		11		10		12			
Missouri Coteau											df = 4, 29	
Perennial-native	19	4.1 (0.5)a	8	1.3 (0.5)b	10	1.4 (0.4)b	7	2.2 (0.6)b	4	1.0 (0.6)b	6.70	**0.0006**
Perennial-introduced	1	0.1 (0.1)	0	0.0 (0.1)	2	0.2 (0.1)	1	0.2 (0.1)	0	0.0 (0.1)	0.73	0.5812
Annual-native	5	0.9 (0.4)b	11	1.8 (0.4)a	13	2.1 (0.4)a	4	1.5 (0.5)ab	4	0.7 (0.5)b	3.20	**0.0272**
Annual-introduced	0	0.0 (0.1)	1	0.2 (0.1)	0	0.0 (0.1)	1	0.2 (0.1)	2	0.3 (0.1)	1.54	0.2167
Total	25	6.0 (0.7)a	20	4.4 (0.7)a	25	5.2 (0.7)a	13	4.7 (0.9)a	10	2.3 (0.8)b	4.04	**0.0101**
n	9		9		11		5		7			
Prairie Coteau											df = 4, 8	
Perennial-native	7	3.0 (0.6)	2	0.7 (0.6)	4	1.3 (0.6)	2	0.7 (0.6)	3	1.3 (0.6)	3.73	0.0536
Perennial-introduced	0	0.0 (0.3)	1	0.3 (0.3)	1	0.3 (0.3)	1	0.3 (0.3)	2	0.7 (0.3)	0.62	0.6579
Annual-native	1	0.3 (0.8)	3	1.3 (0.8)	3	1.0 (0.8)	6	2.7 (0.8)	2	0.7 (0.8)	1.59	0.2677
Annual-introduced	0	0.0 (0.1)	0	0.0 (0.1)	0	0.0 (0.1)	1	0.3 (0.1)	0	0.0 (0.1)	1.00	0.4609
Total	8	4.3 (1.3)	6	3.0 (1.3)	8	3.3 (1.3)	10	4.7 (1.3)	7	4.0 (1.3)	0.32	0.8595
n	3		3		3		3		3			

a n = number of wetland treatment replicates within each region.

most other treatments (Table 14), whereas mean perennial-native taxon richness was statistically similar among nondrained, restored, and drained wetlands. Perennial-native taxon richness was also greater in Prairie Coteau reference wetlands than in other treatments (Table 14). Overall trends among regions indicated that mean taxon richness of annual-natives was lower in reference wetlands than most other treatments, but this was only significant in the Missouri Coteau region. Taxon richness of other plant life history types in the 3 regions did not significantly differ among treatments (Table 14).

Mean C and FQI

In all 3 regions, mean C and FQI estimates were greatest in reference wetlands (Table 15). Mean FQI in all 3 regions was significantly greater in reference wetlands than most other treatments whereas most comparisons of mean FQI among nondrained, restored, and drained wetlands indicated they were statistically similar (Table 15). Trends did indicate that mean C and FQI values in nondrained and restored wetlands in the Glaciated Plain and Missouri Coteau were intermediate between reference and drained wetlands (Figure 25). Drained wetlands in the Prairie Coteau had notably higher mean C and FQI estimates than nondrained and restored wetlands (Figure 25).

Table 15. Least-squares means (± SE) coefficient of conservatism (C) and floristic quality index (FQI) of plants that emerged from the seed banks of seasonal reference, nondrained, restored > 5 year, restored < 5 year, and drained wetlands. Seed bank samples were collected June-September 1997. Wetlands are located in the Glaciated Plain, Missouri Coteau, and Prairie Coteau physiographic regions of the Prairie Pothole Region of the United States. Where significant treatment effects were detected (*P* - values in bold type), means (± SE) within rows with a common letter are not significantly (*P* > 0.05) different.

	Seasonal wetland treatments						
Region	Reference	Nondrained	Restored > 5 years	Restored < 5 years	Drained	ANOVA	
Index	Mean	Mean	Mean	Mean	Mean	*F*	*P*
Glaciated Plain						df = 4, 41	
C	3.0 (0.3)a	2.1 (0.3)bc	2.3 (0.3)ab	2.0 (0.3)bc	1.5 (0.3)c	4.03	**0.0075**
FQI	6.6 (0.6)a	4.5 (0.6)b	5.0 (0.7)ab	3.8 (0.7)b	3.5 (0.6)b	3.77	**0.0106**
n[a]	12	12	11	10	12		
Missouri Coteau						df = 4, 29	
C	3.5 (0.4)a	2.4 (0.4)b	2.0 (0.3)b	2.0 (0.5)b	1.8 (0.4)b	3.00	**0.0344**
FQI	8.0 (0.8)a	5.0 (0.8)b	4.6 (0.7)b	4.5 (1.1)b	3.1 (0.9)b	5.15	**0.0029**
n	9	9	11	5	7		
Prairie Coteau						df = 4, 8	
C	3.8 (0.8)	2.4 (0.8)	1.6 (0.8)	0.6 (0.8)	2.7 (0.8)	2.20	0.1597
FQI	7.7 (1.2.)a	3.2 (1.2)bc	3.5 (1.2)bc	1.4 (1.2)c	5.3 (1.2)ab	4.35	**0.0368**
n	3	3	3	3	3		

a n = number of wetland treatment replicates within each region.

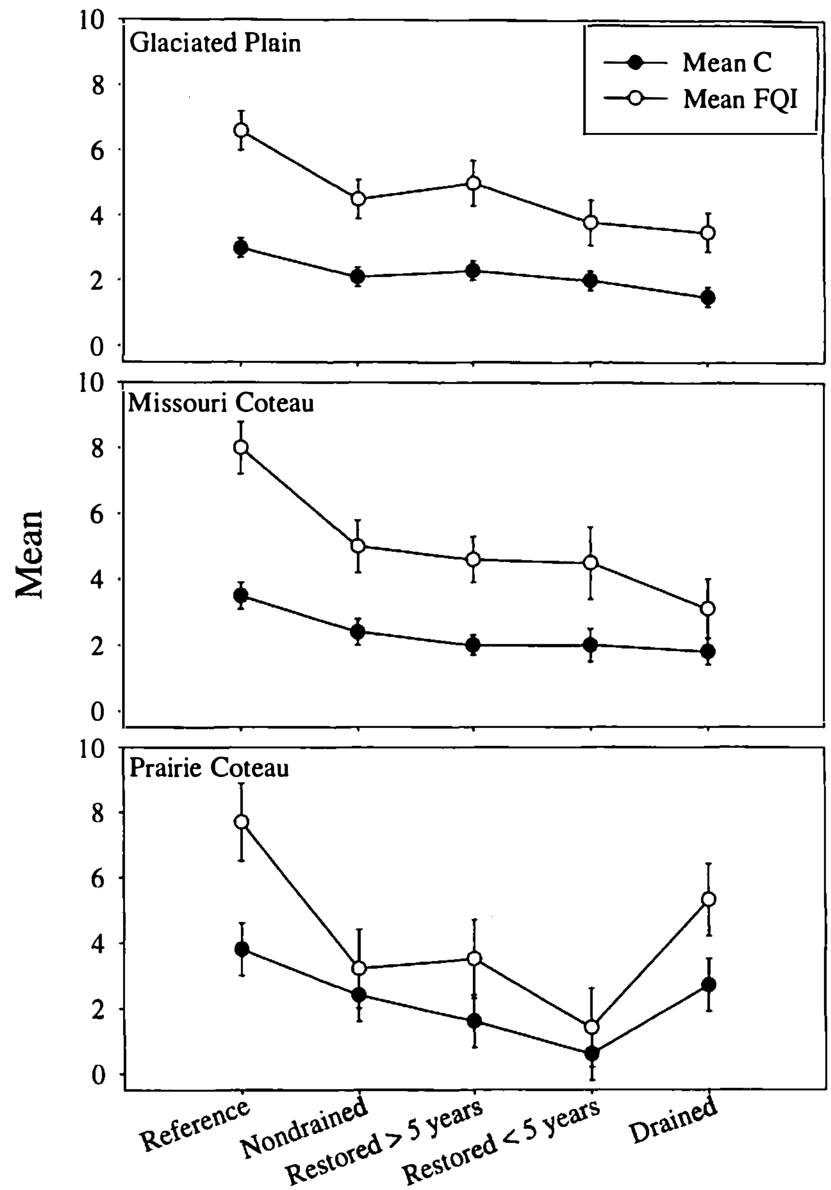

Figure 25. Mean (± SE) coefficient of conservatism (C) and floristic quality index (FQI) for native plants that emerged from the seed banks of seasonal reference, nondrained, restored > 5 year, restored < 5 year, and drained wetlands. Seed bank samples were collected June-September 1997. Wetlands are located in the Glaciated Plain, Missouri Coteau, and Prairie Coteau physiographic regions of the Prairie Pothole Region of the United States. Replication of treatments by region and wetland class are shown in Table 15.

Taxonomic Composition

Glaciated Plain Wetlands: Ordination of plant species grouped reference wetlands better than other treatments (Figure 26). Mean C, mean FQI, and percent perennial species best described the nature of the groupings (based on joint plot vectors) among reference wetlands. Most other treatments tended to be more variable in species composition (i.e., lacked grouping), and were better described by the presence of introduced and annual species. Examination of annual (Figure 27) and perennial (Figure 28) species among treatments showed more perennial species and fewer annual species in reference wetlands than in other treatments. Eighty-eight percent of the 17 perennial-native species occurred in reference wetlands, followed by drained (60%), nondrained (53%), restored > 5 year (47%) and restored < 5 year (35%) wetlands (Figure 28). In contrast, only 29% of the annual-native species occurred in reference wetlands, and 82% occurred in restored < 5 year wetlands, 59% in nondrained, restored > 5 year, and drained treatments (Figure 27). Perennial-natives represented in reference wetlands but occurring in ≤1 of the other treatments included: *Carex spp*., *Epilobium* spp., *Scirpus pungens*, *Sparganium eurycarpum*, *Agrostis hyemalis*, and *Oxalis stricta* (Figure 28).

Missouri Coteau Wetlands: Ordination of plant species grouped most reference wetlands better than other treatments (Figure 29). Percent native species, mean C, and FQI best described associations of reference wetlands. Examination of annual (Figure 30) and perennial species (Figure 31) showed reference wetlands to have fewer annuals and more perennial species than other treatments. Of the 14 annual-native taxa that

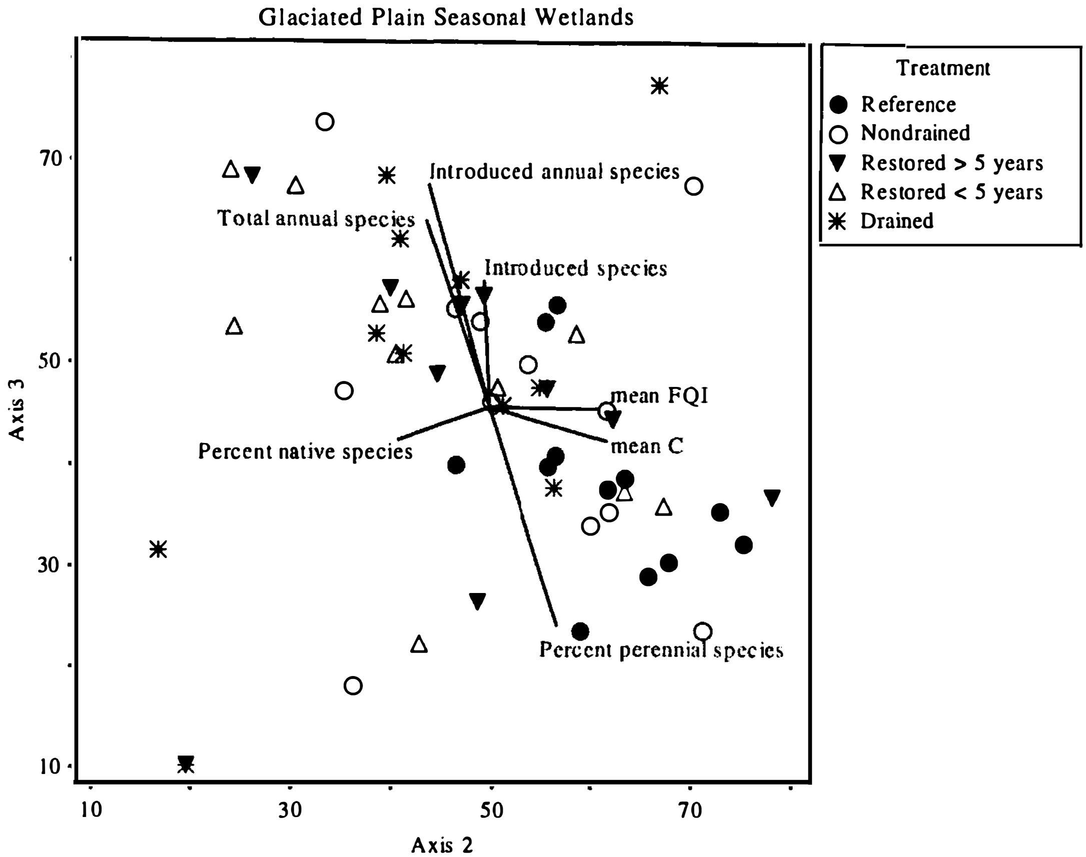

Figure 26. Ordination of plant species (presence or absence) that emerged from the seed banks of seasonal reference (n = 12), nondrained (n = 12), restored > 5 year (n = 11), restored < 5 year (n = 10), and drained wetlands (n = 12). Seed bank samples were collected June-September 1997. Wetlands are located in the Glaciated Plain physiographic region of the Prairie Pothole Region of the United States. Symbols indicate location of each treatment within the species space. Angle and length of radiating lines (i.e., joint plot vectors) indicate the strength and direction of plant types within the species space.

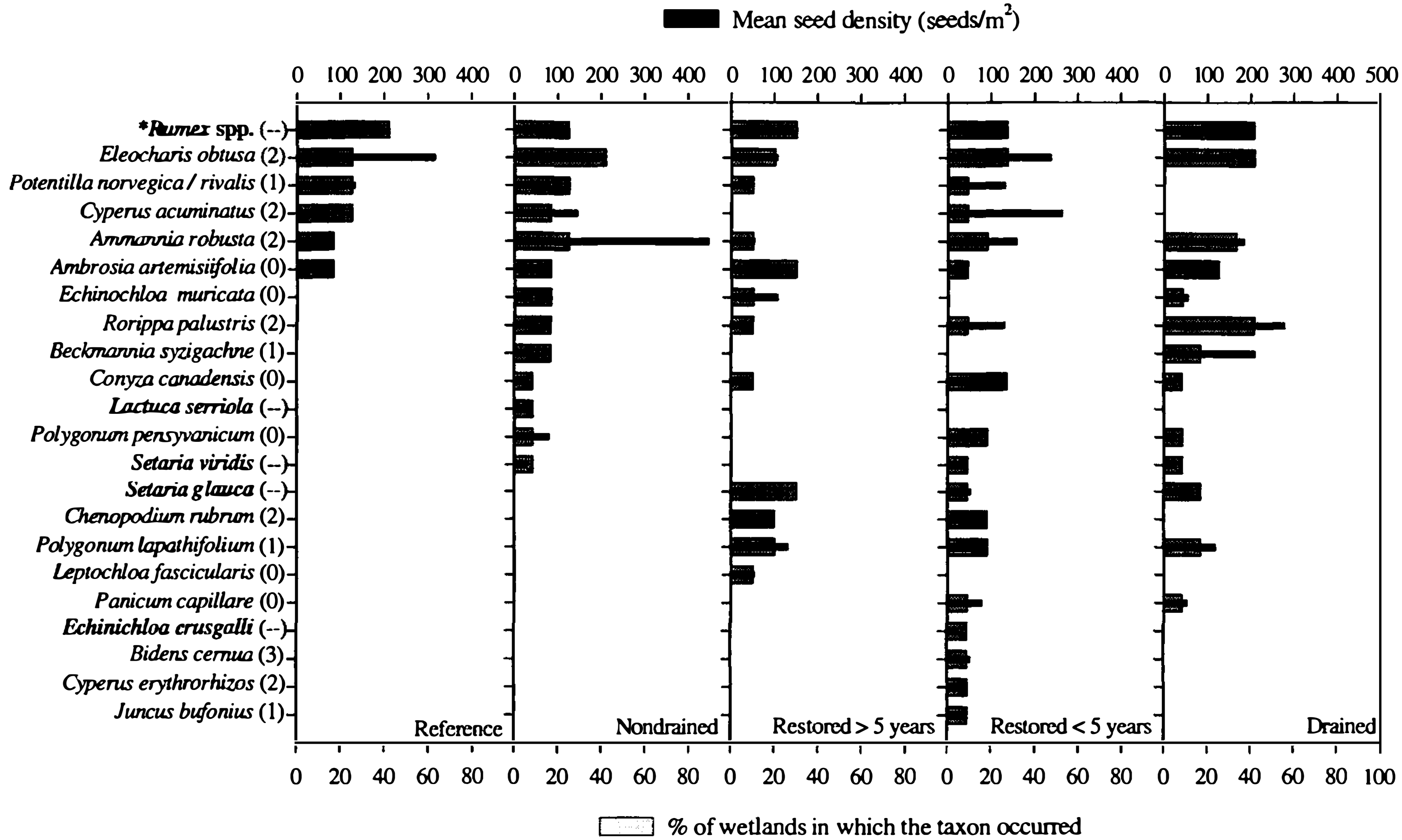

Figure 27. Seed density and % occurrence of native and introduced (bold type) annual plants that emerged from the seed banks of seasonal reference (n = 12), nondrained (n = 12), restored > 5 year (n = 11), restored < 5 year (n = 10), and drained wetlands (n = 12). Seed bank samples were collected June-September 1997. Wetlands are located in the Glaciated Plain physiographic region of the Prairie Pothole Region of the United States. Number in parentheses next to each species is the coefficient of conservatism (C-values) assigned to that species. Introduced species are not assigned C-values (--). An * next to species names indicates it may include introduced, native, and perennial species.

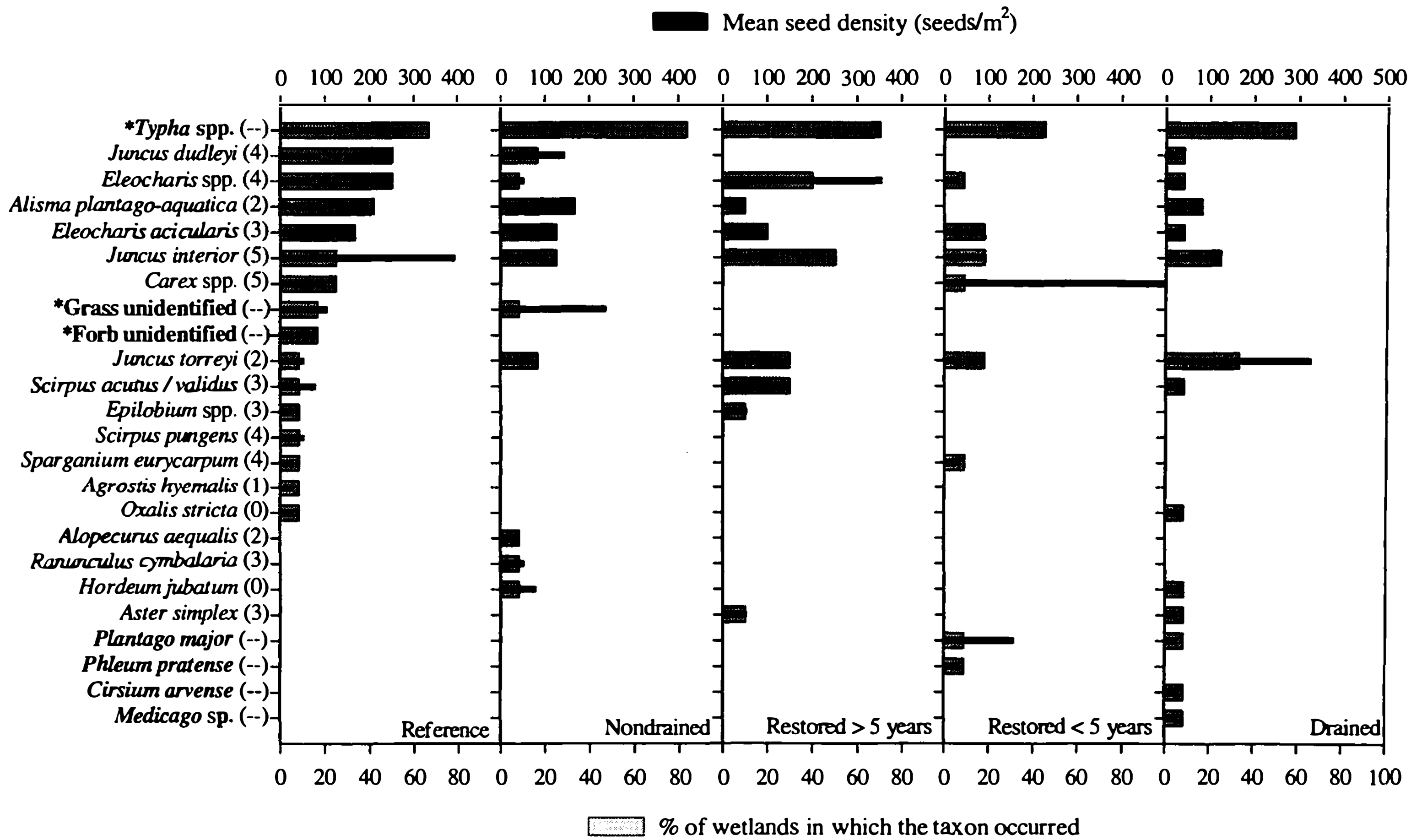

Figure 28. Seed density and % occurrence of native and introduced (bold type) perennial plants that emerged from the seed banks of seasonal reference (n = 12), nondrained (n = 12), restored > 5 year (n = 11), restored < 5 year (n = 10), and drained wetlands (n = 12). Seed bank samples were collected June-September 1997. Wetlands are located in the Glaciated Plain physiographic region of the Prairie Pothole Region of the United States. Number in parentheses next to each species is the coefficient of conservatism (C-values) assigned to that species. Introduced species are not assigned C-values (--). An * next to species names indicates it may include introduced and native species, and for unidentified forbs and grasses annual species.

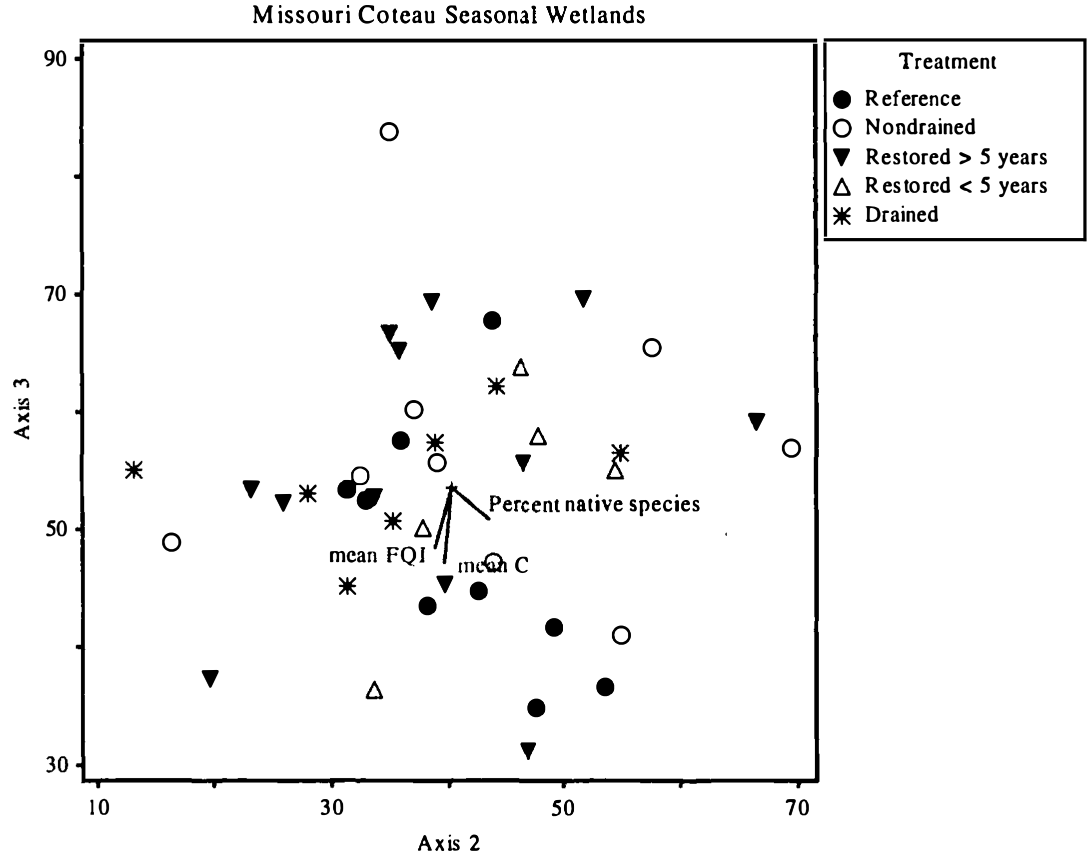

Figure 29. Ordination of plant species (presence or absence) that emerged from the seed banks of seasonal reference (n = 9), nondrained (n = 9), restored > 5 year (n = 11), restored < 5 year (n = 5), and drained wetlands (n = 7). Seed bank samples were collected June-September 1997. Wetlands are located in the Missouri Coteau physiographic region of the Prairie Pothole Region of the United States. Symbols indicate location of each treatment within the species space. Angle and length of radiating lines (i.e., joint plot vectors) indicate the strength and direction of plant types within the species space.

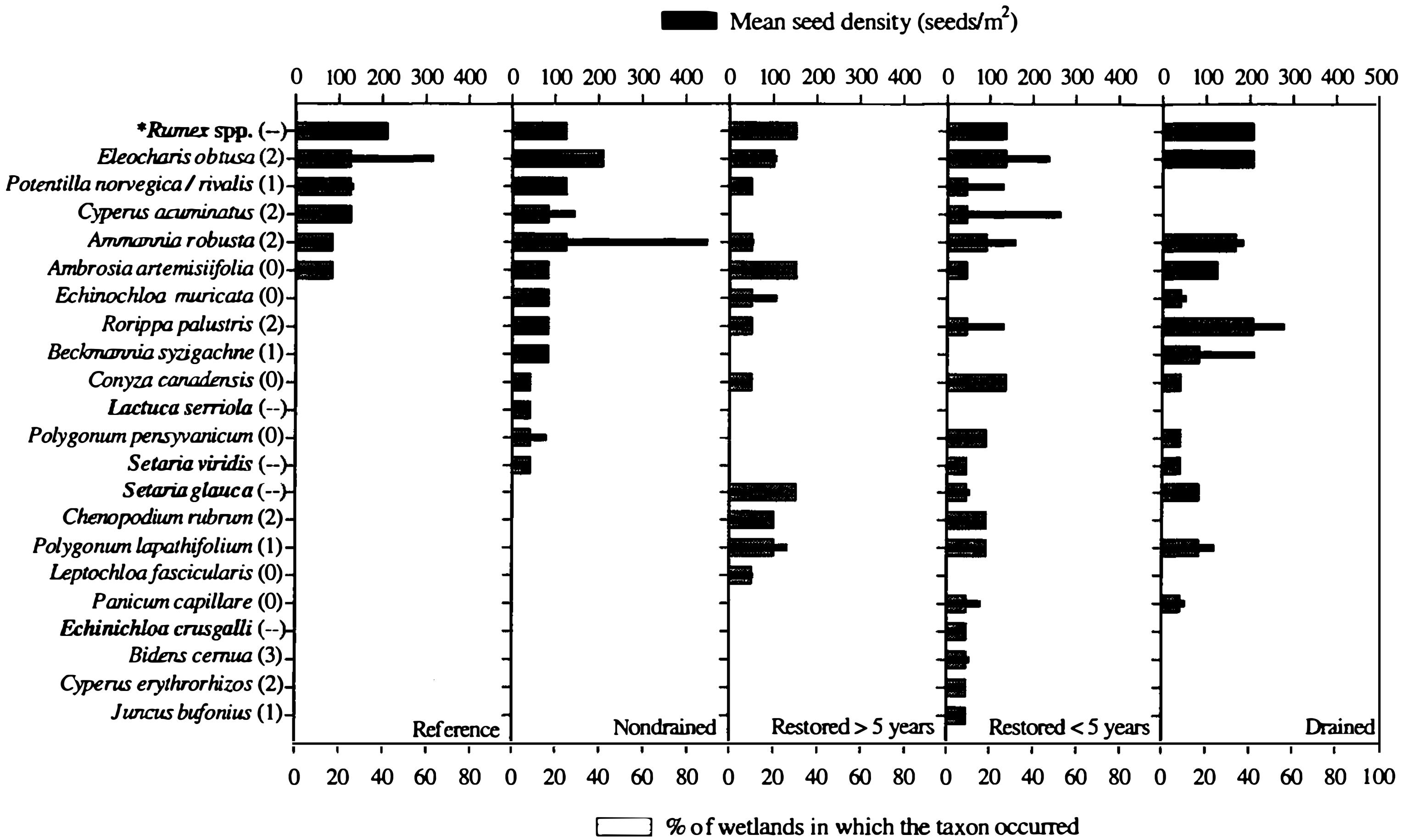

Figure 30. Seed density and % occurrence of native and introduced (bold type) annual plants that emerged from the seed banks of seasonal reference (n = 9), nondrained (n = 9), restored > 5 year (n = 11), restored < 5 year (n = 5), and drained wetlands (n = 7). Seed bank samples were collected June-September 1997. Wetlands are located in the Missouri Coteau physiographic region of the Prairie Pothole Region of the United States. Number in parentheses next to each species is the coefficient of conservatism (C-values) assigned to that species. Introduced species are not assigned C-values (--). An * next to species names indicates it may include introduced, native, and perennial species.

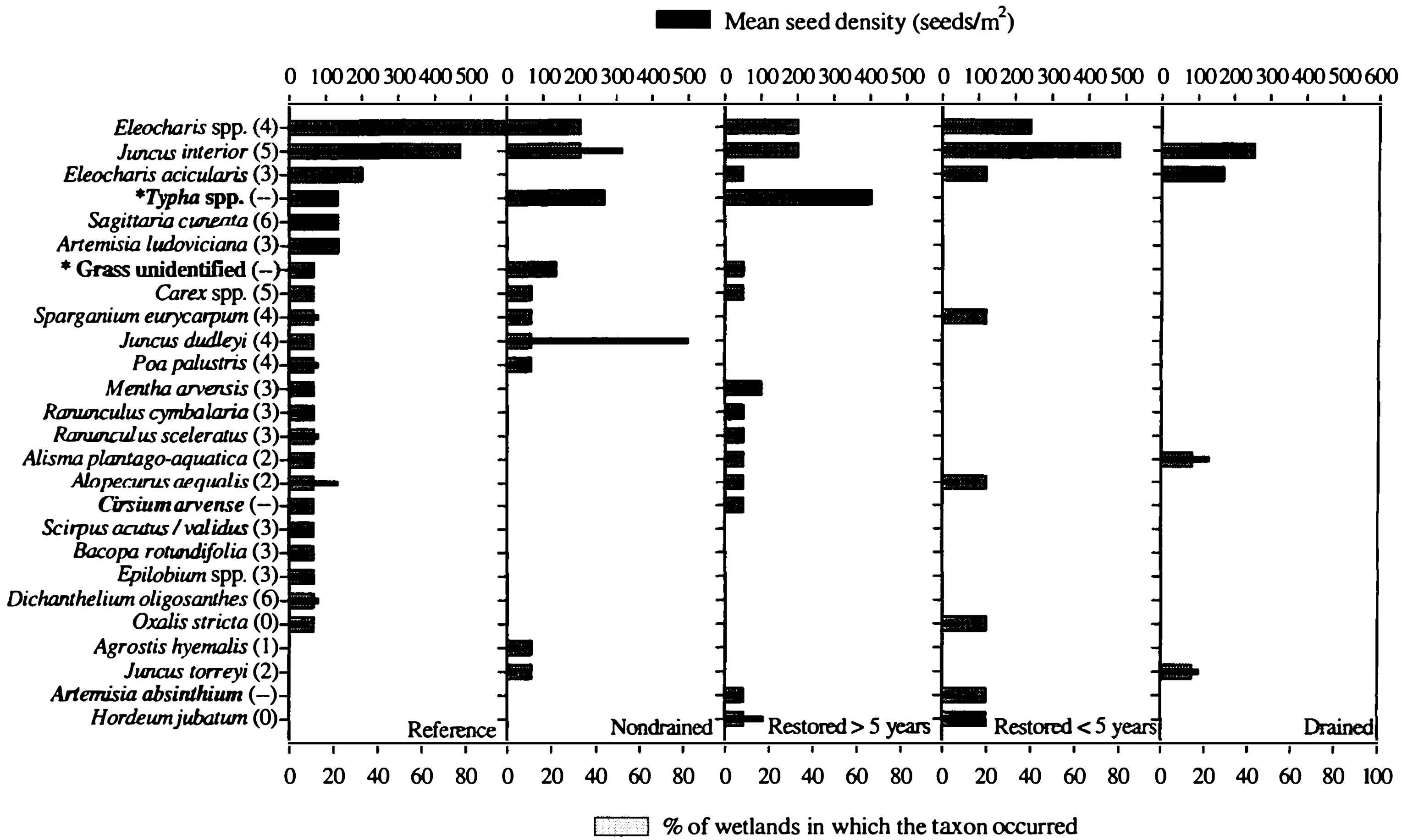

Figure 31. Seed density and % occurrence of native and introduced (bold type) perennial plants that emerged from the seed banks of seasonal reference (n = 9), nondrained (n = 9), restored > 5 year (n = 11), restored < 5 year (n = 5), and drained wetlands (n = 7). Seed bank samples were collected June-September 1997. Wetlands are located in the Missouri Coteau physiographic region of the Prairie Pothole Region of the United States. Number in parentheses next to each species is the coefficient of conservatism (C-values) assigned to that species. Introduced species are not assigned C-values (--). An * next to species names indicates it may include introduced and native species, and for unidentified forbs and grasses annual species.

occurred, 92% occurred in restored < 5 year wetlands, followed by nondrained (78%), reference (36%), restored > 5 year (39%), and drained wetlands (39%) (Figure 30). Of the 22 perennial-native species found, 86% occurred in reference wetlands, 45% in restored > 5 year, 36% in nondrained, 32% in restored < 5 year, and 15% in drained wetlands (Figure 31). Perennial-native species present in reference wetlands but represented in ≤ 1 of the other treatments included: *Sagittaria cuneata*, *Artemisia ludoviciana*, *Juncus dudleyi*, *Poa palustris*, *Mentha arvensis*, *Ranunculus cymbalaria*, *Rununculus sceleratus*, *Scirpus acutus / validus*, *Bacopa rotundifolia*, *Epilobium* spp., *Dichanthelium oligosanthes*, and *Oxalis stricta* (Figure 31).

Prairie Coteau Wetlands: Ordination of species in seasonal Prairie Coteau wetlands was limited because of the small sample size (Figure 32). The loose groupings showed several restored > 5 year and reference wetlands to be associated with percent perennial species, whereas a few other restored < 5 year old wetlands were associated with annual and introduced species. Few annual-native species emerged from the seed banks of Prairie Coteau wetlands, and none of the taxa were common to all treatments (Figure 33). *Eleocharis obtusa* was the only annual-native that occurred in reference wetlands, 6 of the 10 annual-native species occurred in restored < 5 year wetlands, 3 in nondrained and restored > 5 year wetlands, and 2 in drained wetlands. No perennial-native species were common to all treatments (Figure 34). *Typha* spp. occurred in all treatments, but this group likely contained introduced/hybrid species. Species found in reference wetlands, but poorly represented in most other treatments (≤ 1) included: *Juncus*

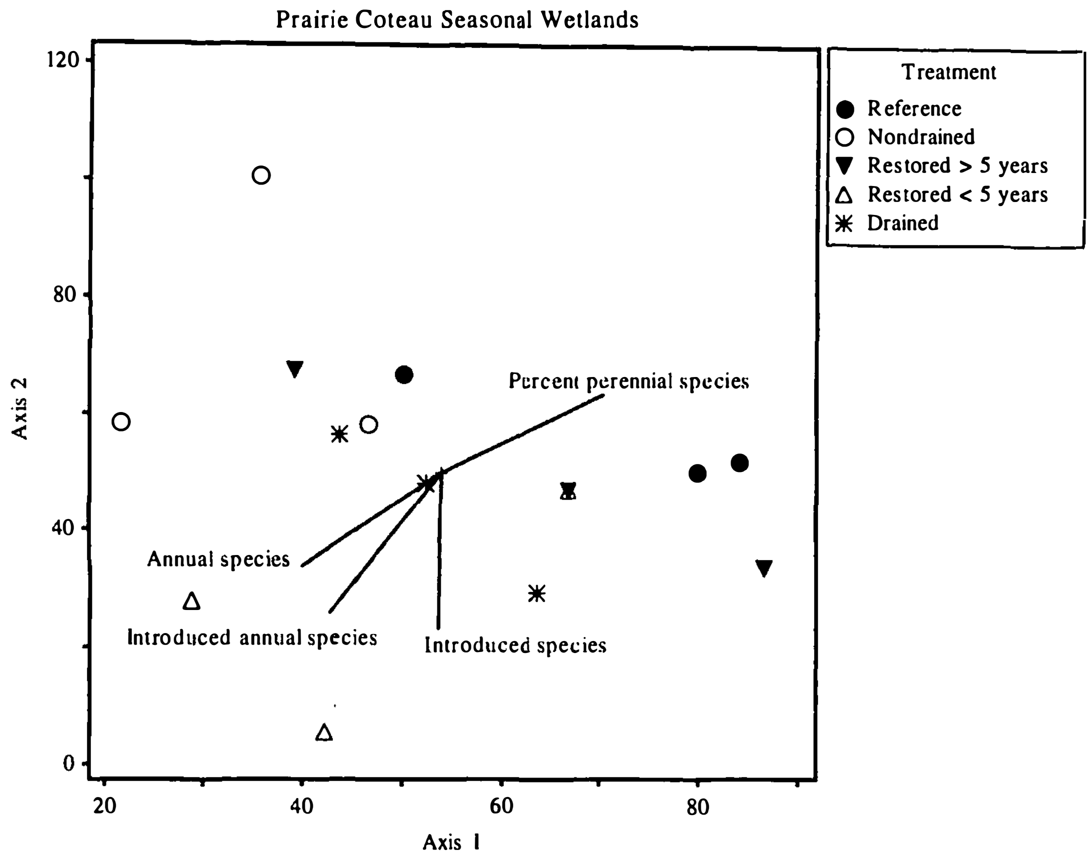

Figure 32. Ordination of plant species (presence or absence) that emerged from the seed banks of seasonal reference (n = 3), nondrained (n = 3), restored > 5 year (n = 3), restored < 5 year (n = 3), and drained wetlands (n = 3). Seed bank samples were collected June-September 1997. Wetlands are located in the Prairie Coteau physiographic region of the Prairie Pothole Region of the United States. Symbols indicate location of each treatment within the species space. Angle and length of radiating lines (i.e., joint plot vectors) indicate the strength and direction of plant types within the species space.

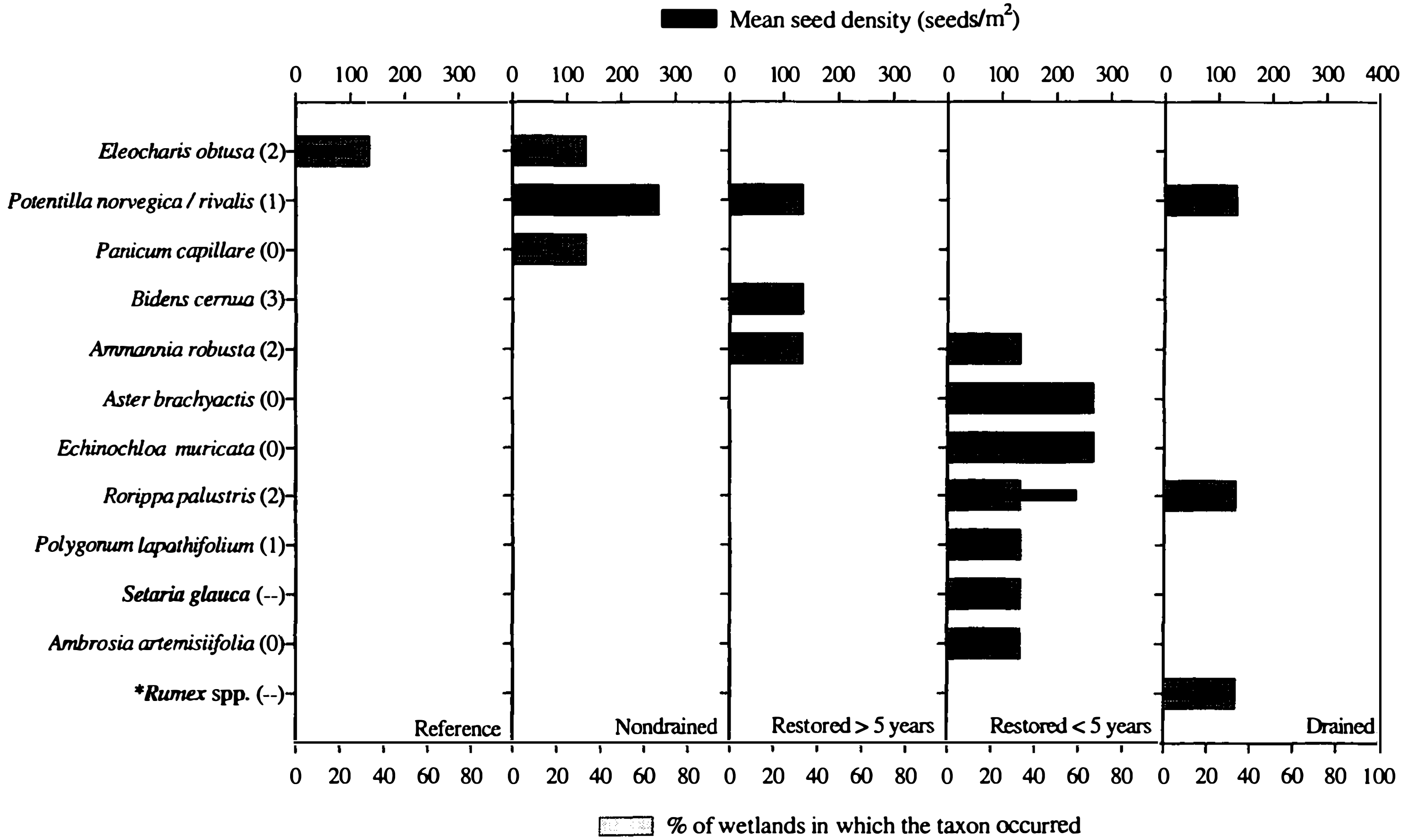

Figure 33. Seed density and % occurrence of native and introduced (bold type) annual plants that emerged from the seed banks of seasonal reference (n = 3), nondrained (n =3), restored > 5 year (n = 3), restored < 5 year (n = 3), and drained wetlands (n = 3). Seed bank samples were collected June-September 1997. Wetlands are located in the Prairie Coteau physiographic region of the Prairie Pothole Region of the United States. Number in parentheses next to each species is the coefficient of conservatism (C-values) assigned to that species. Introduced species are not assigned C-values (--). An * next to species names indicates it may include introduced, native, and perennial species.

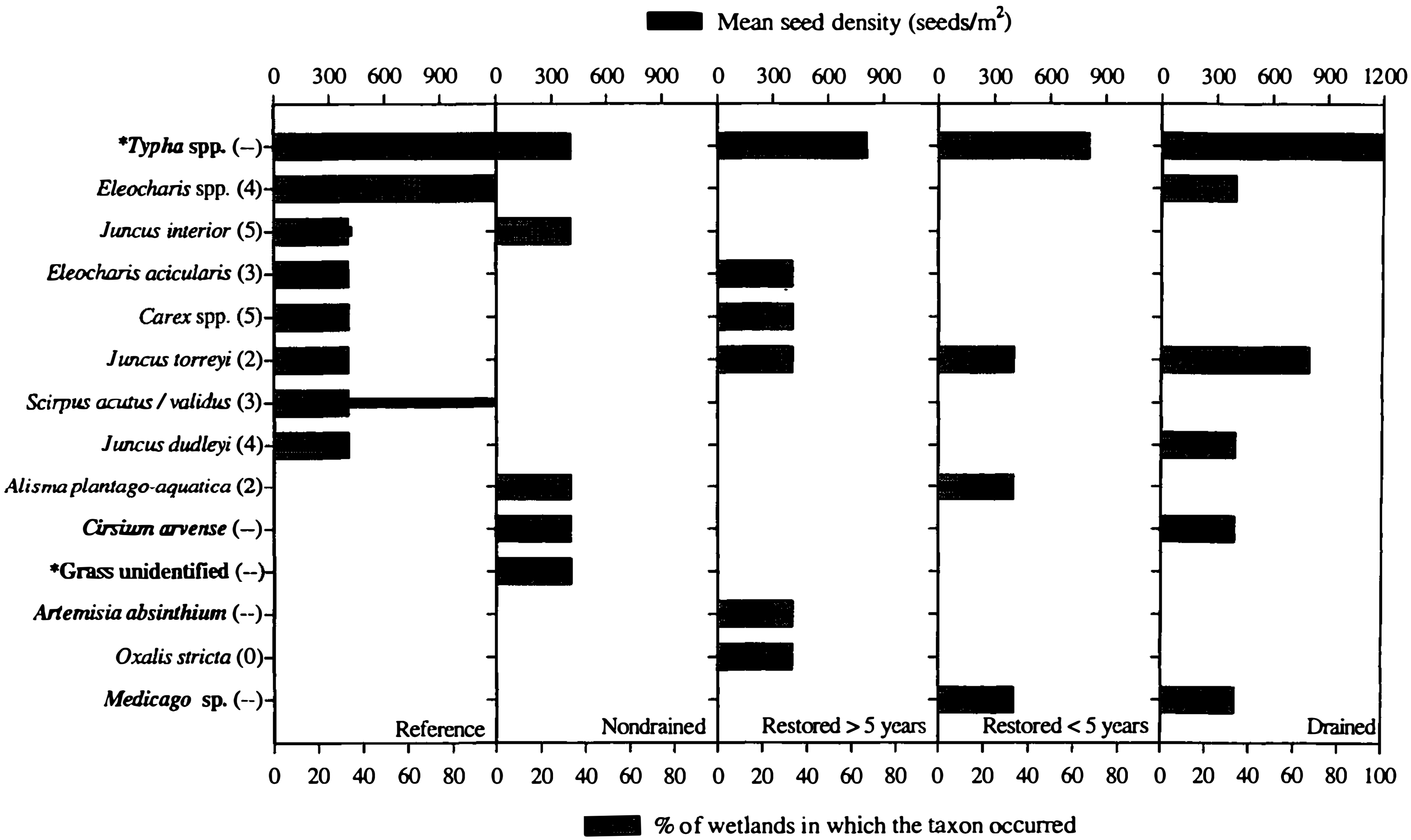

Figure 34. Seed density and % occurrence of native and introduced (bold type) perennial plants that emerged from the seed banks of seasonal reference (n =3), nondrained (n =3), restored > 5 year (n = 3), restored < 5 year (n = 3), and drained wetlands (n = 3). Seed bank samples were collected June-September 1997. Wetlands are located in the Prairie Coteau physiographic region of the Prairie Pothole Region of the United States. Number in parentheses next to each species is the coefficient of conservatism (C-values) assigned to that species. Introduced species are not assigned C-values (--). An * next to species names indicates it may include introduced and native species, and for unidentified forbs and grasses annual species.

interior, *Eleocharis acicularis*, *Carex* spp., *Scirpus acutus / validus*, and *Juncus dudleyi* (Figure 34). Seven of the 9 perennial-native species occurred in reference wetlands, 4 in restored > 5 year, 3 in drained, and 2 in nondrained and restored < 5 year wetlands.

Semipermanent Wetlands

Seed Density by Plant Type

Overall trends showed seed density of perennial-native plants in semipermanent wetlands to be greater in reference wetlands than most other treatments, but this was only significant in the Missouri Coteau region (Table 16). In all 3 regions seed density of annual-natives was lower in reference wetlands than most other treatments, but these differences were not significant. Seed bank density of other plant life history types in the 3 regions did not significantly differ among treatments (Table 16).

Taxon Richness by Plant Type

Mean taxon richness did not significantly differ among treatments in any region (Table 17). However, highest perennial-native and lowest annual-native taxon richness occurred in reference wetlands. In the Glaciated Plain, total number of perennial-native taxa was greatest in reference wetlands, followed by nondrained, restored, and drained wetlands. Total number of perennial taxa varied little among treatments in the Missouri and Prairie Coteau. Likewise, total number of perennial and annual introduced, and annual native taxa varied little among treatments in all 3 regions (Table 17).

Table 16. Transformed [(seeds + 0.5)$^{0.5}$] least-squares means (± SE) seed bank density (no. seeds/m^2) of perennial and annual introduced and native plant taxa that emerged from the seed banks of semipermanent seasonal reference, nondrained, restored > 5 year, restored < 5 year, and drained wetlands. Seed bank samples were collected June-September 1997. Wetlands are located in the Glaciated Plain, Missouri Coteau, and Prairie Coteau physiographic regions of the Prairie Pothole Region of the United States. Where significant treatment effects were detected (*P* - values in bold type), means (± SE) within rows with a common letter are not significantly (*P* > 0.05) different.

Region Plant type	Semipermanent wetland treatments Reference Mean seed density	 Nondrained Mean seed density	 Restored > 5 years Mean seed density	 Restored < 5 years Mean seed density	 Drained Mean seed density	ANOVA *F*	 *P*
Glaciated Plain						df = 4, 26	
Perennial-native	14.8 (2.2)	7.7 (2.3)	9.9 (2.2)	7.5 (3.5)	10.2 (2.3)	1.65	0.1909
Perennial-introduced	1.2 (0.4)	0.7 (0.4)	0.7 (0.4)	1.8 (0.6)	1.2 (0.4)	0.90	0.4787
Annual-native	7.7 (2.9)	8.3 (3.0)	6.7 (2.9)	13.1 (4.3)	8.3 (3.0)	0.48	0.7520
Annual-introduced	3.0 (0.9)	1.2 (0.9)	2.4 (0.9)	1.8 (1.1)	1.7 (0.9)	1.81	0.1570
Total	18.9 (2.8)	13.1 (2.9)	14.1 (2.7)	17.3 (4.0)	14.7 (2.9)	0.91	0.4731
n[a]	10	9	10	4	9		
Missouri Coteau						df = 4, 20	
Perennial-native	22.9 (2.8)a	14.2 (3.0)b	10.4 (3.1)b	11.4 (3.9)b	17.5 (4.4)ab	4.08	**0.0140**
Perennial-introduced	1.2 (0.4)	1.3 (0.4)	0.7 (0.4)	0.7 (0.6)	0.7 (0.7)	0.43	0.7886
Annual-native	7.1 (2.2)	9.0 (2.3)	11.2 (2.4)	8.5 (3.2)	10.8 (3.7)	0.51	0.7314
Annual-introduced	1.6 (0.6)	0.8 (0.6)	1.7 (0.6)	0.5 (0.8)	1.0 (0.9)	0.84	0.5171
Total	24.8 (3.0)	18.6 (3.1)	16.5 (3.3)	13.7 (4.1)	21.2 (4.6)	2.44	0.0808
n	9	8	8	3	3		
Prairie Coteau						df = 4, 8	
Perennial-native	14.5 (2.8)	15.3 (3.4)	10.3 (2.8)	6.6 (2.8)	8.1 (2.5)	1.70	0.2431
Perennial-introduced	0.7 (0.7)	0.7 (0.9)	0.7 (0.7)	0.7 (0.7)	1.9 (0.6)	0.68	0.6224
Annual-native	0.7 (3.0)	13.4 (3.7)	12.0 (3.0)	7.6 (3.0)	5.8 (2.7)	2.81	0.0996
Annual-introduced	4.4 (1.5)	0.7 (1.8)	2.9 (1.5)	0.7 (1.5)	1.8 (1.3)	1.04	0.4447
Total	15.3 (3.4)	20.6 (4.2)	17.8 (3.4)	10.8 (3.4)	10.6 (3.0)	1.59	0.2668
n	3	3	3	3	3		

a n = number of wetland treatment replicates within each region.

Table 17. Total numbers and least-squares means (± SE) taxon richness of perennial and annual introduced and native plant taxa that emerged from the seed banks of semipermanent reference, nondrained, restored > 5 year, restored < 5 year, and drained wetlands. Seed bank samples were collected June-September 1997. Wetlands are located in the Glaciated Plain, Missouri Coteau, and Prairie Coteau physiographic regions of the Prairie Pothole Region of the United States. Means (± SE) within rows were not significantly ($P > 0.05$) different.

	Semipermanent wetland treatments											
	Reference		Nondrained		Restored > 5 years		Restored < 5 years		Drained		ANOVA	
Region / Plant type	No. taxa	Mean richness	No. taxa	Mean richness	No. taxa	Mean richness	No. taxa	Mean richness	No. taxa	Mean richness	F	P
Glaciated Plain											df = 4, 26	
Perennial-native	13	2.5 (0.4)	10	1.7 (0.4)	7	1.3 (0.4)	5	1.5 (0.6)	6	1.3 (0.4)	1.56	0.2146
Perennial-introduced	1	0.1 (0.1)	0	0.0 (0.1)	0	0.0 (0.1)	1	0.3 (0.1)	1	0.1 (0.1)	0.90	0.4787
Annual-native	7	1.1 (0.4)	7	1.1 (0.5)	8	1.6 (0.4)	5	1.3 (0.6)	12	1.9 (0.5)	0.85	0.5038
Annual-introduced	2	0.4 (0.2)	2	0.2 (0.2)	2	0.2 (0.2)	0	0.2 (0.2)	1	0.2 (0.2)	1.06	0.3963
Total	23	5.1 (0.7)	19	4.3 (0.7)	17	3.8 (0.7)	11	3.5 (1.0)	20	4.2 (0.7)	0.81	0.5295
n[a]	10		9		10		4		9			
Missouri Coteau											df = 4, 20	
Perennial-native	9	2.4 (0.3)	9	1.8 (0.4)	9	1.5 (0.4)	5	2.0 (0.5)	5	2.0 (0.6)	0.94	0.4596
Perennial-introduced	1	0.1 (0.1)	1	0.1 (0.1)	0	0.0 (0.1)	0	0.0 (0.1)	0	0.0 (0.1)	0.43	0.7886
Annual-native	8	1.1 (0.4)	5	1.3 (0.4)	9	1.9 (0.4)	6	1.8 (0.6)	4	2.0 (0.6)	0.95	0.4560
Annual-introduced	1	0.2 (0.1)	0	0.0 (0.1)	1	0.2 (0.1)	0	0.0 (0.1)	0	0.0 (0.2)	0.85	0.5108
Total	19	4.5 (0.6)	15	4.0 (0.6)	19	4.5 (0.6)	11	4.4 (0.9)	9	5.4 (1.0)	0.35	0.8378
n	9		8		8		3		3			
Prairie Coteau											df = 4, 8	
Perennial-native	6	3.0 (0.7)	5	2.5 (1.0)	6	2.3 (0.7)	4	1.7 (0.7)	5	1.8 (0.6)	0.58	0.6887
Perennial-introduced	0	0.0 (0.2)	0	0.0 (0.2)	0	0.0 (0.2)	0	0.0 (0.2)	1	0.3 (0.1)	0.68	0.6224
Annual-native	0	0.0 (0.5)	2	1.3 (0.6)	4	1.3 (0.5)	5	1.7 (0.5)	2	0.6 (0.5)	2.45	0.1310
Annual-introduced	1	0.7 (0.3)	0	0.0 (0.3)	1	0.3 (0.3)	0	0.0 (0.3)	1	0.3 (0.2)	1.02	0.4522
Total	7	4.7 (1.2)	7	5.5 (1.5)	11	5.3 (1.2)	9	4.0 (1.2)	9	4.3 (1.0)	0.27	0.8916
n	3		3		3		3		3			

a n = number of wetland treatment replicates within each region.

Mean C and FQI

In all 3 regions, mean C and FQI estimates were greatest in reference wetlands (Table 18). Mean FQI in Glaciated Plain reference wetlands was similar to restored < 5 year wetlands, but significantly greater than, nondrained, restored > 5 year and drained wetlands (Table 18). Mean FQI in Prairie Coteau reference sites was similar to nondrained and restored > 5 year wetlands and significantly greater than restored < 5 year and drained wetlands (Table 18). Most mean FQI estimates in nondrained. restored, and drained wetlands within the Glaciated Plain and Prairie Coteau were statistically similar. I found no significant difference in mean C and FQI among Missouri Coteau treatments. Overall trends showed little difference in mean C and FQI among nondrained, restored, and drained wetlands in the Glaciated Plain and Missouri Coteau regions (Figure 35) whereas mean C and FQI tended to be greater in nondrained and restored > 5 year wetlands than in restored < 5 year and drained wetlands (Figure 35).

Taxonomic Composition

Glaciated Plain Wetlands: Ordination of plants species indicated that reference wetlands were best grouped by native perennials, whereas restored wetlands were grouped more with native species, annual species and introduced annuals (Figure 36). No annual-native species were found to occur in all treatments in the Glaciated Plain (Figure 37). *Rumex* spp. occurred in all treatments but this taxa likely included both annual and introduced species. Most of the 18 annual-native species were found in drained wetlands

Table 18. Least-squares means (± SE) coefficient of conservatism (C) and floristic quality index (FQI) of plants that emerged from the seed banks of semipermanent reference, nondrained, restored > 5 year, restored < 5 year, and drained wetlands. Seed bank samples were collected June-September 1997. Wetlands are located in the Glaciated Plain, Missouri Coteau, and Prairie Coteau physiographic regions of the Prairie Pothole Region of the United States. Where significant treatment effects were detected (*P* - values in bold type), means (± SE) within rows with a common letter are not significantly (*P* > 0.05) different.

	Semipermanent wetland treatments						
Region	Reference	Nondrained	Restored > 5 years	Restored < 5 years	Drained	ANOVA	
Index	Mean	Mean	Mean	Mean	Mean	*F*	*P*
Glaciated Plain						df = 4, 26	
C	3.2 (0.3)a	2.1 (0.3)b	1.9 (0.3)b	3.0 (0.5)ab	1.8 (0.3)b	3.36	**0.0241**
FQI	7.1 (0.7)a	4.4 (0.7)b	3.8 (0.7)b	4.6 (1.1)ab	3.6 (0.7)b	4.02	**0.0114**
n[a]	10	9	10	4	9		
Missouri Coteau						df = 4, 20	
C	3.3 (0.3)	2.2 (0.3)	2.5 (0.3)	2.1 (0.4)	2.3 (0.5)	2.44	0.0807
FQI	6.9 (0.7)	4.6 (0.7)	5.3 (0.7)	4.5 (1.1)	5.2 (1.2)	1.63	0.2055
n	9	8	8	3	3		
Prairie Coteau						df = 4, 8	
C	4.4 (0.5)a	2.5 (0.7)ab	3.3 (0.5)a	1.4 (0.5)b	1.5 (0.5)b	5.54	**0.0195**
FQI	9.4 (1.2)a	5.9 (1.4)ac	7.0 (1.2)ab	3.2 (1.2)c	3.6 (1.0)bc	5.07	**0.0248**
n	3	3	3	3	3		

a n = number of wetland treatment replicates within each region.

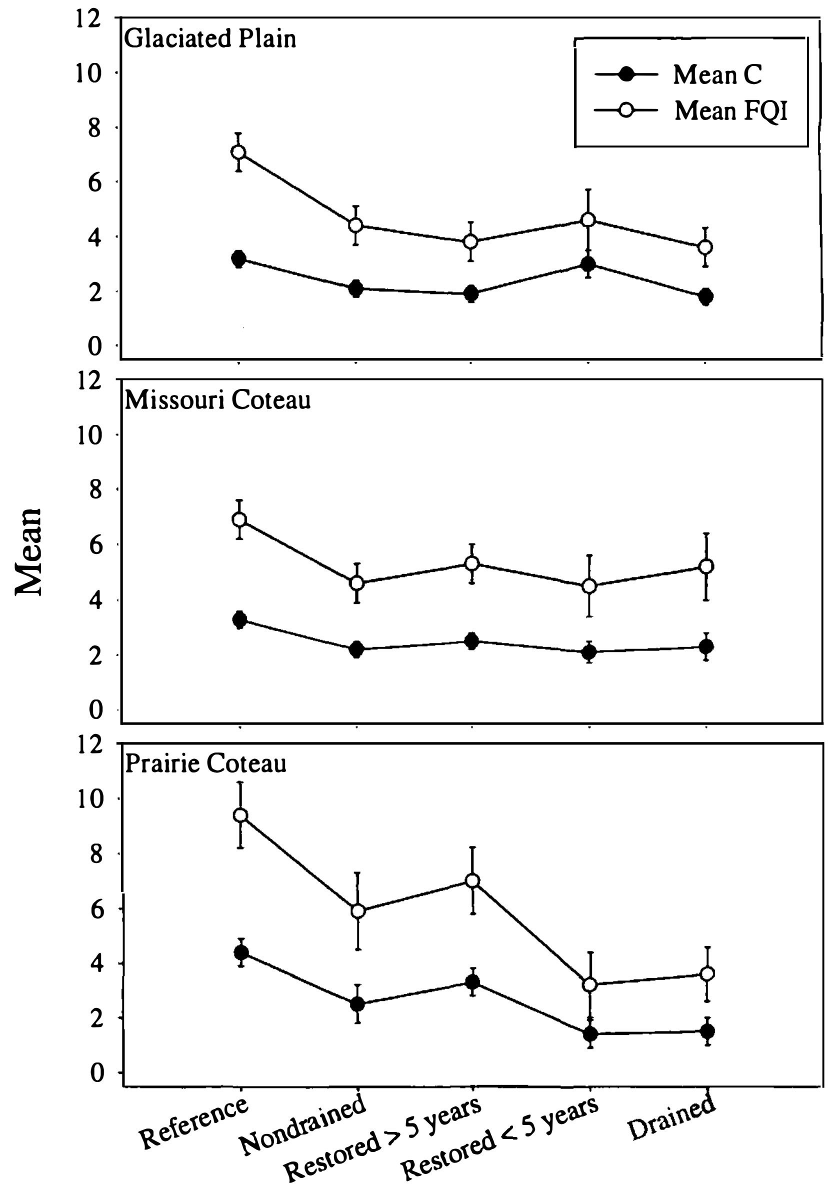

Figure 35. Mean (± SE) coefficient of conservatism (C) and floristic quality index (FQI) for native plants that emerged from the seed banks of semipermanent reference, nondrained, restored > 5 year, and restored < 5 year, and drained wetlands. Seed bank samples were collected June-September 1997. Wetlands are located in the Glaciated Plain, Missouri Coteau, and Prairie Coteau physiographic regions of the Prairie Pothole Region of the United States. Replication of treatments by region and wetland class are shown in Table 18.

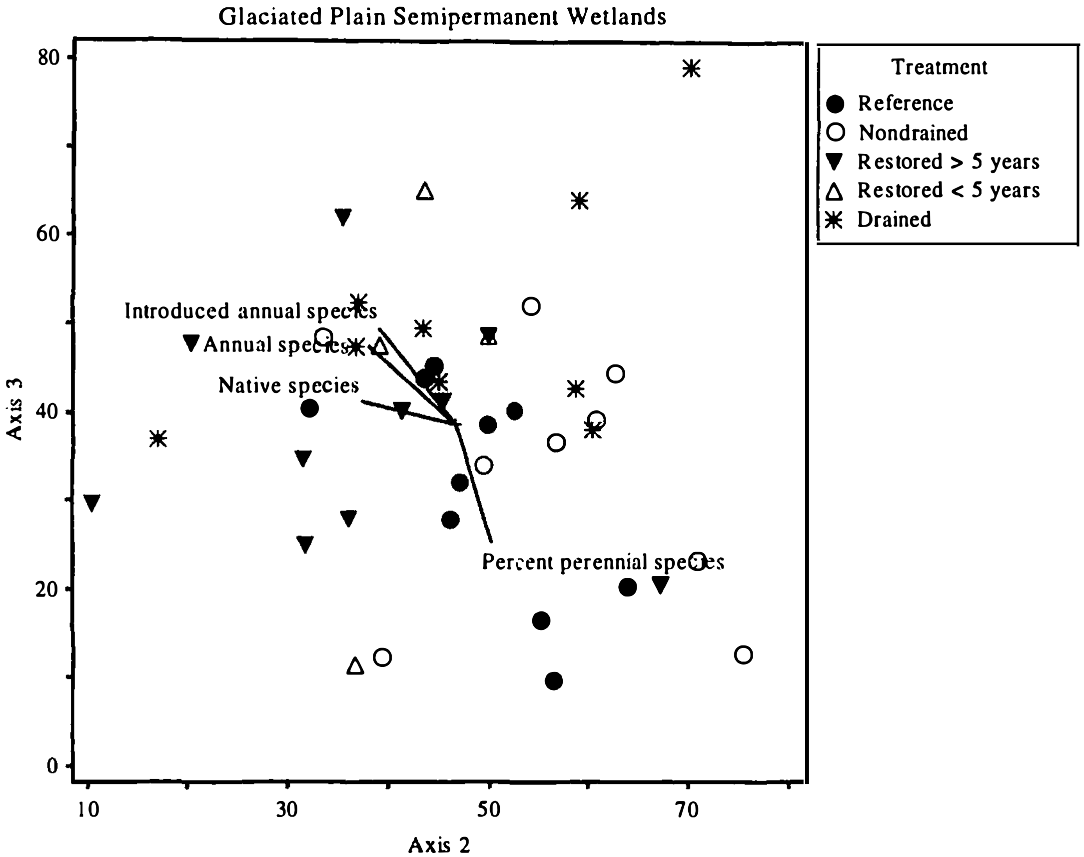

Figure 36. Ordination of plant species (presence or absence) that emerged from the seed banks of semipermanent reference (n = 10), nondrained (n = 9), restored > 5 year (n = 10), restored < 5 year (n = 4), and drained wetlands (n = 9). Seed bank samples were collected June-September 1997. Wetlands are located in the Glaciated Plain physiographic region of the Prairie Pothole Region of the United States. Symbols indicate location of each treatment within the species space. Angle and length of radiating lines (i.e., joint plot vectors) indicate the strength and direction of plant types within the species space.

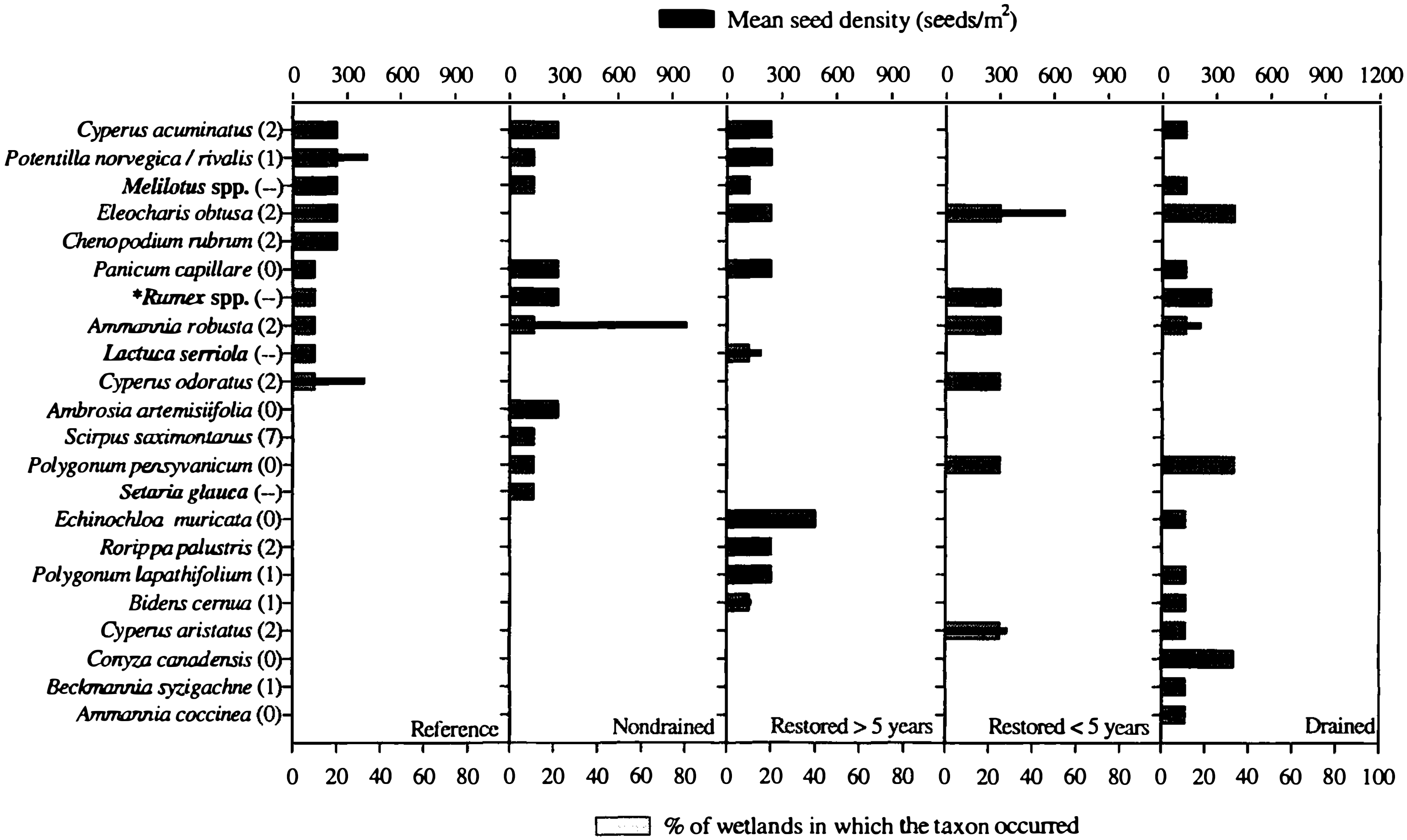

Figure 37. Seed density and % occurrence of native and introduced (bold type) annual plants that emerged from the seed banks of semipermanent reference (n = 10), nondrained (n = 9), restored > 5 year (n = 10), restored < 5 year (n = 4), and drained wetlands (n = 9). Seed bank samples were collected June-September 1997. Wetlands are located in the Glaciated Plain physiographic region of the Prairie Pothole Region of the United States. Number in parentheses next to each species is the coefficient of conservatism (C-values) assigned to that species. Introduced species are not assigned C-values (--). An * next to species names indicates it may include introduced, native, and perennial species.

(67%), followed by nondrained and reference wetlands (38%), restored > 5 year (28%), and restored < 5 year wetlands (Figure 37). *Eleocharis spp.* and *Juncus torreyi* were the only perennial-native species found in all treatments in the Glaciated Plain (Figure 38). Perennial-native taxa that occurred in reference wetlands, but were absent from most other treatments included: *Sagittaria cuneata*, *Scirpus pungens*, *Mentha arvensis*, *Carex* spp., *Sparganium eurycarpum*, *Ranunculus cymbalaria*, and *Hordeum jubatum*. Seventy-two percent of the 18 perennial-native species occurred in reference wetlands, followed by nondrained (56%), restored > 5 year (39%), drained (33%), and restored < 5 year wetlands (Figure 38).

Missouri Coteau Wetlands: Species ordinations indicated high variability among treatments. Some reference wetlands grouped in association with mean C, mean FQI, native species, and native annual species; other treatments were more widely scattered (Figure 39). Of the 15 annual-native species that occurred, none were found in all treatments (Figure 40). Sixty-percent of the annual native species occurred in restored > 5 year wetlands, followed by reference wetlands (53%), restored < 5 year (40%), drained (27%), and nondrained (27%). *Cyperus odoratus*, *Ammannia coccinea*, *Cyperus aristatus, Scirpus saximontanus*, *Echinochloa muricata* and *Polygonum pensylvanicum* occurred in reference wetlands, but were poorly represented in other treatments (Figure 40). *Juncus interior* was the only perennial-native to occur in all treatments (Figure 41). Perennial-native species in reference wetlands, but mostly absent from most other treatments, included *Mentha arvensis* and *Alisma plantago-aquatica*. Percent of

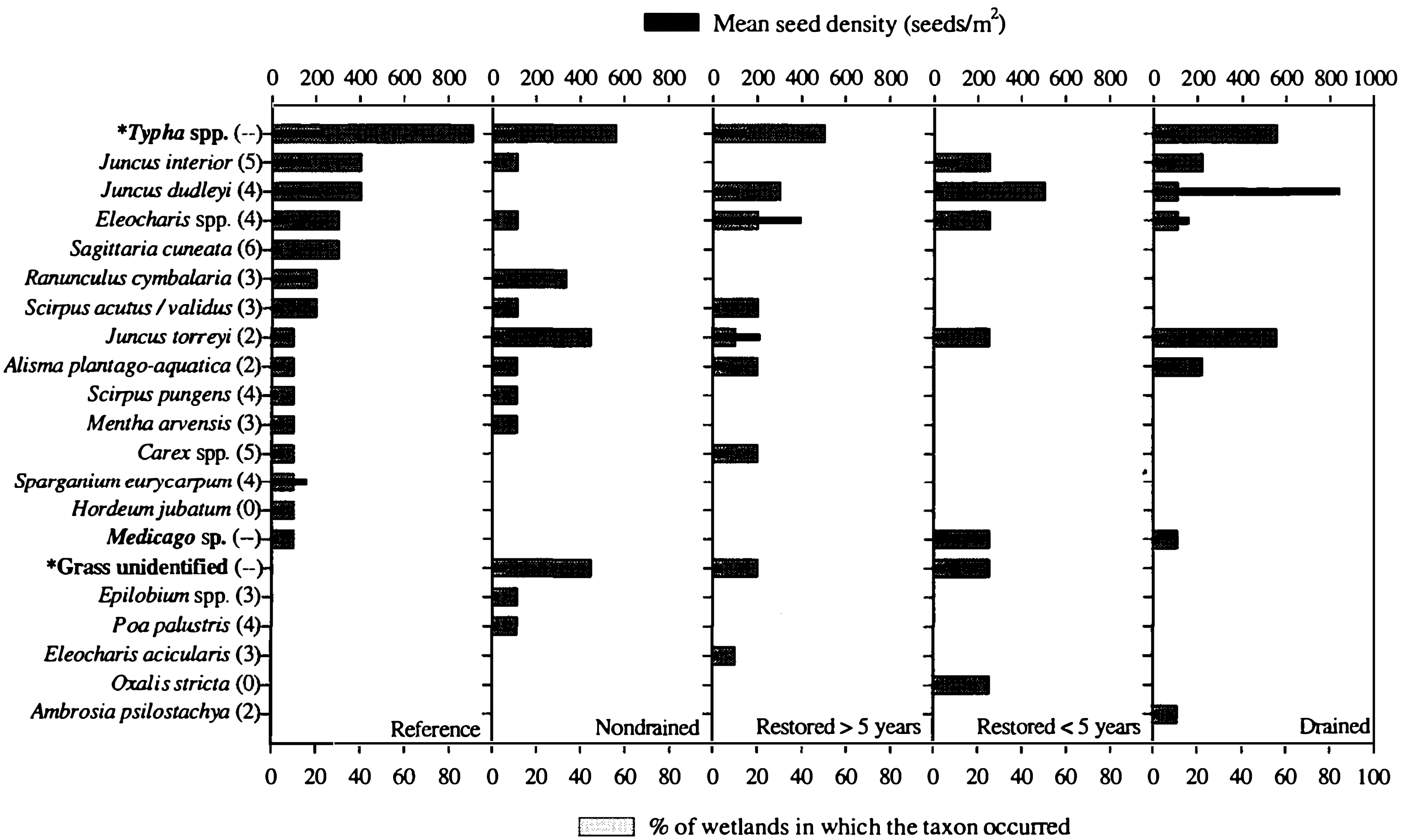

Figure 38. Seed density and % occurrence of native and introduced (bold type) perennial plants that emerged from the seed banks of semipermanent reference (n = 10), nondrained (n = 9), restored > 5 year (n = 10), restored < 5 year (n = 4), and drained wetlands (n = 9). Seed bank samples were collected June-September 1997. Wetlands are located in the Glaciated Plain physiographic region of the Prairie Pothole Region of the United States. Number in parentheses next to each species is the coefficient of conservatism (C-values) assigned to that species. Introduced species are not assigned C-values (--). An * next to species names indicates it may include introduced, native, and perennial species.

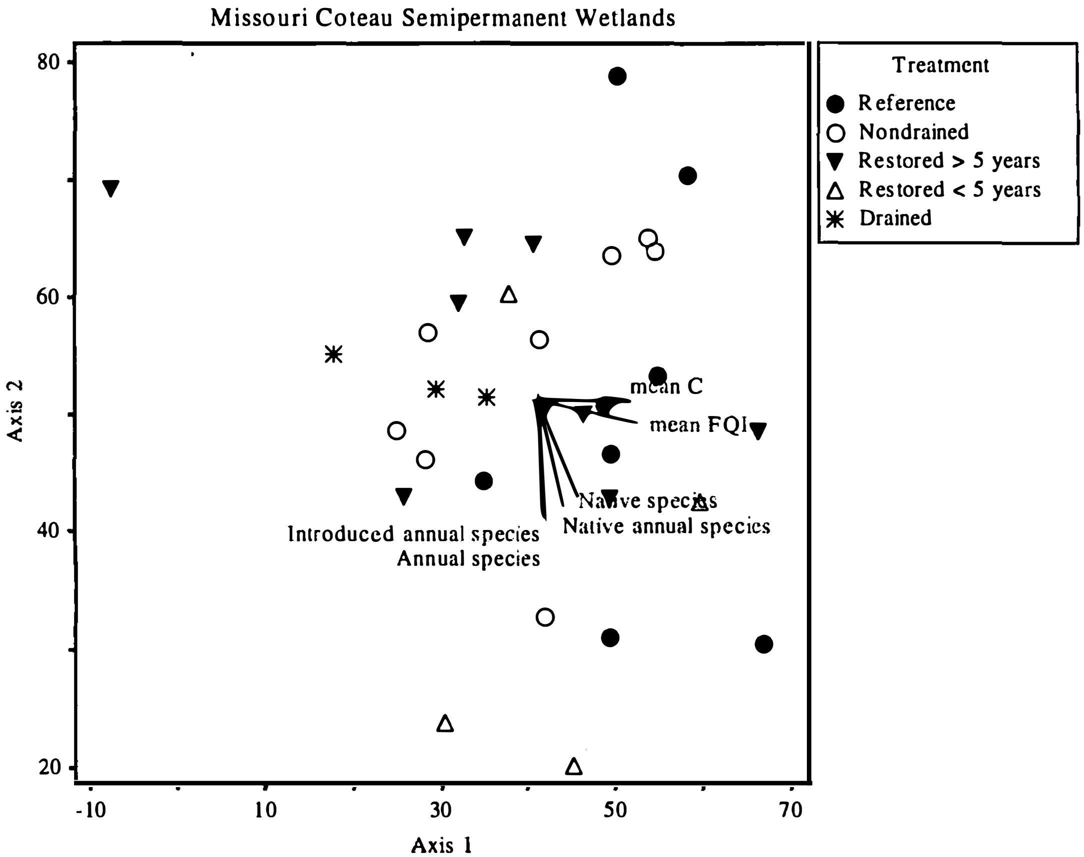

Figure 39. Ordination of plant species (presence or absence) that emerged from the seed banks of semipermanent reference (n = 9), nondrained (n = 8), restored > 5 year (n = 8), restored < 5 year (n = 3), and drained wetlands (n = 3). Seed bank samples were collected June-September 1997. Wetlands are located in the Missouri Coteau physiographic region of the Prairie Pothole Region of the United States. Symbols indicate location of each treatment within the species space. Angle and length of radiating lines (i.e., joint plot vectors) indicate the strength and direction of plant types within the species space.

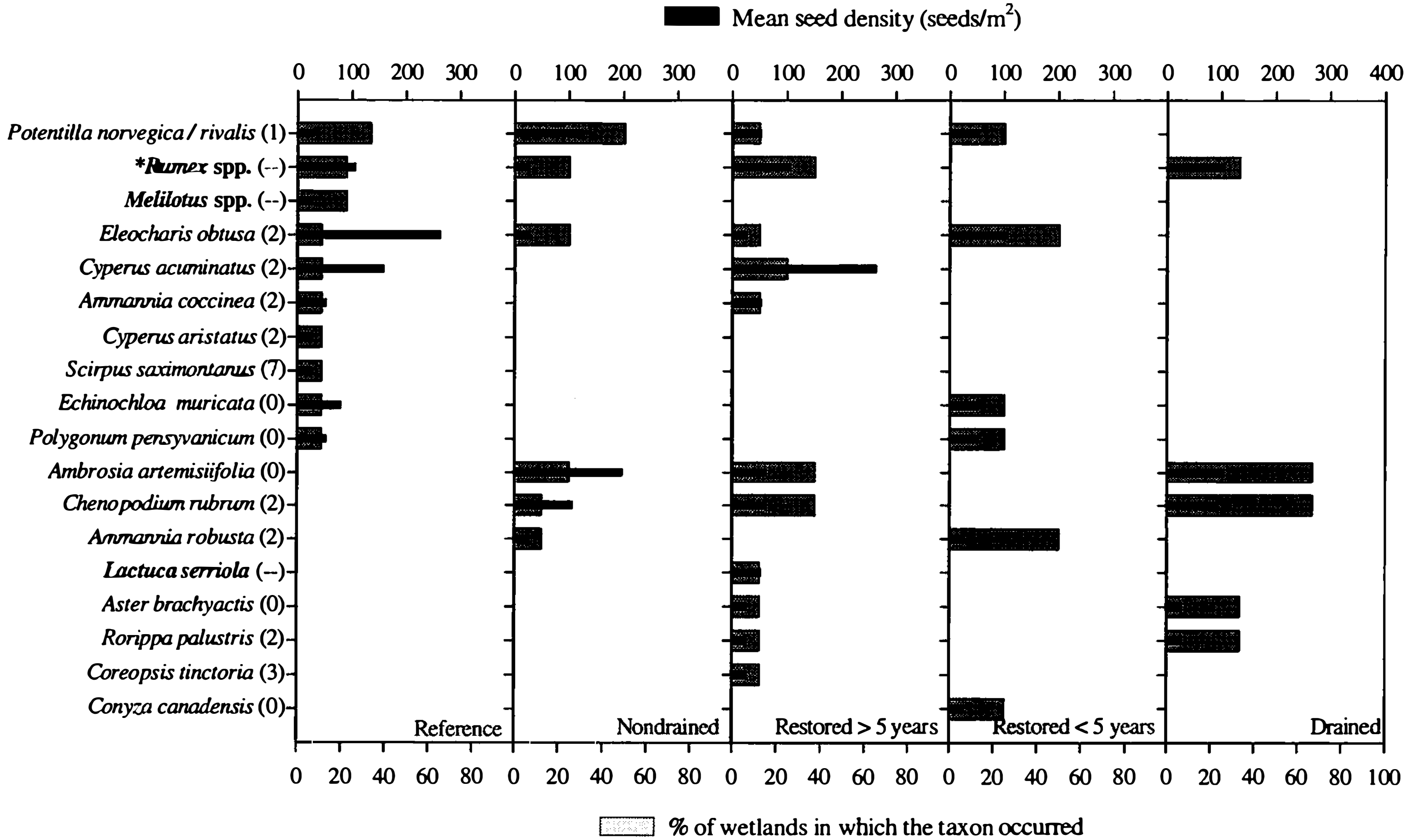

Figure 40. Seed density and % occurrence of native and introduced (bold type) annual plants that emerged from the seed banks of semipermanent reference (n = 9), nondrained (n = 8), restored > 5 year (n = 8), restored < 5 year (n = 3), and drained wetlands (n = 3). Seed bank samples were collected June-September 1997. Wetlands are located in the Missouri Coteau physiographic region of the Prairie Pothole Region of the United States. Number in parentheses next to each species is the coefficient of conservatism (C-values) assigned to that species. Introduced species are not assigned C-values (--). An * next to species names indicates it may include introduced, native, and perennial species.

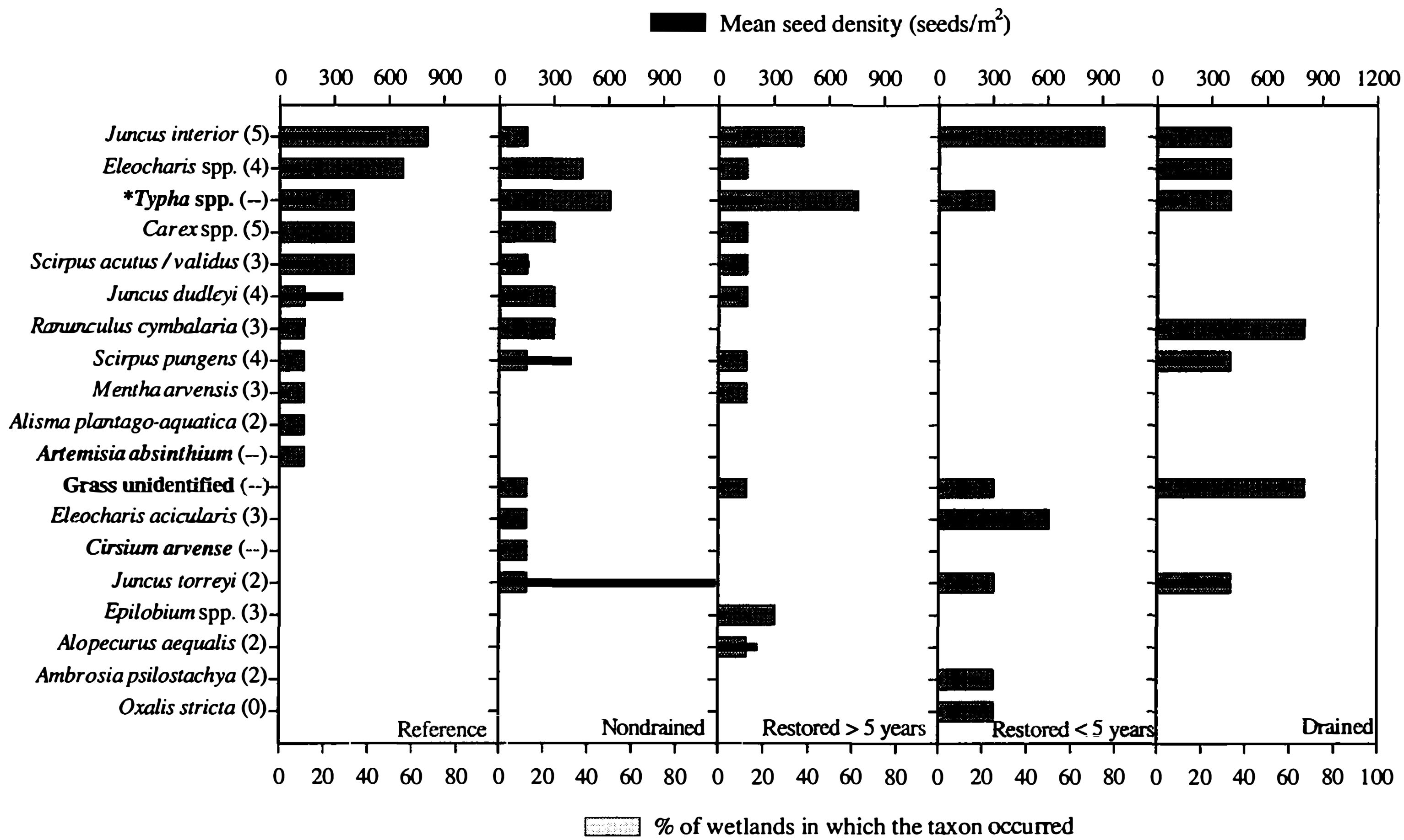

Figure 41. Seed density and % occurrence of native and introduced (bold type) perennial plants that emerged from the seed banks of semipermanent reference (n = 9), nondrained (n = 8), restored > 5 year (n = 8), restored < 5 year (n = 3), and drained wetlands (n = 3). Seed bank samples were collected June-September 1997. Wetlands are located in the Missouri Coteau physiographic region of the Prairie Pothole Region of the United States. Number in parentheses next to each species is the coefficient of conservatism (C-values) assigned to that species. Introduced species are not assigned C-values (--). An * next to species names indicates it may include introduced, native, and perennial species.

perennial-natives (14) that occurred was similar among reference, nondrained, and restored > 5 year wetlands (64%), whereas fewer were found in restored < 5 year (44%) and drained wetlands (44%) (Figure 41).

Prairie Coteau Wetlands: Species ordination resulted in few tight groupings of wetland treatments (Figure 42). Though scattered, associations of reference wetlands was best described by mean C and percent perennial species, whereas several restored wetlands were associated with introduced and annual species (Figure 42). No annual-native species emerged from the seed banks of reference wetlands and no annual-native species were common to nondrained, restored, and drained wetlands (Figure 43). Of the 9 annual-native species that emerged from seed banks, 5 occurred in restored < 5 year, 4 in restored > 5 year, 3 in drained, and 2 in drained wetlands. Likewise, no perennial-native species were found in all treatments in the Prairie Coteau and only *Carex spp*., *Ranunculus cymbalaria*, and *Artemisia ludoviciana* were unique to reference wetlands (Figure 44). Six of the perennial-native species (out of 14) occurred in reference wetlands, 6 in restored > 5 year, 5 in nondrained, 4 in restored < 5 year, and 3 in drained (Figure 44).

Effects of Restoration on Mean C and FQI:

Seasonal Wetlands: Mean C and FQI in seasonal restored wetlands did not show an increase with increasing restoration age (Figure 45a-f). Thirty-eight percent, 39% and 20% of the restored wetlands in the Glaciated Plain, Missouri Coteau, and Prairie Coteau,

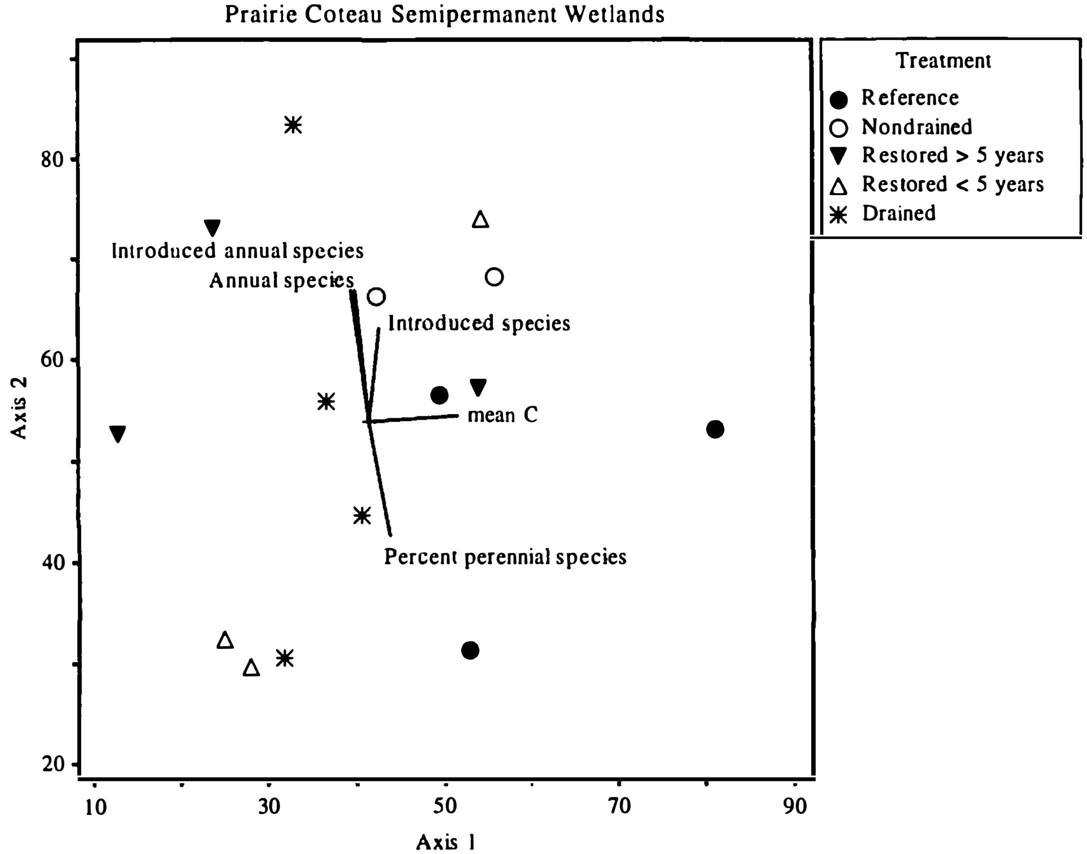

Figure 42. Ordination of plant species (presence or absence) that emerged from the seed banks of semipermanent reference (n = 3), nondrained (n = 3), restored > 5 year (n = 3), restored < 5 year (n = 3), and drained wetlands (n = 3). Seed bank samples were collected June-September 1997. Wetlands are located in the Prairie Coteau physiographic region of the Prairie Pothole Region of the United States. Symbols indicate location of each treatment within the species space. Angle and length of radiating lines (i.e., joint plot vectors) indicate the strength and direction of plant types within the species space.

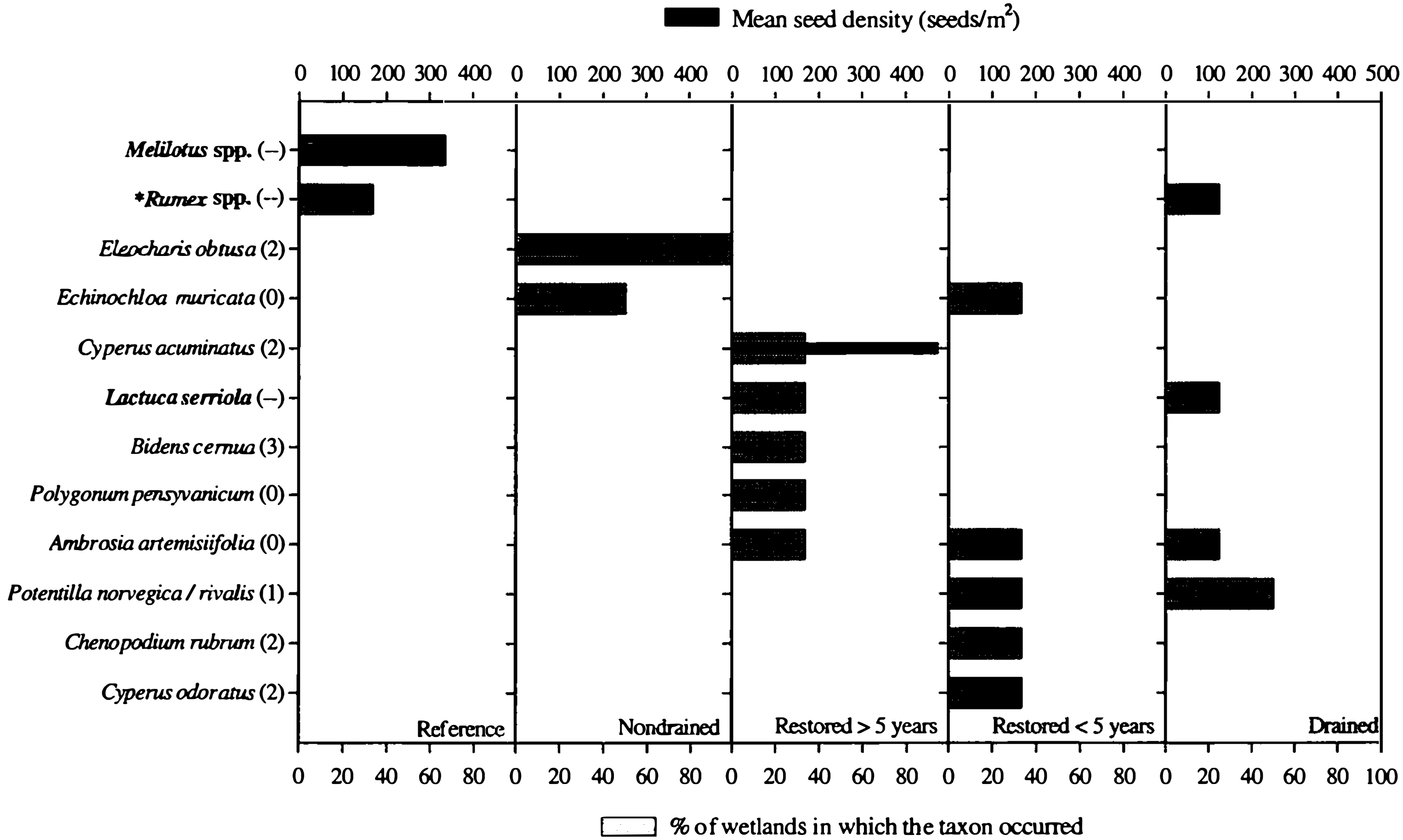

Figure 43. Seed density and % occurrence of native and introduced (bold type) annual plants that emerged from the seed banks of semipermanent reference (n = 3), nondrained (n = 3), restored > 5 year (n = 3), restored < 5 year (n = 3), and drained wetlands (n = 3). Seed bank samples were collected June-September 1997. Wetlands are located in the Prairie Coteau physiographic region of the Prairie Pothole Region of the United States. Number in parentheses next to each species is the coefficient of conservatism (C-values) assigned to that species. Introduced species are not assigned C-values (--). An * next to species names indicates it may include introduced, native, and perennial species.

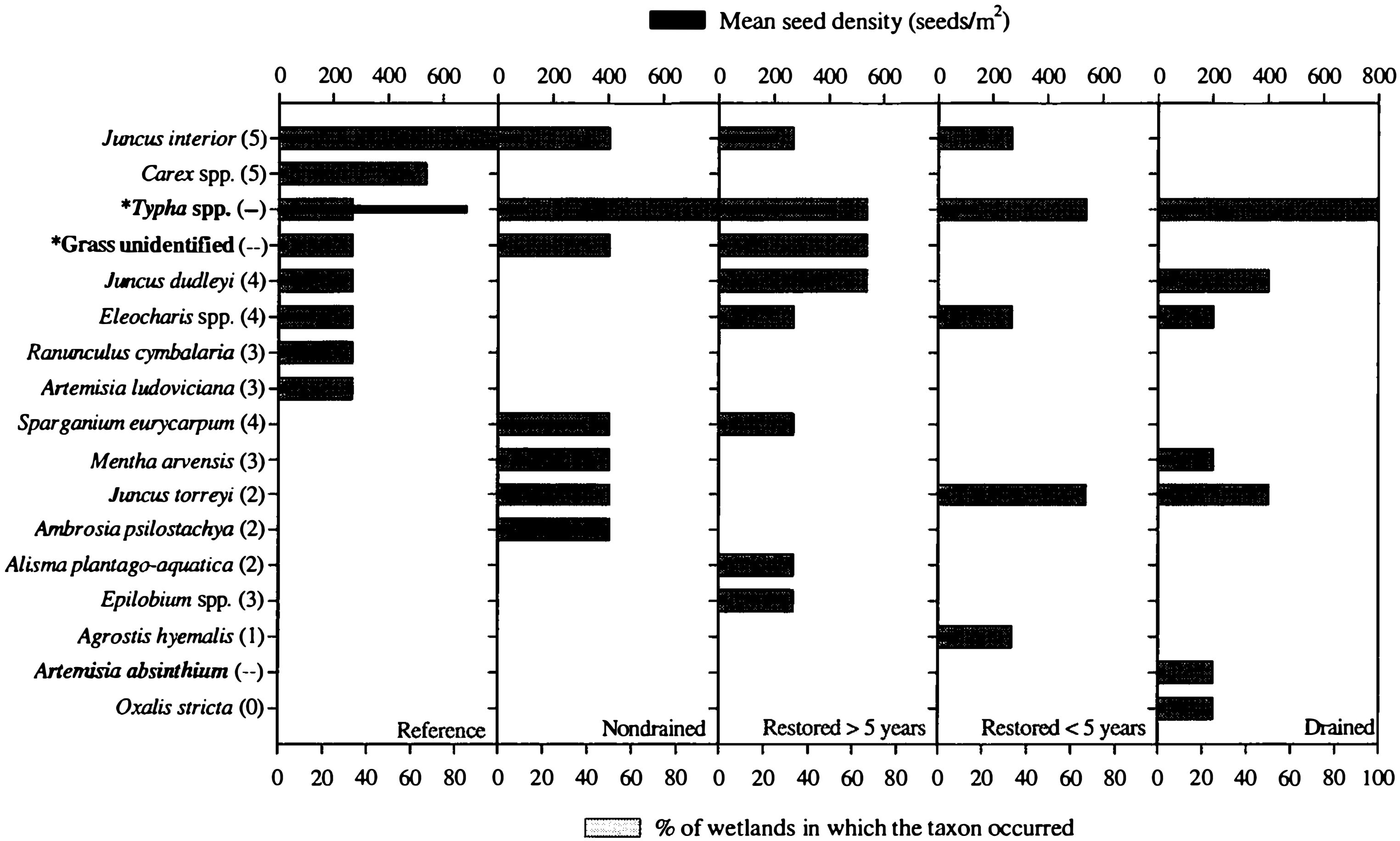

Figure 44. Seed density and % occurrence of native and introduced (bold type) perennial plants that emerged from the seed banks of semipermanent reference (n = 3), nondrained (n = 3), restored > 5 year (n = 3), restored < 5 year (n = 3), and drained wetlands (n = 3). Seed bank samples were collected June-September 1997. Wetlands are located in the Prairie Coteau physiographic region of the Prairie Pothole Region of the United States. Number in parentheses next to each species is the coefficient of conservatism (C-values) assigned to that species. Introduced species are not assigned C-values (--). An * next to species names indicates it may include introduced, native, and perennial species.

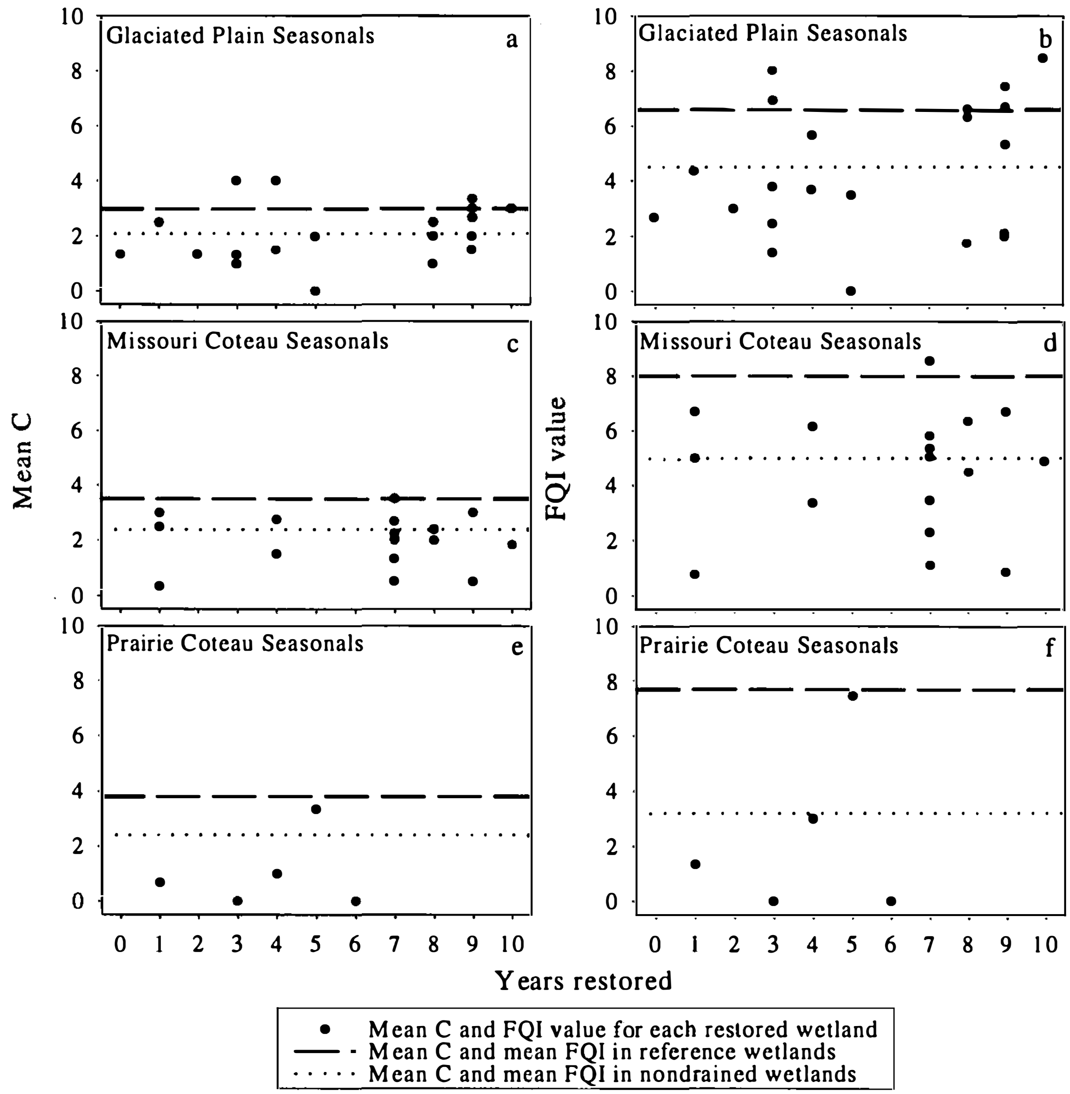

Figure 45a-f. Relationship between restoration age and mean coefficient of conservatism (C) and floristic quality index (FQI) for plants that emerged from the seed banks of restored seasonal wetlands. Seed bank samples were collected June-September 1997. Wetlands are located in the Glaciated Plain (a-b), Missouri Coteau (c-d), and Prairie Coteau (e-f) physiographic regions of the Prairie Pothole Region of the United States. Horizontal lines are the mean C and FQI for reference and nondrained treatments.

respectively, had mean C-values ≥ to mean C of nondrained treatments (Figure 45a, c, e). Similarly, 43%, 50%, and 20% of the restored wetlands had FQI-values ≥ mean FQI of nondrained treatments (Figure 45b, d, f).

Semipermanent Wetlands: Mean C and FQI in restored semipermanent wetlands in the Glaciated Plain and Missouri Coteau did not show an increase with increasing restoration age (Figure 46a-d). There was some indication that mean C and FQI in restored Prairie Coteau wetlands increased with restoration age, however, the small sample size limits the validity of this relationship (Figure 46e-f). Forty-three percent, 42% and 20% of the restored wetlands in the Glaciated Plain, Missouri Coteau, and Prairie Coteau, respectively, had C-values ≥ to mean C of nondrained treatments (Figure 46a, c, e). Similarly, 43%, 50%, and 50% of the restored wetlands had FQI-values ≥ mean FQI of nondrained treatments (Figure 46 b, d, f).

Effects of Sediment Load on Seedling Emergence

Covering wetland soils with a sediment depth of 0.5 cm, 1 cm, and 2 cm significantly reduced emergence of seedlings from soil seed banks (Table 19). A total of 784 seedlings emerged from the 0-cm treatment, 65 from the 0.5-cm treatment, 19 from the 1-cm treatment, and 11 from the 2-cm treatment (Table 19). Of the 40 plant species that emerged from the 0-cm treatment, 10, 7, and 4 emerged from the 0.5, 1, and 2-cm treatments, respectively (Table 19). The 7 species that emerged from the 1-cm treatment included: *Eleocharis* spp., *Juncus interior*, *Juncus dudleyi*, *Alisma plantago-aquatica*,

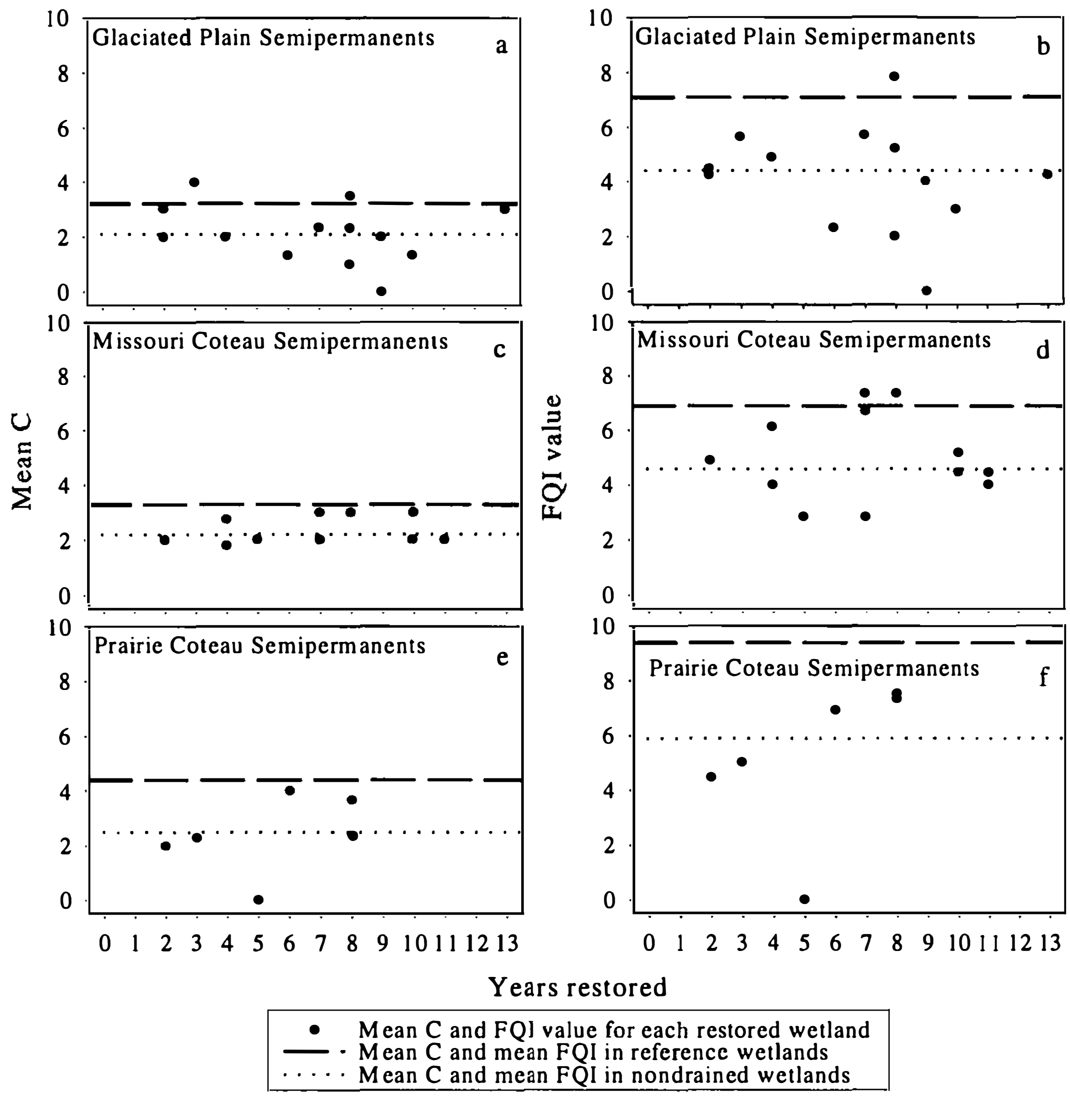

Figure 46a-f. Relationship between restoration age and mean coefficient of conservatism (C) and floristic quality index (FQI) for plants that emerged from the seed banks of restored semipermanent wetlands. Seed bank samples were collected June-September 1997. Wetlands are located in the Glaciated Plain (a-b), Missouri Coteau (c-d), and Prairie Coteau (e-f) physiographic regions of the Prairie Pothole Region of the United States. Horizontal lines are the mean C and FQI for reference and nondrained treatments.

Table 19. Total and mean number of seedlings that emerged from wetland seed banks in each sediment load treatment (n = number of wetlands out of 36 in which species occurred).

	Sediment depth (cm)								
	0		0.5		1		2		
Species	Mean	Total	Mean	Total	Mean	Total	Mean	Total	n
Eleocharis spp.	3.6	76	1.2	26	0.1	2	0.0	0	21
Typha spp.	7.1	150	0.0	0	0.0	0	0.0	0	21
Juncus interior	7.5	143	0.1	2	0.1	2	0.1	1	19
Juncus dudleyi	5.1	76	1.1	17	0.1	2	0.1	1	15
Rumex spp.	1.6	19	0.0	0	0.0	0	0.0	0	12
Alisma plantago-aquatica	1.4	13	1.0	9	0.3	3	0.0	0	9
Carex spp.	1.3	12	0.0	0	0.0	0	0.0	0	9
Eleocharis acicularis	0.9	8	0.0	0	0.0	0	0.0	0	9
Eleocharis obtusa	9.2	55	0.2	1	0.0	0	0.0	0	6
Potentilla spp.	6.0	36	0.0	0	0.0	0	0.0	0	6
Scirpus acutus/validus	12.0	72	0.8	5	1.0	6	1.3	8	6
Sagittaria cuneata	1.4	7	0.2	1	0.6	3	0.0	0	5
Ambrosia artemisiifolia	2.8	11	0.0	0	0.0	0	0.0	0	4
Cyperus acuminatus	1.5	6	0.0	0	0.0	0	0.0	0	4
Melilotus spp.	1.2	5	0.0	0	0.0	0	0.0	0	4
Sparganium eurycarpum	2.5	10	0.0	0	0.2	1	0.2	1	4
Ammannia robusta	1.3	4	0.0	0	0.0	0	0.0	0	3
Artemisia ludoviciana	1.3	4	0.0	0	0.0	0	0.0	0	3
Ranunculus cymbalaria	4.7	14	0.0	0	0.0	0	0.0	0	3
Beckmannia syzigachne	3.0	6	0.0	0	0.0	0	0.0	0	2
Epilobium spp.	1.0	2	0.0	0	0.0	0	0.0	0	2
Juncus torreyi	2.0	4	0.0	0	0.0	0	0.0	0	2
Mentha arvensis	2.0	4	0.0	0	0.0	0	0.0	0	2
Oxalis stricta	1.5	3	0.0	0	0.0	0	0.0	0	2
Ranunculus sceleratus	2.5	5	0.0	0	0.0	0	0.0	0	2
Scirpus pungens	1.0	2	0.5	1	0.0	0	0.0	0	2
Agrostis hyemalis	1.0	1	0.0	0	0.0	0	0.0	0	1
Alopecurus aequalis	5.0	5	2.0	2	0.0	0	0.0	0	1
Bacopa rotundifolia	2.0	2	1.0	1	0.0	0	0.0	0	1
Chenopodium rubrum	1.0	1	0.0	0	0.0	0	0.0	0	1
Cirsium arvense	1.0	1	0.0	0	0.0	0	0.0	0	1
Cyperus odoratus	15.0	15	0.0	0	0.0	0	0.0	0	1
Dichanthelium oligosanthes	3.0	3	0.0	0	0.0	0	0.0	0	1
Echinochloa muricata	1.0	1	0.0	0	0.0	0	0.0	0	1
Hordeum jubatum	2.0	2	0.0	0	0.0	0	0.0	0	1
Lactuca serriola	1.0	1	0.0	0	0.0	0	0.0	0	1
Medicago spp.	1.0	1	0.0	0	0.0	0	0.0	0	1
Panicum capillare	1.0	1	0.0	0	0.0	0	0.0	0	1
Polygonum pensylvanicum	2.0	2	0.0	0	0.0	0	0.0	0	1
Rorippa palustris	1.0	1	0.0	0	0.0	0	0.0	0	1
Total emergence	21.8	784	1.9	65	0.5	19	0.3	11	
Number of species	5.0	40	0.8	10	0.3	7	0.2	4	

Scirpus acutus / validus, *Sagittaria cuneata*, and *Sparganium eurycarpum*. All of these 7 taxa showed some decreased emergence when covered with 0.5 cm of sediment (Figure 47). The 2-cm treatment stopped seedling emergence of *Sagittaria cuneata* and *Alisma plantago-aquatica*; whereas, seedling emergence of *Scirpus acutus / validus* and *Sparganium eurycarpum* was not completely eliminated by the 2-cm depth treatment (Figure 47). *Alisma plantago-aquatica*, *Sagittaria cuneata*, *Scirpus acutus / validus*, and *Sparganium eurycarpum* showed more resilience to sediment depth than *Eleocharis spp*., *Juncus interior*, and *Juncus dudleyi* (Figure 47). Seedling emergence of *Eleocharis* spp., *Juncus dudleyi*, and *Juncus interior* was essentially eliminated by the 1-cm treatment.

DISCUSSION

My study showed that prior land-use has had a similar effect on nondrained, restored, and drained wetlands relative to reference wetlands, across all regions, and for both wetland classes. Trends showed that reference wetlands had greater perennial-native seed density, taxon richness, mean-C and FQI values, and fewer annual species than nondrained, restored, and drained wetlands. Conversely, most comparisons of perennial-native response variables were found to be similar among nondrained, restored, and drained wetlands. This suggests that overall agricultural land-use impacts (e.g., cultivation, sedimentation) rather than drainage history alone, have had a major impact on prairie wetland seed banks.

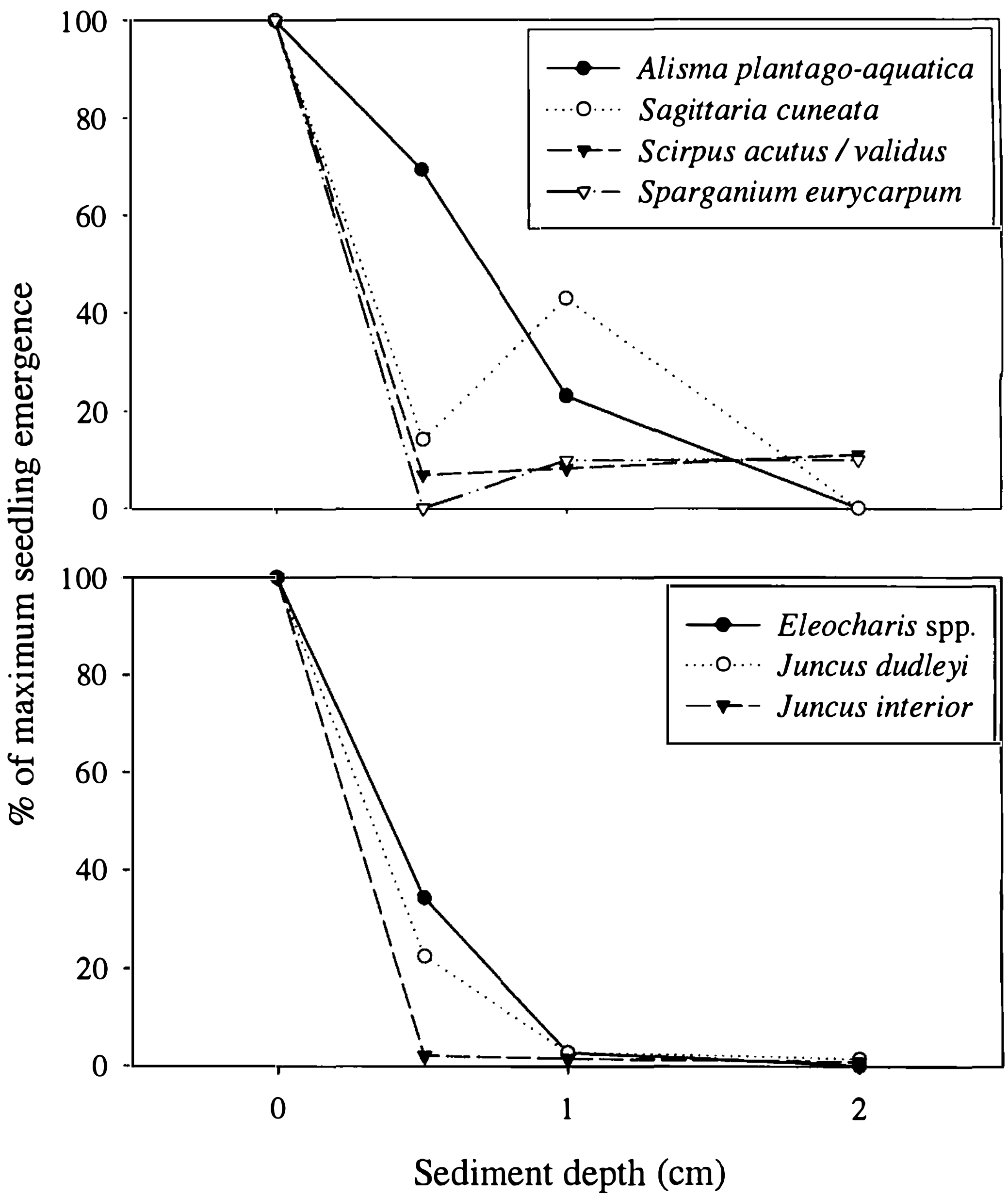

Figure 47. Effect of sediment depth on % emergence by plant species. Percent emergence of seedlings in the 0.5, 1, and 2-cm treatments is relative to maximum emergence of seedlings in the 0-cm treatment.

Both seasonal and semipermanent wetlands showed similar trends with respect to perennial-native response variable differences between reference wetland seed banks and other treatments. However, differences were more pronounced and statistically significant in seasonal wetlands (Table 14-15) than in semipermanent wetlands (Table 16-17). Seasonal wetlands seed banks thus appear to have been impacted more by prior land-use than semipermanent wetlands. Because seasonal wetlands go dry more frequently than semipermanent wetlands, prior agricultural activities (e.g., cultivation) in seasonal wetlands basins have been more frequent and intense. Also, seasonal wetlands are often drained more completely than semipermanent wetlands. Studies have shown that duration of drainage and cultivation reduce species richness and abundance of seed banks (Erlandson 1987, Wienhold and van der Valk 1989).

Similar to my results, Galatowitsch and van der Valk (1996) found higher densities of mudflat annuals in the seed banks of restored wetlands than in natural wetlands. Mudflat annuals that were found in nearly all of my treatments at some point, include: *Cyperus acuminatus*, *Echinochloa muricata*, *Polygonum pensylvanicum / lapathifolium*, *Rorippa palustris*, *Ammannia robusta*, and *Eleocharis obtusa*. Perennial species that were well represented in most of my treatments included: *Juncus interior*, *Juncus dudleyi*, *Juncus torreyi*, *Eleocharis* spp. and *Typha* spp. Galatowitsch and van der Valk (1996) also found *Juncus dudleyi* and *Juncus torreyi* to be represented in their restored wetland seed banks.

Research has suggested that with the exception of some annuals, seed banks in restored wetlands will contribute little to revegetation (Galatowitsch and van der Valk 1994, 1996). If restored and nondrained wetlands are to develop communities similar to reference wetlands, species absent from the seed banks will have to be dispersed into wetlands from surrounding sources (Galatowitsch and van der Valk 1996). The dispersal process is believed to be dependent on time and availability of propagules in the landscape. In the Missouri and Prairie Coteau regions where there are high densities of wetlands in the landscape, the recovery process would be expected to occur more rapidly than in the Glaciated Plain where wetland drainage has been more severe. My results showed the percent of restored wetlands that attained FQI values similar to nondrained or reference wetlands to vary little among regions (Figure 45-46). Thus, even in areas with high wetland densities, seed banks in restored wetlands are still highly variable. This suggests that establishment factors may be more important than time and dispersal limitations.

A great many factors have contributed to loss or maintenance of perennial-native seeds in nondrained, restored, and drained wetlands. Kantrud and Newton (1996) compared composition of plants in wetlands in grassland watersheds to cropland watersheds and found more perennial-native species were associated with wetlands in grassland watersheds. This implies that agricultural land-use of wetlands and their catchments has altered wetland plant communities. Wienhold and van der Valk (1989) found that prolonged drainage and possibly cultivation reduced seed bank species richness and abundance. Mudflat annuals were also found to have the greatest seed longevities (Wienhold and van der Valk 1989). Freeland et al. (1999), showed that prior land-use resulted in elevated P and N, and altered soil texture of wet-meadow zones. Consequently, agricultural land-use alters soil structure, chemistry, and seed bank composition which may prevent perennial-natives from becoming established. For example, these new altered conditions may be preferred by more invasive species (e.g., *Phalaris arundinacea*) that preempt establishment of more preferred species (e.g., *Carex* spp.) (Galatowitsch and van der Valk 1994, 1996; Franke 1997, Galatowitsch et al. 1999). Moreover, most species that emerged from seed banks in my study become established during natural wetland drawdowns on exposed mudflats. Perennial species that need drawdown conditions to become established, may be out-competed by the plethora of annuals that occur in the seed banks of nondrained and restored wetlands.

Another impact is the potential for eroded agricultural soils to cover seed banks, thereby making them unavailable for revegetation. My work clearly showed the potential impact of sedimentation on seed banks. All but a few species were completely eliminated by a sediment depth of 0.5 cm (Table 19). I found 7 species that were capable of emerging from the 1-cm depth treatment (Figure 47). These species varied in their ability to emerge from sediment depths, with *Scirpus acutus / validus*, *Sparganium eurycarpum*, *Sagittaria cuneata*, and *Alisma plantago-aquatica* having more resilience to sediment loads than *Eleocharis* spp., *Juncus dudleyi*, and *Juncus interior*.

Studies have indicated that seeds with the largest mass often are least effected by burial (Jurik et al 1994, Wang et al. 1994, Dittmar and Neely 1999). I did not determine seed mass during my study, but relative seed lengths (as a proxy of mass) from species descriptions (Larson 1993) did suggest some relationship between seed size and resilience to burial. *Juncus torreyi* and *Juncus interior* both have smaller seeds (0.3-0.4 mm) than *Eleocharis* sp. (1.4-1.7 mm -- based on *E. macrostachya*) which was more resilient to burial (Figure 47). All 3 of these species were less resilient to burial than larger-seeded species (*Scirpus acutus / validus* = 1.5-2.2 mm, *Alisma plantago-aquatica* = 2-2.5 mm, *Sagittaria cuneata* = 2-3 mm, *Sparganium eurycarpum* 6-8 mm). Three species showed some increase in emergence with moderate burial (*Sparganium eurycarpum*, *Scirpus acutus / validus*, and *Sagittaria cuneata*). Jurik et. al (1994) also found *Sagittaria* spp. emergence to increase with moderate burial (0.5 cm).

Of the 7 species resilient to burial, smaller-seeded species occurred more often in non-reference (e.g., treatments with farmed histories) wetlands than larger-seeded species; *Juncus interior* occurred in seed banks of 43 non-reference wetlands, *Juncus dudleyi* in 32, *Eleocharis* spp. in 30, *Alisma plantago-aquatica* in 17, *Scirpus acutus / validus* in 9, *Sparganium eurycarpum* in 5, and *Sagittaria cuneata* was found only in reference wetlands. In contrast to resilience of plants to sediment burial, smaller-seeded species were able to persist or recolonize agricultural wetlands better than larger-seeded species. It is likely that smaller-seeded species are more easily dispersed than larger-seeded species into agricultural wetlands by wind, water, and animals. Smaller-seeded species also tend to produce more seeds than larger-seeded species which increases their availability in the landscape for dispersal into wetlands. Coefficient of conservatism (C-values) was highest for *Sagittaria cuneata* (6), followed by *Juncus interior* (5), *Juncus dudleyi* (4), *Eleocharis* spp. (4), *Sparganium eurycarpum* (4), *Scirpus acutus / validus* (3), *Alisma plantago- aquatica* (2). With the exception of *Sagittaria cuneata*, smaller-seeded species that were more frequent in non-reference wetlands had the higher C-values. Thus, some species that are more conservative and produce many small seeds may be able to recolonize disturbed sites better than less conservative species that produce fewer and larger seeds.

Dittmar and Neely (1999) showed that seed mass was positively correlated with emergence of seedlings at moderate sediment loads (0.5 cm), whereas at control (0 cm) levels and high sediment loads (1 cm) seed mass was not related to seedling emergence. My results showed similar trends (Figure 47). Consequently, at higher sediment loads even species with larger seeds have no advantage over small-seeded species. But following sedimentation events or even cultivation events (i.e., disturbance), smaller seeded species are at a competitive advantage because of greater seed production and availability in the landscape. This is especially true for annual species that can quickly produce many seeds that quickly ripen, whereas, most perennial-natives take longer to produce seeds and often produce fewer seeds. Perennial-natives that have life-histories more similar to annual species would be expected to recolonize disturbed sites more frequently than long-lived species that produce fewer seeds. For example, *Juncus interior* and *Juncus dudleyi* appear to have those traits (i.e., producing many small seeds that quickly ripen) and were frequently found in non-reference wetlands.

SUMMARY AND MANAGEMENT IMPLICATIONS

Many studies examining areal vegetation of restored wetlands have found that certain groups of species do not naturally revegetate restored prairie potholes (Delphey 1991, Galatowitsch and van der Valk 1994, 1996). Most often, perennial species associated with low-prairie and wet-meadow zones in natural wetlands were absent from restored wetlands. These studies generally showed that annual species (especially mudflat annuals) quickly repopulated and dominated restored wetlands. These studies are in agreement with trends observed in my seed bank results. My research showed that seed banks of farmed wetlands have been converted from a predominantly perennial-native community (as in reference wetlands) to a predominantly annual-native/introduced community (as in nondrained, restored, and drained wetlands). The establishment and recovery of perennial-native species in restored wetlands did not show a relationship with restoration age. This trend was consistent across regions that varied in wetland densities, and presumably, seeds that were available for dispersal into restored wetlands, suggesting that establishment factors may be more important than time and dispersal limitations. Cultivation and sedimentation associated with farmed wetlands have altered soil texture, chemistry, and seed bank composition facilitating establishment of annual species. Propagules of perennial-native species that are dispersed to farmed wetlands may not become established because of altered soil conditions or competition with annuals and other invasive species. Examination of life history strategies within the context of my sediment load experiments indicated that perennial-native species with life-history strategies similar to annual plants may be better adapted to recolonization of agricultural wetlands. Whereas, longer-lived species that produce fewer larger seeds, or produce few seeds and are established through vegetative processes, are less likely to establish themselves in agricultural wetlands.

If plant composition found in natural wetlands is desired in restored or nondrained wetlands, then seeding or active plantings will be necessary. Some research on seed germination requirements has been conducted, including the influence of seeding date and water level fluctuations on the establishment of *Carex* spp. (Budelsky and Galatowitsch 1999, Yetka and Galatowitsch 1999, van der Valk et al. 1999). I also found 1 study that examined a combination of seeding-mixtures and disturbance treatments to restore temporary wetlands colonized by *Phalaris arundinacea*, an extremely invasive species (Franke 1997). These studies suggest that methods employed to revegetate restored wetlands (e.g., by donor seed banks or rhizome plantings) vary by species. Further, technology will need to be developed to remove persistent perennial species (e.g., *Phalaris arundinacea*). Consequently, much more research is needed to identify optimal strategies to restore vegetation of nondrained and restored wetlands back to reference wetland conditions.

CHAPTER 5

GENERAL SUMMARY AND CONCLUSIONS

The main objectives of my research were to evaluate invertebrate egg and seed bank composition among reference, nondrained, restored, and drained wetlands and to evaluate the potential effect of sedimentation on recolonization of hydrophytes and aquatic invertebrates in wetlands. Based on accretion rates in cultivated wetlands, 50% of the estimated wetland pool volume (203 hectare-meters) from 134 wetlands would be lost over the next 200 years. In contrast, only 20% of the estimated wetland pool volume would be lost over that same time based on accretion rates from reference wetlands. Presumably, the loss of water storage capacity in wetlands from accelerated sedimentation would substantially increase the risk of flooding and associated economic loss at a regional scale. Studies evaluating the effects of wetland drainage and land-use on increased flooding (Brun et al. 1981, Miller and Nudds 1996) have not considered the subtle but significant loss in water storage capacity of wetlands from accelerated sedimentation.

Invertebrate egg bank hatching success in seasonal wetlands in all regions was lower in drained wetlands than in other treatments. Drained and restored semipermanent wetlands in the Glaciated Plain and Missouri Coteau also had lower hatching success than reference and nondrained wetlands. Of the few significant differences in taxon richness and invertebrate abundance detected, most occurred among treatments in the Glaciated Plain. Within 5 years after restoration, most restored seasonal wetlands contained viable invertebrate egg banks, but I was unable to detect a significant increase in taxon richness and invertebrate abundance with restoration age. Relative to Glaciated Plain wetlands, more seasonal wetlands in the Coteau regions attained taxon richness values similar to reference and nondrained wetlands. Overall trends suggest that agricultural impacts on invertebrate egg bank have been more severe in the Glaciated Plain than in the Coteau regions and that active inoculation of invertebrate egg banks may be necessary for rapid recovery of restored wetlands. Examination of the effect of sediment load showed that sediment depths as low as 0.5 cm effectively halted 84% of the invertebrate emergence from invertebrate egg banks. My results demonstrate the potential impact of sediment load on invertebrate emergence and suggests that future studies are needed to evaluate the impact of agricultural erosion and accelerated sedimentation on invertebrate productivity in prairie wetlands.

My evaluation of seed banks demonstrated that reference wetlands had greater perennial-native seed density, taxon richness, mean-C and FQI values, and fewer annual species than nondrained, restored, and drained wetlands. In contrast, most comparisons of perennial-native response variables were found to be similar among nondrained, restored, and drained wetlands. These trends were consistent across regions, but differences between reference wetlands and other treatments were more pronounced in seasonal than in semipermanent wetlands. Hence, seasonal wetland seed banks have likely been impacted more by prior land-use than semipermanent wetlands. Floristic quality in restored wetlands did not show a relationship with restoration age. This trend was consistent across regions that had different wetland densities, and presumably, seeds available for dispersal into restored wetlands would correlate positively with wetland density. Thus, establishment factors may be more important than time and dispersal limitations.

Overall, my research showed that seed banks of farmed wetlands have been converted from a predominantly perennial-native community (as in reference wetlands) to a predominantly annual-native/introduced community (as in nondrained, restored, and drained wetlands). Cultivation and sedimentation associated with farmed wetlands have altered soil texture, chemistry, and seed bank composition which has in turn facilitated establishment of annual species. Propagules of perennial-native species that are dispersed to farmed wetlands may not become established because of altered soil conditions or competition with annuals and invasive species. Examination of the effects of sediment depth on emergence of seedlings indicated that all but a few species were completely eliminated by a sediment depth of 0.5 cm. I found 7 species that were capable of emerging from the 1-cm depth treatment. These species varied in their ability to emerge from sediment depths, with larger-seeded species showing the most resilience to burial.

Prior studies evaluating recovery of restored wetlands have typically compared restored wetlands to high quality reference wetlands (i.e., native prairie wetlands). Such comparisons generally indicated that plant communities in restored wetlands were less diverse than reference wetlands (Galatowistch and van der Valk 1994, 1996). My seed banks results were in agreement with those studies. However, I also compared restored wetlands to nondrained wetlands that had a farmed land-use history similar to restored wetlands, but differed only in drainage history. Results indicated that most restored wetlands had seed bank composition similar to nondrained wetlands, the most common type of wetland in the PPR. Therefore, when comparing restored wetlands to wetlands that have been farmed, but never drained, most restorations would be considered successful. If plant composition found in natural wetlands is desired in restored or nondrained wetlands, than seeding or active plantings will be necessary. However, much more research is needed to identify optimal strategies to restore vegetation of nondrained and restored wetlands back to reference wetland conditions.

In conclusion, I demonstrated that the recovery of invertebrate egg and seed banks in nondrained and restored wetlands is highly variable. There is much uncertainty as to whether natural processes would ever result in full recovery to nonfarmed conditions. Apparently, land-use effects such as cultivation, drainage, and focusing of sediments and agrochemicals into wetlands have impeded natural recovery processes. If invertebrate and plant communities are to attain reference wetland conditions, then more proactive and intensive restoration methods will need to be employed (e.g., donor seed banks and active planting). However, research has not identified optimal methods and strategies to restore plant or invertebrate communities. Intensive efforts to restore wetland communities probably could not be justified for wetlands that are in short-term contracts such as the Conservation Reserve Program. However, there are many wetlands with farmed histories in restored grasslands under federal, state, and private ownership by conservation agencies that would benefit from intensive methods to improve overall wetland quality. Such sites would provide excellent outdoor laboratories to test new methods for restoring wetland communities.

Successional change in plant and invertebrate communities in response to natural disturbances (i.e., wet/dry cycles) is largely dependent on soil-born propagules. My research showed that sedimentation will greatly impede emergence of plants and invertebrates, and presumably alter natural successional changes that occur during wet/dry cycles. Moreover, accelerated sedimentation of prairie wetlands from agricultural practices will ultimately fill wetlands and hence shorten their life span. In addition to identifying strategies to restore wetland communities, much more effort should be directed toward conserving wetlands in agricultural landscapes. This is especially important for conservation of nondrained wetlands in agricultural fields that are filling with anthropogenic sediments. Nondrained wetlands are the most common wetland type remaining in the PPR, and as a population, they are the most important group of wetlands providing wetland functions of societal interest. These nondrained wetlands need to be protected from accelerated sedimentation and other non-point source pollutants. A variety of agricultural practices have been developed that reduce soil erosion and maintain soil tilth (e.g., Bills and Heimlich 1984, Isenee and Sasdeghi 1993, Fawcett et al. 1994). These practices will likely reduce sedimentation of wetlands, however they generally have been only evaluated from an agricultural perspective. Thus, future research is needed to integrate both agricultural and wetland interests, to evaluate and implement management strategies that sustain both agriculture and wetlands.

LITERATURE CITED

Adomaitis, V. A., H. A. Kantrud, and J. A. Shoesmith. 1967. Some chemical characteristics of aeolian deposits of snow-soil on prairie wetlands. Proceedings of the North Dakota Academy of Science 21:65-69.

Baskin, C. C., and J. M. Baskin. 1998. Seeds: ecology, biogeography, and evolution of dormancy and germination. Academic Press, San Diego, California, USA.

Beule, J. D. 1979. Control and management of cattails in southeastern Wisconsin wetlands. Department of Natural Resources, Technical Report Number 112, Madison, Wisconsin, USA.

Bills, N. L., and R. E. Heimlich. 1984. Assessing erosion on U.S. cropland: land management and physical features. Natural Resources Economics Division, Economic Research Service, U.S. Department of Agriculture. Agricultural Economic Report No. 513.

Brady, N. C. 1984. The nature and properties of soils, 9th edition. Macmillan, New York, New York.

Brown, S. C., K. Smith, and D. Batzer. 1997. Macroinvertebrate responses to wetland restoration in northern New York. Environmental Entomology 26:1016-1024.

Brun, L. J., J. L. Richardson, J. W. Enz, and J. K. Larsen. 1981. Stream flow changes in the southern Red River Valley of North Dakota. North Dakota Farm Research Bulletin 38:11-14.

Bryson, A., and T. J. Murray. 1977. Climates of hunger. University of Wisconsin Press, Madison, Wisconsin, USA.

Budelsky, R. A., and S. M. Galatowitsch. 1999. Effects of moisture, temperature, and time on seed germination of five wetland carices: implications for restoration. Restoration Ecology 7:86-97.

Burras, C. L., and W. H. Scholtes. 1987. Basin properties and postglacial erosion rates of minor morianes in Iowa. Soil Science Society of America Journal 51:1541-1547.

Cowardin, L. M., V. Carter, F. C. Golet, and E. T. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United States. FWS/OBS-79/31.

_____, D. S. Gilmer, and L. M. Mechlin. 1981. Characteristics of central North Dakota wetlands determined from sample aerial photographs and ground study. Wildlife Society Bulletin 9:280-88.

Cvancara, A. M., L. Clayton, W. B. Bickley, Jr., A. F. Jacob, C. T. Shay, L. D. Delorme, and G. E. Lammers. 1971. Paleolimnology of late quaternary deposits: Seibold site, North Dakota. Science 171:172-174.

Dahl, T. E. 1990. Wetland losses in the United States 1780's to 1980's. U.S. Department of Interior, Fish and Wildlife Service., Washington, D.C.

_____, and C. E. Johnson. 1991. Status and trends of wetlands in the coterminous United States, mid-1970's to mid-1980's. U.S. Department of Interior, Fish and Wildlife Service, Washington, D.C.

DeLaune, R. D., J. H. Whitcomb, W. H. Patrick, Jr., J. H. Pardue, and S. R. Pezeshki. 1989. Accretion and canal impacts in a rapidly subsiding wetland: I. ^{137}Cs and ^{210}Pb techniques. Estuaries 12:247-259.

Delphey, P. J. 1991. A comparison of the bird and aquatic macroinvertebrate communities between restored and natural Iowa prairie wetlands. Thesis, Iowa State University, Ames, Iowa, USA.

_____, and J. J. Dinsmore. 1993. Breeding bird communities of recently restored and natural prairie potholes. Wetlands 13:200-206.

Dieter, C. E. 1991. Water turbidity in tilled and untilled prairie wetlands. Journal of Freshwater Ecology. 6:185-189.

Dittmar, L. A., and R. K. Neely. 1999. Wetland seed bank response to sedimentation varying in loading and texture. Wetlands 19:341-351.

Dornfeld, R., and R. Warhurst. 1988. A cooperative program for restoring drained wetlands in Minnesota. North American Wildlife and Natural Resource Conference 53:454-462.

Dryer, P., L. Brooks, and N. Dietz. 1996. 1995 report: vegetation and sedimentation monitoring of undisturbed, cropland, and waterbank wetlands in Wells County, North Dakota. Bluestem Incorporated, Bismark, North Dakota, USA.

Erlandson, C. S. 1987. The potential role of seed banks in the restoration of drained prairie wetlands. Thesis, Iowa State University, Ames, Iowa, USA.

Euliss, N. H. Jr., and D. M. Mushet. 1996. Water-level fluctuation in wetlands as a function of landscape condition in the prairie pothole region. Wetlands 16:587-593.

_____, and _____. 1999. Influence of agriculture on aquatic invertebrate communities of temporary wetlands in the prairie pothole region of North Dakota, USA. Wetlands 19:578-583.

_____, and _____. 2001 In Press. Use of macroinvertebrates to identify cultivated wetlands in the prairie pothole region. Wetlands 21:

_____, D. A. Wrubleski, and D. M. Mushet. 1999. Wetlands in the prairie pothole region: invertebrate species composition, ecology, and management. In Invertebrates in Freshwater Wetlands of North America: Ecology and Management, ed. D. P. Batzer, R. B. Rader, and S. A. Wissinger, 471-514. John Wiley & Sons, Inc.

Fawcett, R. S., B. R. Christensen, and D. P. Tierney. 1994. The impact of conservation tillage on pesticide runoff into surface water: a review and analysis. Journal of Soil and Water Conservation 49:126-135.

Franke, D. C. 1997. Enhancement of floral species richness in glaciated prairie temporary wetlands. Thesis, South Dakota State University, Brookings, South Dakota, USA.

Freeland, J. A., J. L. Richardson, and L. A. Foss. 1999. Soil indicators of agricultural impacts on northern prairie wetlands: Cottonwood Lake Research Area, North Dakota, USA. Wetlands 19:56-64.

Galatowitsch, S. M., N. O. Anderson, P. D. Ascher. 1999. Invasiveness in wetland plants in temperate North America. Wetlands 19:733-755.

_____, and A. G. van der Valk. 1994. Restoring prairie wetlands: An ecological approach. Iowa State University Press, Ames, Iowa, USA.

_____, and _____. 1996. The vegetation of restored and natural prairie wetlands. Ecological Applications 6:102-112.

Galinato, M. I., and A. G. van der Valk. 1986. Seed germination traits of annuals and emergents recruited during drawdowns in the Delta Marsh, Manitoba, Canada. Aquatic Botany 26: 89-102.

Gleason, R. A. 1996. Influence of agricultural practices on sedimentation rates, aquatic invertebrates, and bird-use in prairie wetlands. Thesis, Humboldt State University, Arcata, California, USA.

_____, and N. H. Euliss, Jr. 1996. Impact of agricultural land-use on prairie wetland ecosystems: Experimental design and overview. Proceedings of the North Dakota Academy of Science 50:103-107.

_____, and _____. 1997. Sedimentation of prairie pothole wetlands: the need for integrated research by agricultural and wildlife interests. In Water for Agriculture and Wildlife and the Environment Win-Win Opportunities, eds. J. Schaack and S. S. Anderson, 107-114. Proceedings of the U.S. Committee of Irrigation and Drainage.

_____, and _____. 1998. Sedimentation of prairie wetlands. Great Plains Research 8:97-112.

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

Grue, C. E., L. R. DeWeese, P. Mineau, G. A. Swanson, J. R. Foster, P. M. Arnold, J. N. Huckins, P. J. Sheehan, W. K. Marshall, and A. P. Ludden. 1986. Potential impacts of agricultural chemicals on waterfowl and other wildlife inhabiting prairie wetlands: an evaluation of research needs and approaches. Transactions of the North American Wildlife and Natural Resources Conference 51:357-383.

Hartleb, C. F., J. D. Madsen, and C. W. Boylen. 1993. Environmental factors affecting seed germination in *Myriophyllum spicatum* L. Aquatic Botany 45:15-25.

Hemesath, L. M. 1991. Species richness and nest productivity of marsh birds on restored prairie potholes in northern Iowa. Thesis, Iowa State University, Ames, Iowa, USA.

Holmes, C. W. 1998. Short-lived isotopic chronometers: a means of measuring decadal sedimentary dynamics. U.S. Geological Survey, Fact Sheet FS-073-98.

Hubbard, D. E. 1988. Glaciated prairie wetland functions and values: a synthesis of the literature. Washington, D.C.: U.S. Fish and Wildlife Service Biological Report 88(43).

_____, and R. L. Linder. 1986. Spring runoff retention in prairie pothole wetlands. Journal of Soil and Water Conservation 41:122-125.

Interagency committee on wetlands restoration and creation. 1992. A national program for wetlands restoration and creation. U.S. Government, Washington, D.C.

Isenee, A. R., and A. M. Sadeghi. 1993. Impact of tillage practice on runoff and pesticide transport. Journal of Soil and Water Conservation 48:523-527.

Jurik, T. W., S. C. Wang, and A. G. van der Valk. 1994. Effects of sediment load on seedling emergence from wetland seed banks. Wetlands 14:159-165.

Kantrud, H. K. 1986. Effects of vegetation manipulation on breeding waterfowl in prairie wetlands: a literature review. U.S Fish and Wildlife Service, Technical Report 3, Washington, D.C.

_____, G. L. Krapu, and G. A. Swanson. 1989. Prairie basin wetlands of the Dakotas: a community profile. U.S Fish and Wildlife Service Biological Report 85(7.28).

_____, and W. E. Newton. 1996. A test of vegetation-related indicators of wetland quality in the prairie pothole region. Journal of Aquatic Ecosystem Health 5:177-191.

Kern, J. S., and M . G. Johnson. 1993. Conservation tillage impacts on national soil and atmospheric levels. Soil Science Society of America Journal 57:200-210.

Krull, J. N. 1970. Aquatic plant-macroinvertebrate associations and waterfowl. Journal of Wildlife Management 34:707-718.

LaGrange, T. G., and J. J. Dinsmore. 1989. Plant and animal community responses to restored Iowa wetlands. Prairie Naturalist 21:39-48.

Laird, K. R., S. C. Fritz, K. A. Maasch, and B. F. Cumming. 1996. Greater drought intensity and frequency before AD 1200 in the northern great plains, USA. Nature 384:552-554.

Larson, G. E. 1993. Aquatic and wetland vascular plants of the northern Great Plains. General Technical Report RM-238. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Linz, G. M., R. A. Dolbeer, J. J. Hanzel, and L. E. Huffman. 1996. Controlling blackbird damage to sunflower and grain crops in the northern Great Plains. U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Agriculture Information Bulletin No. 679.

Ludden, A. P., D. L. Frink, and D. H. Johnson. 1983. Water storage capacity of natural wetland depressions in the Devils Lake Basin of North Dakota. Journal of Soil and Water Conservation 38:45-48.

Luo, Hong-Ren, L. M. Smith, B. L. Allen, and D. A. Haukos. 1997. Effects of sedimentation on playa wetland volume. Ecological Applications 7:247-252.

Malo, D. D. 1988. The Holocene sedimentation environment in a seasonal wetland in eastern North Dakota. Soil Survey Horizons 29:141-152.

Martin, D. B., and W. A. Hartman. 1987. The effect of cultivation on sediment composition and deposition in prairie pothole wetlands. Water, Air, and Soil Pollution. 34:45-53.

McCune, B., and M. J. Mefford. 1999. PC-ORD. Multivariate analysis of ecological data, version 4. MjM Software Design, Gleneden Beach, Oregon, USA.

Merritt, R. W., K. W. Cummins, and T. M. Burton. 1984. The role of aquatic insects in the processing and cycling of nutrients. Pg. 134-163 *In* Resh, V. H. and D. M. Rosenburg, ed. The Ecology of Aquatic Insects. Praeger, New York, New York, USA.

Miller, M. W., and T. D. Nudds. 1996. Prairie landscape change and flooding in the Mississippi River Valley. Conservation Biology 10:847-853

Milliken, G. A., and D. E. Johnson. 1984. Analysis of messy data, Volume 1: designed experiments. Van Nostrand Reinhold Company. New York, New York, USA. 473 pp.

Mutcher, C. K., C. E. Murphree, and K. C. McGregor. 1994. Laboratory and field plots for erosion research. In Soil Erosion Research, 2nd edition, ed. R. Lal, 11-37. Soil and Water Conservation Society and St. Lucie Press.

National Research Council. 1992. Restoration of Aquatic Ecosystems. National Academy Press, Washington, D.C., USA.

Neely, R. K., and J. L. Baker. 1989. Nitrogen and phosphorus dynamics and the fate of agricultural runoff. In Northern Prairie Wetlands, ed. A. G. van der Valk, 92-131. Iowa State University Press, Ames, Iowa, USA.

Northern Great Plains Floristic Quality Assessment Panel. 2001 In Press. Coefficients of conservatism for the vascular flora of North Dakota, South Dakota (excluding the Black Hills), and adjacent grasslands. U.S. Geological Survey Information and Technology Report XX.

Northern Prairie Wildlife Research Center (NPWRC). 1997. Study Plan 168.01: Evaluation of restored wetlands in the prairie pothole region of the United States. (On file, NPWRC, Jamestown, North Dakota, USA).

Novotny, V., and G. Gordon. 1989. Delivery of sediment and pollutants from nonpoint sources: a water quality perspective. Journal of Soil and Water Conservation 44:568-576.

Pennak, R. W. 1989. Fresh-water invertebrates of the United States. 3rd edition, John Wiley and Sons, New York, New York, USA.

Renard, K. G., G. R. Foster, G. A. Weesies, D. K. McCool, and D. C. Yoder, coordinators. 1997. Predicting soil erosion by water: a guide to conservation planning with the revised universal soil loss equation (RUSLE). U.S. Department of Agriculture, Agriculture Handbook No. 703.

Richardson, J. L., J. L. Arndt, and J. Freeland. 1994. Wetland soils of the prairie pothole region. Advances in Agronomy 52:121-171.

Ritchie, J. C., and J. R. McHenry. 1990. Application of radioactive fallout cesium-137 for measuring soil erosion and sediment accumulation rates and patterns: a review. Journal of Environmental Quality 19:215-233.

SAS Institute, Inc. 1989. SAS/STAT user's guide, version 6, fourth edition, volume 2. SAS Institute, Cary, North Carolina, USA.

_____. 1997. SAS/STAT software: changes and enhancements through release 6.12. SAS Institute., Cary, North Carolina, USA.

Sewell, R. W. 1989. Floral and faunal colonization of restored wetlands in west-central Minnesota and northeastern South Dakota. Thesis, South Dakota State University, Brookings, South Dakota, USA.

SigmaPlot. 2000. SigmaPlot 2000 user's guide, version 6. SPSS Science software products, Chicago, Illinois.

Steel, R. G. D., and J. H. Torrie. 1980. Principles and procedures of statistics: a biometrical approach. McGraw Hill, New York, New York, USA.

Stevens, T. H., S. Benin, and J. S. Larson. 1995. Public attitudes and economic values for wetland preservation in New England. Wetlands 15:226-231.

Stewart, R. E., and H. A. Kantrud. 1971. Classification of natural ponds and lakes in the glaciated prairie region. U.S. Fish and Wildlife Service Resource Publication 92.

_____, R. E., and H. A. Kantrud. 1973. Ecological distribution of breeding waterfowl in the prairie pothole region of North Dakota. Journal of Wildlife Management 37:39-50.

Swanson, G. A. 1985. Invertebrates consumed by dabbling ducks (Anatinae) on the breeding grounds. Journal of Minnesota Academy of Sciences. 50:37-40.

van der Kamp, G., W. J. Stolte, and R. G. Clark. 1999. Drying out of small prairie wetlands after conversion of their catchments from cultivation to permanent brome grass. Hydrological Sciences Journal 44:387-397.

van der Valk, A. G. 1981. Succession in wetlands: a Gleasonian approach. Ecology 62:688-696.

_____, T. L. Bremholm, and E. Gordon. 1999. The restoration of sedge meadows: seed viability, seed germination requirements, and seedling growth of *Carex* species. Wetlands 4:756-764.

_____, and C. B. Davis. 1978. The role of seed banks in the vegetation dynamics of prairie glacial marshes. Ecology 59:322-335.

VanRees-Siewert, K. L. 1993. The influence of wetland age on bird and macroinvertebrate use of restored Iowa wetlands. Thesis, Iowa State University, Ames, Iowa, USA.

Van Stempvoort, D. R., T. W. D. Edwards, M. S. Evans, and W. M. Last. 1993. Paleohydrology and paleoclimate records in a saline prairie lake core: mineral, isotope, and organic indicators. Journal of Paleolimnology 8:135-147.

Voights, D. K. 1976. Aquatic invertebrate abundance in relation to changing marsh vegetation. American Midland Naturalist 95:313-322.

Wang, Shih-Chin, T. W. Jurik, and A. G. van der Valk. 1994. Effects of sediment load on various stages in the life and death of cattail (Typha x Glauca). Wetlands 14:166-173.

Weller, M. W. 1987. Fresh Water Marshes: Ecology and Wildlife Management, 2nd edition. University of Minnesota Press, Minneapolis, Minnesota, USA.

Wienhold, C. E., and A. G. van der Valk. 1989. The impact of duration of drainage on the seed banks of northern prairie wetlands. Canadian Journal of Botany 67:1878-1884.

Wiggins, G. B., R. J. Mackay, and I. M. Smith. 1980. Evolutionary and ecological strategies of animals in annual temporary pools. Archiv für Hydrobiologie Supplement 58:97-206.

Winter, T. C. 1989. Hydrologic studies of wetlands in the Northern Prairie. Pp. 17-54 *in* van der Valk, ed. Northern Prairie Wetlands. Iowa State University Press, Ames, Iowa, USA.

Wischmeier, W. H., and D. D. Smith. 1978. Predicting rainfall erosion losses: a guide to conservation planning. Agricultural Handbook 537. U.S. Department of Agriculture, Washington, D.C.

Yetka, L. A., and S. M. Galatowitsch. 1999. Factors affecting revegetation of *Carex lacustris* and *Carex stricta* from rhizomes. Restoration Ecology 7:162-171.

Appendix A. Lead-210 and Cesium-137 analysis methods, U.S. Geological Survey's Center for Marine and Coastal Research Laboratory, St. Petersburg, Florida.

ANALYTICAL

Total extracted lead-210

The analysis of sediments at the USGS laboratory is based on counting of Po-210, in secular equilibrium with its parent Pb-210, and exploits the ability of polonium to self-plate onto silver and certain other metals (Flynn 1968). Five grams of the > 62 micrometer dried, ground sample was transferred to a 100ml Teflon beaker and mixed with 5-10 ml of reagent grade 16N nitric acid. An amount of NIST-calibrated Po-209 spike was added and the sample swirled to mix the spike. The beaker was covered with a watch glass and allowed to stand overnight. The solution with solids was allowed to evaporate under heat lamps at 90 deg. C. The sample was washed from the sides of the beaker using 8N hydrochloric acid and swirled again to insure proper mixing. The solution is evaporated again and allowed to cool. One ml of 30% hydrogen peroxide was the added to the sample and the resulting mixture evaporated to dryness. These latter steps, adding peroxide and drying the mixture were repeated an additional two times. The 8N HCl was added to the sample and allowed to dry out. This step was repeated so as to ensure that nitric acid, which hinders efficient plating is virtually eliminated from the mixture. Finally 5 ml of 8 HCl were added to the dried sample and the mixture transferred to a 100 ml beaker using additional amounts of de-ionized water to insure essentially complete transfer. To minimize interference of several ions with plating, 5 ml of hydroxylamine hydrochloride and 2 ml of 25% sodium citrate were added to each sample. Additionally, 1 ml of a hold back carrier, bismuth nitrate, was added to prevent deposition of Bi-212. A plastic coated magnetic bar was added to each beaker for stirring during autoplating. The pH of the solution was adjusted to between 1.85 and 1.95 using ammonium hydroxide. The beaker was placed on a hot plate and heated between 85 and 90oC for 5 minutes to reduce iron, chromium and oxidants present. Then a Teflon holder which exposes one side of a silver foil disc was placed in the solution for a minimum of 90 minutes. Rinsed and air-dried silver discs were then counted for polonium isotopes by alpha spectroscopy. Combined analytical and counting errors in determining lead-210 values are about 3%.

Lead-210, cesium-137 and radium-226

A larger aliquot, 50 grams of dried fraction were transferred to a plastic counting jar with a tight sealing plastic screw cap. Sealed counting jars were stored for at least 20 days to allow for the in-growth of radium-222 and lead-214 to approximate equilibrium values. Samples were counted on a gamma detector system consisting of a germanium detector for low energy gamma rays (2000 mm2 area) and a 4096 channel multichannel analyzer. Samples were typically counted for 48 hours (depending on sample size) or until counting errors were <5%. The system has been calibrated using Oxford standard ore in the same geometry as the samples. Specific activity of radium-226 was determined from counts associated with the gamma photopeaks of Pb-214 (295 and 351 keV) and Bi-214 (609 KeV). Cesium-137 was determined at by counting the 661.7 KeV gamma ray. Activities calculated from the three peaks were combined to yield a weighted mean reported value and standard deviation. The system was calibrated and frequently recalibrated by counting standards prepared by doping portions of sediment with precisely known amounts of a radium standard solution (NIST SRM-4959). This solution has a 0.4% uncertainty in activity at the 99% confidence level due to random errors and an additional 0.8% uncertainty due to assessable systematic errors. Reported standard deviations in radium activity, including random errors associated with detector calibration, were typically 5-7%. The limit of detection was about 0.1 dpm/g for this matrix.

Flynn, W. W. 1968. The determination of low levels of polonium-210 in environmental materials. Analytica Chimica Acta 43:221-227.