# INFLUENCES ON PLANT SPECIES DISTRIBUTIONS AND SOIL ORGANIC CARBON IN PLAYA CATCHMENTS OF THE HIGH PLAINS

By

JESSICA L. O'CONNELL

Bachelor of Arts in Biology
Sonoma State University
Cotati, CA
2003

Master of Science
Louisiana State University
Baton Rouge, LA
2006

Submitted to the Faculty of the
Graduate College of the
Oklahoma State University
in partial fulfillment of
the requirements for
the Degree of
DOCTOR OF PHILOSOPHY
May, 2012

# INFLUENCES ON PLANT SPECIES DISTRIBUTIONS AND SOIL ORGANIC CARBON IN PLAYA CATCHMENTS OF THE HIGH PLAINS

Dissertation Approved:

Loren Smith

Dissertation Adviser

Scott McMurry

Dave Haukos

Sam Fuhlendorf

Outside Committee Member

Dr. Sheryl A. Tucker

Dean of the Graduate College

# TABLE OF CONTENTS

# LIST OF TABLES

# LIST OF FIGURES

# INTRODUCTION

This work describes interactions among land-use, plant communities and ecosystem function in depressional playa wetlands, with implications for critical societal services and global climate change. There are several major themes in these chapters. First, we suggest depressional wetlands are threatened world-wide by conversion to agriculture, altering wetland processes and degrading societal services (Brinson and Malvárez 2002, Smith et al. 2008). Services are aspects of ecosystem processes that have direct benefits to society, for example, flood water storage or carbon storage for mitigation of global climate change. Further, plant communities interact with abiotic wetland processes. For example, the High Plains, where playas occur in high density, is semiarid with limited surface freshwater. Playas are predominant surface water features and provide water when inundated for people and wildlife. In this work, we demonstrate that upland plant composition influence water and sediments entering depressional wetlands (Chapters I and III), influencing wetland hydroperiods (Tsai et al. 2007), and altering plant communities and wetland processes. We also demonstrate that plant species richness influences soil organic carbon in both playas and uplands (Chapter IV). Thus, determining filters to plant species is critical for enhancing ecosystem services in depressional wetlands (Chapters I, II and III).

Therefore, we identified key aspects influencing plant distributions, including land management (Chapter I), dispersal limitation (Chapter II), and disturbance processes (Chapter I and III). We provide restoration models (Chapter II) and suggestions for remediation of plant communities where appropriate (all chapters). We hope these suggestions may be generally useful for depressional wetland conservation, preserving ecosystem function, maximizing soil organic carbon sequestration, and mitigating global climate change.

## AUTHOR CONTRIBUTIONS

The following chapters were written in manuscript format, and have several co-authors. I am the first author on these manuscripts and wrote the bulk of the text and preformed all (and designed nearly all) statistics. However, this work was highly collaborative.

Drs. Loren Smith, David Haukos and Scott McMurry wrote the grants funding these studies. They generated research questions addressed in Chapters I and III. Smith and McMurry are co-authors on all chapters. Haukos is a co-author on Chapters I, II and III. Dr. Lacrecia Johnson, Dale Daniel and Ben Beas also are co-authors (Johnson on Chapters I, II, and III, Beas on Chapter II, Daniel on Chapters II and III). They combined their research data with mine, allowing us to address larger research questions. Beas contributed plant composition data from the Rainwater Basin. Johnson and Haukos contributed sediment data from half of the Southern High Pains, and Daniels and McMurry collected sediment data in the rest of the High Plains. Johnson collected plant composition data from half of Texas. I collected plant composition data from the rest of the western High Plains. I collected, designed, and processed the soil organic carbon analyses. Smith and McMurry provided funding and equipment for the carbon work. I designed the research questions in Chapters II and IV, but collaboration with Smith, McMurry, and Haukos were essential. Further, while I wrote the following chapters, my co-authors have assisted with editing and improving them. The first chapter is in revision with *Biological Conservation*. Some suggestions from *Biological Conservation* reviewers also were incorporated into this first chapter.

## ACKNOWLEDGMENTS

This research would not have been possible without the kind assistance of so many others. I would like to thank my dissertation advisor, Dr. Loren Smith, whose unfailing support and trust were greatly appreciated. I also would like to thank my many research collaborators, Scott McMurry, Dave Haukos, Lacrecia Johnson, Dale Daniels and Ben Beas. Their assistance with data collection, field equipment, manuscript review, and logistics was invaluable. Further, Scott McMurry, Dave Haukos, and Sam Fuhlendorf were kind enough to serve on my committee, and their careful input has strengthened my research immeasurably.

Others also have been helpful. April Bagwill and Paris Reilly amicably shared field housing with me, and their good humor and excellent cooking helped summer field seasons pass quickly. Ele Nugent volunteered to help collect soil samples in the rain. My field assistants, Amber Staley (now Williams), Marie Russo, and Guido Ufer were excellent traveling companions and cheerful about surveying wetlands in the intense High Plains sun. We traveled over 40,000 miles together in a Toyota Tundra, and I couldn't have asked for better companions. My lab assistants, Michawn Overall, Guido Ufer, Dana Paladino, and Justin Rolen were diligent about helping me process over 2000 soil samples. That was really amazing guys, and I am forever grateful for your help.

The following people also were important. Lynn Nymeyer and Buffalo Lake National Wildlife Refuge provided Texas field housing and warned us when tornados were about to blow through. Joe Hartman and Cimarron National Grassland provided housing in Kansas and helped us fix the soil probe when it broke for the thousandth time. Dr. Jack F. Cully, KSU loaned us the use of his field trailer. William Burnidge and The Nature Conservancy provided housing in Colorado. Randy Stutheit and Nebraska Game and Parks Commission assisted with housing in Nebraska. Nathan Andrews drove us to his favorite TNC playas and worried about us when we turned up late from field work. Comanche National Grasslands assisted with finding grassland field sites. Megan McLachlan assisted with GIS source data. This research was funded by USDA, NRCS-CEAP WETLANDS and Region 6 EPA: project CD-966441-01.

Finally, moral support was provided by April Bagwill, Kim Hays, Marie Perkins, Jason Joines, and Philip and Stephanie O’Connell. Thanks guys. I appreciate you always.

# CHAPTER I

## II. INFLUENCE OF LAND-USE AND CONSERVATION PROGRAMS ON WETLAND PLANT COMMUNITIES OF THE SEMIARID GREAT PLAINS

### ABSTRACT

Depressional wetlands are predominant surface hydrological features providing critical societal ecosystem services in the semiarid United States High Plains. Essential wetland processes may be threatened because this 30 million ha short-grass prairie largely was converted from grassland to cropland. Further, the United States Department of Agriculture enrolled marginal cropland into the Conservation Reserve Program (CRP). CRP reduces topsoil erosion by planting permanent cover on croplands. In the High Plains, introduced tall-grasses primarily were planted in CRP, possibly reducing precipitation runoff, an important hydroperiod driver in wetlands. We assessed land-use influence on important wetland processes (wetland area, inundation, and plant composition) in 261 depressional wetlands called playas (87 each in native grassland, CRP, and cropland). Surveys spanned 6 states within 3 High Plains sub-regions (southern, central and northern). Playas averaged 8 ha in cropland and 16 ha in other land-uses. Plant composition in grassland playas was predominately native perennials, and upland plant cover equaled wetland plant cover. Cropland playas had fewer species/ha, generally more annuals than perennials and 80% greater exposed ground than other land-uses. CRP playas had 400% greater cover of introduced species (mostly upland perennial tall-grasses), which possibly inhibited catchment runoff, as CRP playas were inundated 56% less often than other land-uses. Therefore, tall grasses may be inappropriate in short-grass prairie CRP catchments, as they alter inundation frequency and vegetation communities in embedded wetlands. Conservation programs containing provisions to protect playas, including planting common native species and using grass buffers to control erosion into wetlands, should be promoted.

## INTRODUCTION

Wetlands are important for supporting surrounding ecosystems through their influence on landscape hydrology and biodiversity (Millennium Ecosystem Assessment 2005). Wetlands in similar geomorphic settings often have similar characteristics and face similar threats worldwide (Brinson and Malvárez 2002). For example, depressional wetlands frequently have groundwater connections, occur in fertile landscapes and are modified for agricultural production (Brinson and Malvárez 2002). Further, depressional wetlands are especially vulnerable to activities in surrounding catchments (Smith et al. 2008).

Playas are a depressional wetland type vulnerable to catchment activities. Playas are the dominant hydrogeomorphic feature in the High Plains of the United States Great Plains (Smith 2003). The High Plains is a semiarid short-grass landscape. Playa wetlands are important because they pond water and provide habitat connectivity between water sources in a region where precipitation frequency and quantity are variable and scarce (Bolen et al. 1989, Johnson 2011). Playas also provide ecological services such as biodiversity refugia for wetland plants and animals, biomass production, flood mitigation, water storage, denitrification and carbon storage (Smith et al. 2011a). Moreover, playas recharge the High Plains Aquifer, the main source of water for crop irrigation and human use (Gurdak and Roe 2009). Therefore, playa degradation can have negative ecological and sociological impacts. In this paper, we provide the first evaluation of the effects of crop cultivation and the largest United States Department of Agriculture (USDA) conservation program, the Conservation Reserve Program (CRP), on playa plant communities and inundation frequency across the entirety of the High Plains, a 30 million ha landscape. CRP was implemented to reduce surplus crop production and soil erosion by replacing highly erodible croplands with perennial cover. Recommendations are needed concerning current practices intended to conserve playas. Such suggestions should inform policy on depressional wetlands in most agricultural settings (Smith et al. 2008).

Agricultural development is common in the High Plains (Samson and Knopf 1994), where greater than 15 million ha are cultivated (M. McLachlan, Playa Lakes Joint Venture, personal communication). Croplands can influence playas because playas are depressional recharge wetlands that drain catchments (e.g., are at the lowest elevation in the watershed). As such, hydrologic inputs to playas are precipitation and overland sheet flow, while outputs are limited to evapotranspiration and groundwater recharge (Smith 2003). Crop fields contain extensive bare soil between rows, during plowing, and while fallow. Therefore, crop field runoff transports sediment into playas and sediment accumulation reduces wetland volume, increases water surface area, increases evaporative loss of water and shortens hydroperiods (Luo et al. 1997, Tsai et al. 2007). Shortened hydroperiods influence all other playa ecosystem properties (Smith et al. 2011a). Upland sediments in playas are naturally removed only by wind because playas have no overland water outputs. Native grasslands surrounding playas, rather than cropland, protect playas by providing plant cover that reduces upland soil erosion. Thus, playas and the surrounding catchments are implicitly linked, and catchment alterations, such as crop production, threaten playas.

CRP was initiated by the USDA in 1985 and today is the largest USDA conservation program in the United States (USDA 2011). This program provides landowner incentives (payments) for planting perennial non-crop cover on highly erodible croplands. CRP lands occur in high density in the High Plains, where payments to landowners have totaled $97 million annually (Farm Service Agency 2010). Most CRP plantings in the High Plains were generally introduced (e.g., occurring outside of their historical range) perennial grasses. Thus, CRP influence on playas may be complex because CRP playas were previously cultivated and now often are planted with extensive introduced grass cover. Introduced grasses in CRP plantings may alter resources and plant communities within playas, impacting other ecosystem properties (D'Antonio and Vitousek 1992, Ehrenfeld 2003). However, perennial grass plantings also should reduce wetland sedimentation by providing a barrier to overland sheet flow. Consequently, we should evaluate the effects of CRP on wetlands in the High Plains to ensure efficient use of conservation dollars. Ours is the first evaluation of CRP influence on embedded wetland plant communities in a semiarid landscape.

Land-use alteration of playa ecosystem properties may vary with land management practices in both croplands and CRP. In CRP these practices include planting native vs. introduced grasses. In the High Plains, introduced grasses were planted on CRP lands except in Kansas, where native tall-grass plantings were common (Robel et al. 1998, Hickman et al. 2009), though not planted exclusively. We use “introduced” and “native” as defined by distribution maps in the USDA

PLANTS database (USDA and NRCS 2010). No previous study has evaluated differences among playa plant communities in native and introduced CRP grasslands.

Further, in croplands, alternate land management practices also may influence plant community responses. Alternate management practices in croplands include those provided for by USDA wetland conservation provisions (Smith et al. 2011a). Such provisions are the Highly Erodible Land Conservation and Wetland Conservation Compliance provisions (Swampbuster) that were first introduced in the 1985 Farm Bill. Swampbuster provisions refuse USDA benefits to producers who produce commodities on any wetland after 1990. However, Swampbuster allows crop production on dry wetlands (Glaser 1985), a common condition for playas converted to commodity production prior to 1985. Therefore, Swampbuster provisions may not prevent producers from frequently tilling playas. Further, many wetlands are dry at some stage of their hydrologic cycle (Mitsch and Gosselink 2007). Thus Swampbuster may generally fail to prevent plowing through U.S. depressional wetlands. Finally, we have little evidence that plowing catchments while leaving wetland basins unplowed minimizes alterations to embedded wetlands. Moreover, studies should critically evaluate the effects of catchment plowing on embedded wetlands to ensure current conservation regulations are effective.

In this study, our first objective was to document how vast land-use changes in the U.S. High Plains, such as conversion of native prairie to cropland and CRP, affected wetland area, plant communities and probability of playa inundation. Our second objective was to evaluate whether alternate land management, such as practices provided under USDA programs, could mitigate problems associated with CRP and croplands. To this end, we examined whether native grass CRP mixtures used in Kansas reduced alterations to embedded playa plant communities. We also evaluated whether plowing around playas rather than through them lessened alterations to plant communities in cropland wetlands. Finally, we suggest methods for integrating sustainable land-use practices to preserve playas from future impacts. Because depressional wetlands are common in croplands world-wide (Brinson and Malvárez 2002, Smith et al. 2008), these suggestions may also inform wetland conservation outside the High Plains.

## METHODS

### *Study area*

We sampled playas within the short-grass prairie eco-region of the non-glaciated High Plains. Below the High Plains lie portions of the High Plains Aquifer. The extent of the High Plains largely coincides with the extent of the aquifer because of changes in topography at the aquifer's borders. Up to 60,000 playas occur throughout the High Plains (Playa Lakes Joint Venture, http://pljv.org/) and are dominant sources of surface freshwater. Our surveys encompassed 6 states, and can be considered to contain 3 sub-regions: the northern, central and southern High Plains (Figure II.1). Sub-region boundaries are defined by changes in geomorphology of the High Plains Aquifer (Gurdak and Roe 2009). Climate is semiarid and variable, with average annual precipitation ranging from 38 cm to 63 cm along a west—east gradient (Smith 2003).

We sampled 261 playas: 87 each embedded in native grassland (never previously plowed), USDA CRP (previously plowed and planted to perennial grass), and croplands, in a random design stratified by playa density/county. We selected study sites from a GIS containing playa locations and land-use designations compiled from existing databases (A. Bishop, USFWS). We first randomly selected playas in native grassland due to their limited availability, and then selected nearby cropland and CRP playas, generating geographically associated playa triplets. We confirmed playa presence in the field by utilizing soil cores to verify hydric soils when upland sediments covered wetland basins (e.g., crop and CRP playas). Playa hydric soils are Vertisols, readily identified as dense clays with gleyed matrix color (Luo et al. 1997), and distinct in appearance from non-Vertisol upland soils. Upland soils varied in texture, structure and other properties with land-use, parent material, climate and other properties, but were always distinct from wetland soils.

### *Field surveys*

We verified upland land-use designations in the field with visual assessments and step-point transects (Evans and Love 1957) extending 100 m into uplands from playa basin edges. We also used two step-point transects to estimate plant cover within playas, identifying plants (including crops) approximately every 1 m. Step-point surveys require that surveyors walk transects and identify plants encountered at the tip of each footstep. Playa transects spanned playa diameter between playa visual edges. We determined visual edge by comparing changes in soil type and topography from sloped depression edge to flat upland (Luo et al. 1997). We surveyed playas twice to account for species turnover from cool- (surveyed 10 May – 30 June) to warm-season species (surveyed from 10 July – 31 August) (Smith and Haukos 2002). We list species names as defined in the USDA PLANTS database (USDA and NRCS 2010). USDA PLANTS largely uses taxonomy from the Biota of North America (Kartesz 2011). We collected voucher specimens to verify unknown plants.

We estimated mid-peak growing season (July) aboveground biomass in 30 playa land-use triplets (native grassland, cropland, and CRP land). We collected all biomass (clipped to the soil surface) from one 50 X 50-cm quadrat per wetland. We selected wetland triplets for clip-plots evenly across sub-regions, proportionate to playa density. We clipped quadrats in playas at wetland centers. We used GPS to locate wetland centers. Coordinates for wetlands centers were from the GIS database previously described. We dried clipped biomass at 65˚C until constant weight was achieved. We evaluated oven-dried biomass in our analyses.

### *Playa area differences*

We compared playa area among land-use with analysis of variance (ANOVA) with blocking by triplet. We used total steps surveyed along transects to estimate playa diameter (1 step = approximately 1 m). Playas are typically round (Smith 2003). We used diameter to calculate playa area, using the formula for the area of a circle. We used steps surveyed from transects as our diameter estimate because this better represents area surveyed than diameter derived from soil maps (Smith and Haukos 2002).

### *Plant composition differences*

To determine how land-use influences plant composition, we investigated differences in relationships between species richness, land-use and playa area with analysis of covariance (ANCOVA).We incorporated area in species richness analyses because species richness often increases exponentially with area (Rosenzweig 1995). To account for this, we used the species-area curve to separate area effects from land-use differences. The species-area curve is modeled as $S = cA^z$, where S = species richness, A = area, and c and z are constants (MacArthur and Wilson 1967). C is the rate-determining factor in the species-area curve (i.e., number of species that accumulate per unit area), and z has sometimes been associated with degree of disturbance or isolation, where greater values of z imply more disturbed or more isolated habitats (Rosenzweig 1995). Log-transformation linearizes this relationship, transforming the equation to $\log(S) = z*\log(A) + \log(c)$, allowing linear regression and generating estimates of c and z comparable to literature values (Rosenzweig 1995). To assess differences in intercepts (c-values) among land-use, we coded land-use categories (cropland, grassland, CRP) as separate dummy variables (1 = this land-use, 0 = not this land-use). We also included land-use*area interactions to assess differences in slopes (z-values) among land-use. We again used steps surveyed to estimate playa area.

We used USDA PLANTS to classify wetland indicator status of plants (obligate, facultative wet, facultative, facultative upland, or upland). Upland plants usually had no wetland indicator status in USDA PLANTS; therefore we assumed plants with no data were upland plants in analyses. Data collection spanned multiple geographic regions defined by USDA (regions 5, 6, and 7) and species' wetland indicator status sometimes differs by region. For simplicity, we used the wettest indicator status among surveyed regions for each species. Finally, to simplify analyses, we grouped wetland indicator status into broader categories: wetland (plants ranging from wetland obligate to facultative wet) and upland (plants ranging from facultative upland to upland). Facultative species were excluded from wetland status analyses. We used range maps in USDA PLANTS and descriptions in Flora of the Great Plains (Great Plains Flora Association 1986) to classify plants as annual or perennial, and as native or introduced within the Great Plains region. Biennial species were classified as perennials to simplify analyses.

We calculated percent cover for all species including crops, bare ground, and water by dividing the number of encounters by total steps on both transects. We designated plants observed in playas but not encountered on transects as trace species and gave them a cover of 0.0001. We excluded unidentified plants from analyses.

We compared plant cover among land-use and sub-region (southern, central, and northern as defined on Figure II.1). We assigned playas to sub-regions with overlay analysis of UTM locations on sub-region polygons using ArcInfo 9.3 (ESRI, Redlands, CA). Some playas fell outside the High-Plains aquifer sub-region boundary, probably due to difficulty mapping the exact position of the boundary. We assigned playas outside sub-region borders to the closest sub-region. We used ANOVA with blocking on playa land-use triplet to compare plant biomass among land-use, sub-regions and land-use*sub-region interactions. Additionally, we used separate repeated-measures ANOVAs with blocking on triplet to compare percent cover of wetland, upland, annual, perennial, native and introduced plants among land-use, sub-regions and land-use*sub-region interactions. Early and late-season surveys were the repeated value in these analyses. We square-root or arcsine transformed response variables when appropriate to achieve normalcy of residuals and reduce heterogeneity of variances.

### *Playa inundation*

We recorded whether playas were wet (inundated or surface moist from past inundation) or dry during any field visit. We used a chi-square contingency test to compare the number of playas encountered wet versus dry by land-use.

### *Alternate practices within cropland and CRP*

We compared practices within cropland and CRP playas to determine influences on playa plant communities. Within CRP playas, Kansas planted almost all native CRP mixtures, whereas all other states used mostly introduced grass mixtures. We confirmed CRP mixture characteristics using 100 m step-point transects extending away from playa basins into uplands. To test effects of CRP mixture, we compared aboveground biomass and percent cover of annual, perennial, wetland, upland, native, and introduced plants between Kansas and other states grouped together.

Within croplands, we compared these same plant response variables as well as species richness-area relationships between cultivated and uncultivated playa basins. We considered playas cultivated if there were plow lines or crop rows through playa centers during any field visit.

For all models, we present back-transformed means in the results for ease of interpretation. We used post-hoc tests with Tukey adjustments for significant models to compare responses among land-uses, sub-regions, and land-use*sub-region interactions, as appropriate. Where multiple response variables were modeled for the same independent variables, we used the Holm–Bonferroni method to correct for potential increased Type I error (Holm 1979). We used the Holm-Bonferroni method because it allows comparison with historical literature, such as Smith and Haukos (2002), which used univariate tests (Huberty and Morris 1989, Jaccard and Guilamo-Ramos 2002). We interpret model significance using Holm–Bonferroni correction, but report uncorrected p-values to allow readers to interpret significance using any preferred method.

These analyses assume that cropland, native grassland and CRP are randomly distributed. This may not be true because people select where to cultivate and subjective opinions concerning the best lands for cultivation may cause croplands to be non-randomly distributed in a manner difficult to quantify. Similarly CRP lands were selected using a combination of landowner and USDA opinions on which lands met CRP objectives. However, to evaluate the effects of land-use on playa wetlands, we must use conditions present on the landscape. Though this may not match an ideal scientific sampling design, it is the best information available and therefore is valuable.

## RESULTS

### *Area of wetland habitat*

We detected no difference in playa area among sub-region and land-use*sub-region interactions ($F_{2,252}$ = 1.53, $P$ = 0.22 and $F_{4,252}$ = 0.49, $P$ = 0.74, respectively), but area differed by land-use ($F_{2,251}$ = 6.64, $P$ = 0.002, Figure II.2a). Cropland playas were 52% smaller than grassland and 41% smaller than CRP playas. We detected no difference in area between CRP and grassland playas.

### *Plant community composition*

Species richness varied with playa area in all land-uses ($F_{5,512}$ = 97.8, $P$ < 0.001, $R^2$ = 0.49, Table II.1). Slopes of the relationship between richness and playa area (z-values) were similar for grassland and CRP playas and steeper for cropland playas. Intercepts (c-values) for the relationship between richness and playa area were similar for CRP and grassland, whereas cropland had lower c-values.

We detected no difference in sub-region and land-use*sub-region interactions for plant biomass ($F_{2,52}$ = 0.02, $P$ = 0.98 and $F_{4,52}$ = 0.16, $P$ = 0.96, respectively). However, plant biomass differed by land-use; CRP biomass was twice that of other land-uses ($F_{2,52}$ = 4.4, $P$ = 0.017, Figure II.2b). Wetland plants generally had reduced cover in cropland playas versus other land-uses, except in the northern sub-region, where they were equally low in CRP playas ($F_{4,421}$ = 2.92, $P$ = 0.02, Figure II.3a). We detected no land-use*sub-region interaction for upland plants ($F_{4,421}$ = 1.10, $P$ = 0.36). Upland plant cover differed by land-use and sub-region, and accordingly was 84% less in cropland playas than in grassland and CRP playas, and 28% greater in southern than in central and northern sub-regions (land-use: $F_{2,421} = 83.87$, $P < 0.001$, region: $F_{2,421} = 3.58$, $P = 0.029$, Figure II.3b).

For all other models, plant cover was associated with significant land-use*sub-region interactions. Annual plant cover was greatest in central CRP (31% ± 0.2) and northern grassland playas (24% ± 0.2); elsewhere annual plant cover ranged from 13 – 19% ($F_{4,421} = 4.06$, $P = 0.003$, Figure II.3c). Perennial plant cover was 83% less in cropland than in other land-uses. Perennial cover was similar between grassland and CRP playas except in the central region, where grasslands had 20% greater cover than in CRP playas ($F_{4,421} = 8.36$, $P < 0.001$, Figure II.3d). Native plant cover was 300% greater in other land-uses than in cropland playas. Grassland playas also had greater native cover than did CRP ($F_{4,421} = 5.7$, $P < 0.001$), except in the southern region where native cover was similar between grasslands and CRP (Figure II.3e). Conversely, introduced plant cover was 400% greater in CRP playas, whereas introduced cover generally was similar between grassland and cropland. The exception was in the central region, where croplands had three times greater cover of introduced species than in grassland playas ($F_{4,421} = 3.43$, $P = 0.009$, Figure II.3f).

*Frequency of encountering wet playas*

Playas in CRP land-use were encountered wet 56% less often than other catchments ($n_{grass} = 39$; $n_{cro} = 40$; $n_{CRP} = 22$; $\chi^2 = 9.9$, $df = 2$, $P = 0.007$). We detected no difference in number of inundated playas encountered between grassland and cropland playas.

*Alternate practices in CRP and cropland*

Kansas CRP planting mixtures were associated with greater annual playa plant cover than in other CRP playas (Kansas: 0.29 ± 0.03, $n = 46$; Elsewhere: 0.18 ± 0.02, $n = 130$; $F_{1,172} = 9.46$, $P$

= 0.002). Other response variables were not significant after Holm–Bonferroni correction (biomass: $F_{1,\,27} = 4.62$, $P = 0.04$; wetland plants: $F_{1,\,172} = 1.10$, $P = 0.30$; upland plants: $F_{1,\,172} = 2.26$, $P = 0.13$; perennials: $F_{1,\,172} = 0.45$, $P = 0.50$; natives: $F_{1,\,172} = 5.94$, $P = 0.016$; introduced plants: $F_{1,172} = 1.69$, $P = 0.20$).

In croplands, cultivation through wetlands reduced c-values (intercept) in the species richness-area relationship as compared with unplowed cropland playas ($F_{3,125} = 27.3$, $P < 0.001$, $R^2 = 0.40$, Table II.1). Cultivated playa basins also had reduced cover of all plants except annuals, which were 3% greater than in unplowed basins (Table II.2). We detected no difference in plant biomass between cultivated and uncultivated crop playas ($F_{1,28} = 0.13$, $P = 0.72$, $\overline{X}_{\text{unplowed}} = 260.5\ \text{g/m}^2 \pm 51$, $n = 12$; $\overline{X}_{\text{plowed}} = 330.1\ \text{g/m}^2 \pm 117$, $n = 18$).

## DISCUSSION

### *Area of wetland habitat and species richness*

Cropland playas were smaller than native grassland playas. There are two potential explanations for this. First, playa area, volume and hydroperiod are positively correlated, and smaller playas hold less water and have shorter hydroperiods than larger ones (Guthery and Bryant 1982, Luo et al. 1997, Tsai et al. 2007). As a result, small playas are shallower, dry more often, and easier to plow than large playas. Disproportionate cultivation of small playas may reduce water depth and hydroperiod variability on the landscape. Second, cropland playas may be smaller than elsewhere because watershed cultivation increases sediment accumulation in playa basins (Luo et al. 1999, Tsai et al. 2007). Further, if farmers choose small playas for cultivation over large playas, this may influence the rate of sedimentation in cropland wetlands because of differences in geomorphology among large and small wetlands. Upland sedimentation from croplands into playas is substantial, decreases playa area, and eventually results in complete loss of wetlands. Luo et al. (1997) demonstrated that cropland wetlands sampled in the Southern High Plains had lost more than 100% of their volume, and that sources of these sediments were from surrounding agricultural fields (Luo et al. 1999). Preliminary results from a companion study demonstrate that sedimentation in northern High Plains cropland playas also is substantial (S. McMurry, Unpublished results). Cropland wetlands we surveyed were nearly always covered by upland sediments and sometimes completely infilled.

### *Plant community composition*

Cropland playas had reduced species richness, as reflected in lower intercept (c-values) than observed in other land-uses. Recall that c-values are the intercept in log-log space for the relationship between species richness and area, but reflect the slope of the relationship in arithmetic space (i.e., they are the rate-determining factor in the equation $S = cA^z$). C-values are therefore more important for determining area-corrected species density than z-values (Rosenzweig 1995). Accordingly, species richness per unit area was higher in grassland and CRP than in cropland playas. Consequently, CRP playas had increased richness relative to croplands they replaced, although many CRP plants were introduced, upland species.

Z-values for playa plant richness also varied with land-use, averaging 0.14 in CRP and grassland, and 0.48 in cropland. Z-values typically range from 0.15 to 0.6, with larger values common in isolated areas and smaller values common in areas contiguous to large species pools (Rosenzweig 1995). Larger z-values in cropland playas may reflect increased isolation from non-crop species, causing cropland playas to act more like islands. However, disturbance such as cultivation also can increase z-values. For example, de Bello et al (2007) demonstrated that in semiarid regions, intense grazing disturbance increased z-values for plant species richness. In general, c and z-values estimated in cropland playas imply that both reduced area, as well as ecological processes not associated with area, lowered species richness in croplands.

Plant community cover differed by land-use and sub-region within land-use. We first describe environmental filters to plant community composition in grassland playas, our reference condition. Grassland playas were dominated by perennial, native vegetation. Cover of wetland relative to upland plants was roughly equal, probably reflecting natural fluctuation in hydroperiod. In the semiarid High Plains, precipitation is infrequent and unpredictable. Wetland plants in grassland playas should be common during inundation, when wetland annuals colonize newly wet playas. Extended inundation allows wetland perennials to persist and eventually outcompete annuals. Upland plants germinate during dry periods, with upland annuals colonizing first and perennials persisting during static dry conditions.

Cropland playas, in contrast, had low plant cover and increased bare ground and crop cover. Of non-crop plants present, annuals and introduced species were common. Low prevalence of perennials suggests cultivation disturbance prevented perennial wetland and upland plants from establishing, reducing biodiversity. Moreover, cropland playas were small and shallow because of upland sedimentation (S. McMurry, Unpublished results). This limited water volume in cropland playas and ecosystem functions that rely on wetland plants, such as wetland wildlife habitat, denitrification and carbon sequestration.

CRP playas, however, were dominated by perennials and had 400% greater cover of introduced plants. Introduced species consisted largely of perennial grasses from CRP seed mixtures. These probably persisted because of extended dry conditions and because introduced grasses sometimes were deliberately planted through wetland basins (Smith et al. 2011a). Introduced species other than planted grasses also were present and must have germinated from the seed bank or colonized from outside the wetland. Annuals were equal to perennials only in central CRP playas. However, unlike moist-soil annuals observed in cropland playas, central CRP annuals were predominately upland vegetation (97% ± 3). We provide the first demonstration that practices in CRP lands were associated with altered plant communities within semiarid wetlands.

### *Frequency of encountering wet playas*

CRP playas ponded water 56% less often than other catchments. It is unlikely that CRP was drier because precipitation was lower than in cropland and grassland playas, given our triplet selection methodology. Grassland wetlands were randomly selected and compared with cropland and CRP playas in close proximity. Therefore, factors other than precipitation were probably responsible.

Reduced water ponding might be attributed to lower CRP playa volume. CRP playas generally had sediments over the hydric clay surface (personal observation). Presumably, sediments were deposited during the agricultural phase of CRP history. However, wetland volume and inundation probability are not necessarily correlated. For example, cropland playas were smaller than CRP playas and inundation in croplands was similar to grassland playas. Most likely, factors that limited ponding were unique to CRP, such as high-biomass tall-grasses in both catchments and basins. Dense grass borders intercept overland runoff, preventing it from reaching playas (Detenbeck et al. 2002, van der Kamp et al. 2003). Further, Cariveau et al. (2011) demonstrated that CRP playas in the northern High Plains were less likely to be inundated following high precipitation than cropland or grassland playas. Our study corroborates these results. Reduced playa inundation is problematic in a region where water is limited and cultivation places high demand on water-use (Ryder 1996).

### *Alternate practices in CRP*

Alternate CRP practices, such as planting native rather than introduced grasses in uplands surrounding playas, may reduce introduced species and biomass inside playas. However, our data suggest current practices reduce neither introduced species nor biomass. For example, since the inception of the CRP program in 1985, Kansas used mostly native grass in CRP mixtures. These native grasses included tall-grasses, such as switchgrass (*Panicum virgatum*) and Indiangrass (*Sorghastrum nutans*). Although native to the region, they are not common in short-grass prairie. As elsewhere, grass mixtures often were planted in both uplands and wetlands. Short-grass species would be more appropriate in semiarid prairies and upland grasses should not be planted inside wetlands.

Further, Kansas did not have reduced introduced plant cover relative to states using introduced CRP mixtures. Introduced species in Kansas CRP playas could have germinated from seeds deposited during the cropland phase of CRP history or colonized via dispersal. Native species cover in Kansas also was similar to other states after Holm–Bonferroni correction. Further, native cover was within the range observed in other states (KS: 0.77 ± 0.03, elsewhere, 0.59 — 0.96), suggesting that even without Holm–Bonferroni correction, differences among states were marginal. The co-existence of native and introduced species may suggest playas are not species saturated. Others also have documented that introduced species established without decreasing native species (Tilman 1997, Gurevitch and Padilla 2004). In total, our data imply that planting mixtures in High Plains' CRP lands do not cause plant communities in embedded playas to resemble playas in native grasslands.

Of necessity, our analysis included a region (Kansas vs. other states) as well as treatment difference (native vs. introduced mixture). Therefore climate differences could be confounding. However, average total monthly precipitation during surveyed months was similar among High Plains' states during our survey months (NOAA 2011). We encountered slightly fewer inundated playas in Kansas than elsewhere (inundated in KS: 15% of playas, 9% of CRP playas; Inundated in other states: 22% of playas, 14% of CRP playas), but we detected no difference in cover of wetland species. We therefore argue that average conditions were similar across the High Plains during surveyed months and that our comparison of plant cover and biomass is informative.

### *Alternate practices in croplands*

In croplands, plant communities may more closely resemble playas in native grasslands if catchments are cultivated, but wetlands are unplowed. In our study, unplowed playa basins had higher species richness than plowed playas, but richness still was lower than in other land-uses. In contrast, an earlier study in the Southern and Central High Plains suggested cropland and grassland playas had similar species richness (Smith and Haukos 2002). That early study excluded plowed playas. This does not clearly represent the condition of most cropland playas, because plowing wetlands is common. In our study 59% of surveyed crop playas had plowed basins. Moreover, our analysis shows uncultivated cropland playas still had lower richness than grassland and CRP playas. Therefore, cultivating catchments generally reduces plant richness in embedded playas.

In addition to reduced species richness, both plowed and unplowed cropland playas had reduced plant cover. Reduced plant cover in unplowed playas may be from sediment accumulation in wetland basins. Also, unplowed playas were likely only unplowed when sampled, perhaps because inundation prevented plowing. Corroborating that seasonal inundation inhibited cultivation, wetland plant cover was greater in unplowed cropland playas than plowed, and also was greater than generally observed in grassland playas. Thus, though playas were not plowed when we sampled them, past cultivation may still have influenced observed plant communities.

Plowing through wetlands is allowed under current law because Swampbuster provisions permit cultivating dry wetlands, provided it does not result in “destruction of natural wetland characteristics” (Glaser 1985). Our data are the first to demonstrate that plowing playas caused substantial alteration of plant communities (reduced species richness and cover of plants) throughout the 30 million ha High Plains. Therefore, cultivating playas should be prohibited. We further suggest that plowing through any depressional wetland may generally be a destructive practice.

### *Suggestions for remediation*

Land-use alterations were prevalent in the High Plains and profoundly impacted depressional wetlands. Additionally, watershed erosion from cultivation and subsequent sedimentation eventually could cause permanent loss of all cropland playas within a 100-year period (Luo et al. 1997). CRP also lessened playa inundation because of reduced runoff. Therefore, both CRP and farming may have directly impacted diversity through loss of inundated habitat. Evidence suggests playas are important for recharging the High Plains Aquifer, the main source of water for agriculture and human-uses (Gurdak and Roe 2009, Ganesan 2010). Therefore, loss of inundated wetland area also may impact water available for human consumption and irrigation.

Agricultural production is necessary, but impacts on embedded ecosystems can be lessened by integrated landscape planning (Foley et al. 2005). Here, such planning should involve protecting wetlands remaining in native land-use. Further, USDA programs contain provisions for stewardship of wetlands in CRP and croplands, but these seldom are applied in the High Plains (Smith et al. 2011a). USDA conservation provisions should be promoted, and modified where appropriate, to enhance playa ecosystem services. For example, CRP enrollments should encourage native short-grass species and avoid planting upland species through wetlands. Conservation practices within agriculture should limit plowing of wetlands. Swampbuster restricts conversion of wetlands to produce commodity crops, but permits cultivating wetlands dry through natural conditions. Swampbuster would be more effective were it modified to prohibit cultivation of wetlands with hydric soils (i.e., those ponding water during wet years). Sediment accumulation in cropland wetlands also may be minimized by short-grass buffer strips surrounding wetlands (Skagen et al. 2008). USDA programs offer payment incentives for planting grass buffers in croplands (USDA 2003), but this incentive is rarely utilized (Smith et al. 2011a). Grasses in either CRP catchments or cropland buffer strips should be similar to species in surrounding native prairie. In the High Plains, common species include buffalo grass (*Buchloe dactyloides*) and blue grama (*Bouteloua gracilis*). Conservation practices outside the High Plains should use native species common to that region. Additionally, the USDA’s Wetland Reserve Program (WRP) provides land-owner incentives for wetland protection and enhancements, such as wetland revegetation and sediment removal. Promotion and utilization of conservation programs within the High Plains, as in other regions, would lead to a more stable and diverse local economy (Smith et al. 2011a).

The High Plains is a highly altered landscape and the unique habitat contained therein could soon be lost. Playas are similar to depressional wetlands worldwide (Smith et al. 2008), in that they are characterized by groundwater connections to important water sources and are located in fertile soils heavily impacted by agriculture (Brinson and Malvárez 2002). As such, lessons concerning playas should be applicable to depressional wetlands in other settings. Integrating sustainable agricultural practices to preserve wetlands warrants immediate attention.

Table II.1. Log-log relationship of plant species richness with playa area (ha) among land-use ($n = 174$ surveys, 2 surveys/playa). Cropland playas are subset into plowed basins ($n = 103$ surveys, 2 surveys/playa) and unplowed ($n = 71$ surveys, 2 surveys/playa). Upper-case letters indicate significant differences among land-uses ($P < 0.05$), lower-case letters indicate significant differences between plowed and unplowed playas within croplands.

| Land-use | Slope (z) | 95% CI of slope | Intercept (c) | 95% CI of intercept |
|---|---|---|---|---|
| Grassland | 0.12 A | 0.06 – 0.18 | 2.67 A | 2.52 – 2.83 |
| CRP | 0.15 A | 0.09 – 0.21 | 2.55 A | 2.41 – 2.69 |
| Cropland | 0.48 B | 0.39 – 0.57 | 1.22 B | 1.03 – 1.42 |
| Playa plowed | 0.40 a | 0.25 – 0.55 | 1.16 a | 0.91 – 1.41 |
| Playa unplowed | 0.31 a | 0.21 – 0.42 | 1.89 b | 1.61 – 2.17 |

Table II.2. Plant cover, mean ± SE, in playas within croplands. Playas either were plowed (n = 103 surveys, 2 surveys/playa) or unplowed (n = 71 surveys, 2 surveys/playa).

| Response | Playa unplowed | Playa plowed | F | P |
|---|---|---|---|---|
| Perennial | 0.25 ± 0.03 | 0.03 ± 0.01 | 70.53 | < 0.0001 |
| Annual | 0.03 ± 0.03 | 0.07 ± 0.01 | 52.02 | < 0.0001 |
| Native | 0.45 ± 0.04 | 0.07 ± 0.01 | 100.54 | < 0.0001 |
| Introduced | 0.11 ± 0.02 | 0.04 ± 0.01 | 16.31 | < 0.0001 |
| Wetland | 0.37 ± 0.04 | 0.04 ± 0.01 | 109.39 | < 0.0001 |
| Upland | 0.13 ± 0.02 | 0.05 ± 0.01 | 16.75 | < 0.0001 |

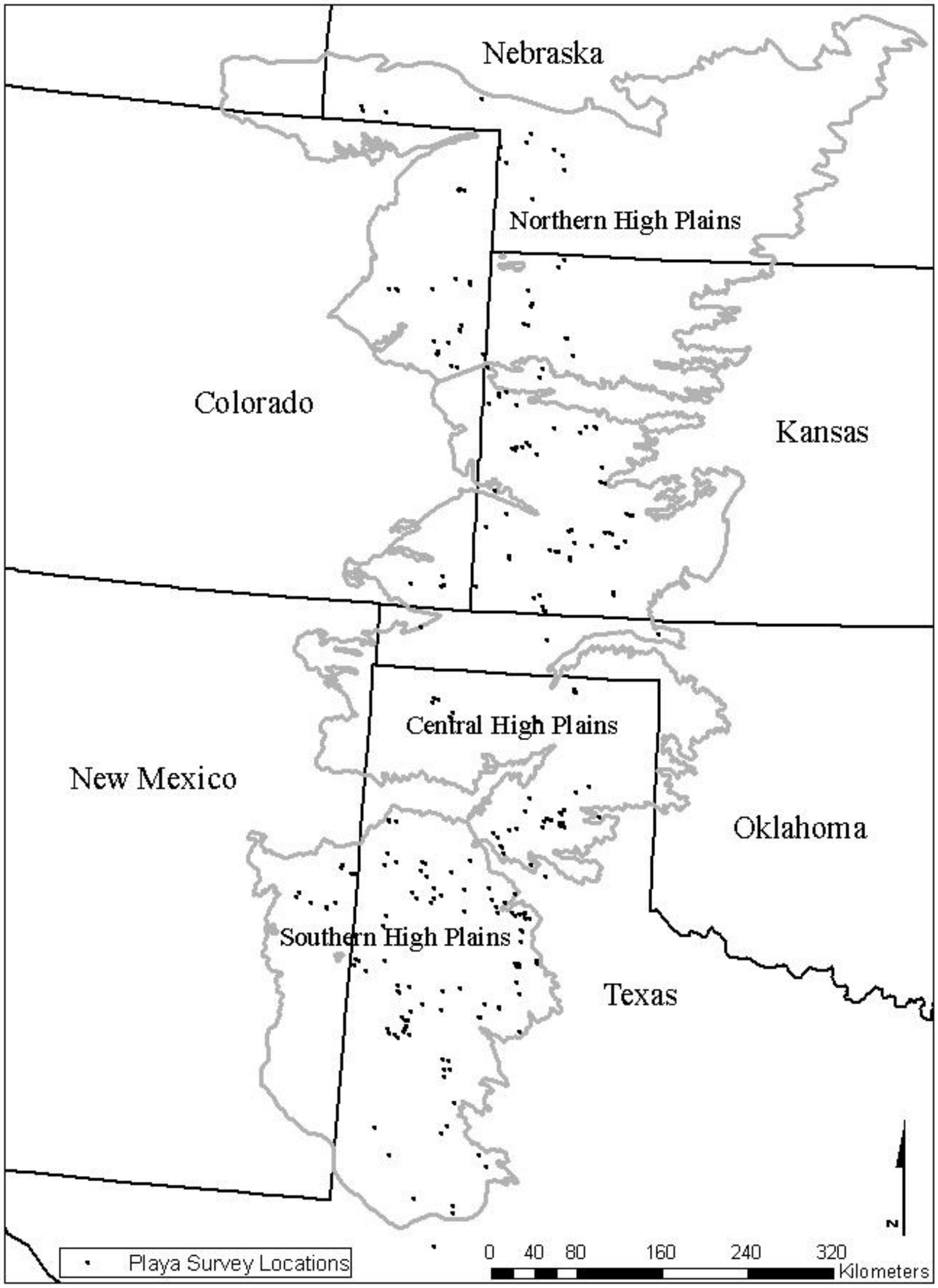


Figure II.1. Locations of playas surveyed (n = 261) within the non-glaciated High Plains of the United States. The High Plains Aquifer delineates the border of the short-grass in eco-region. Aquifer outline provided by USGS and modified by M. McLachlan, PL JV.

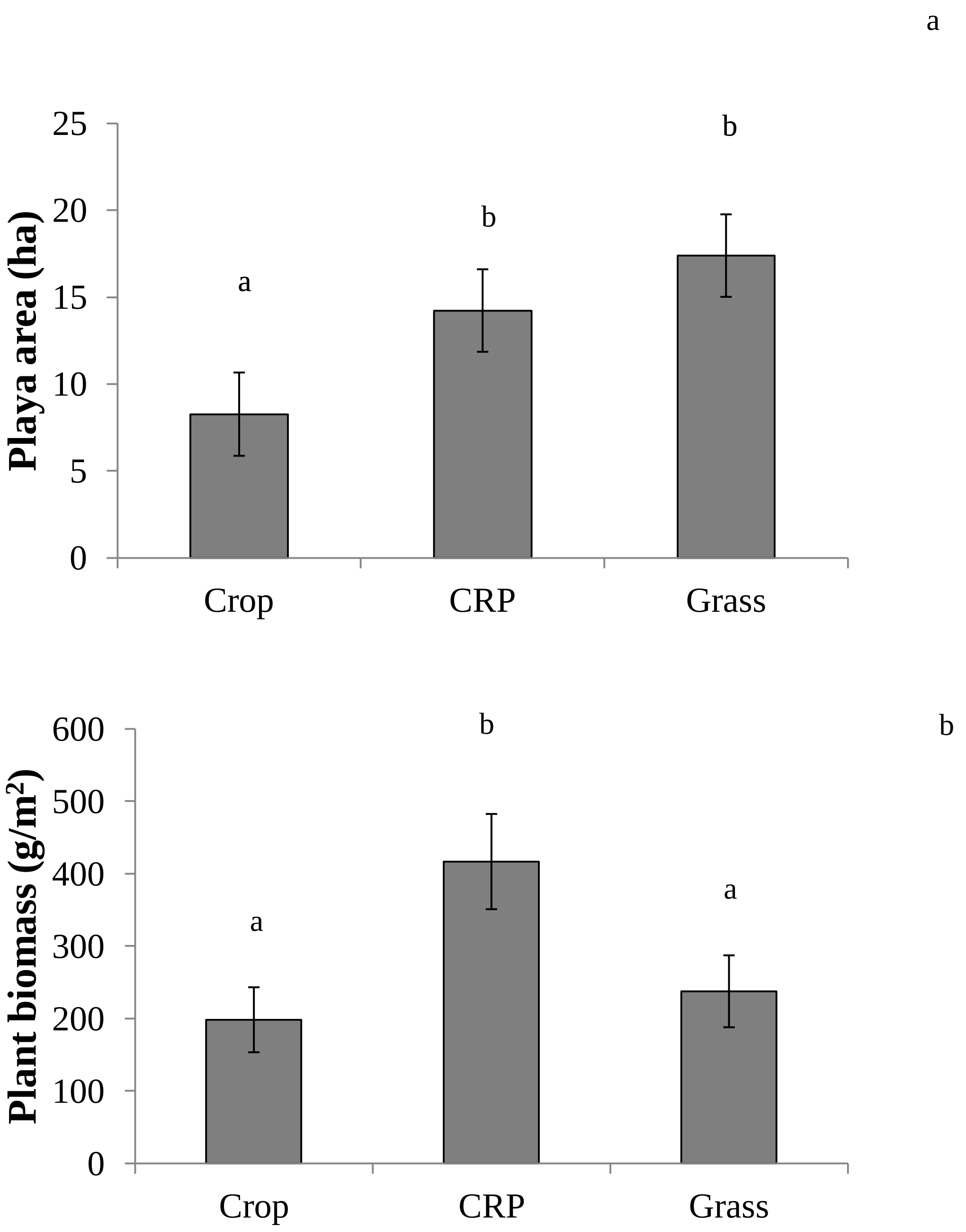
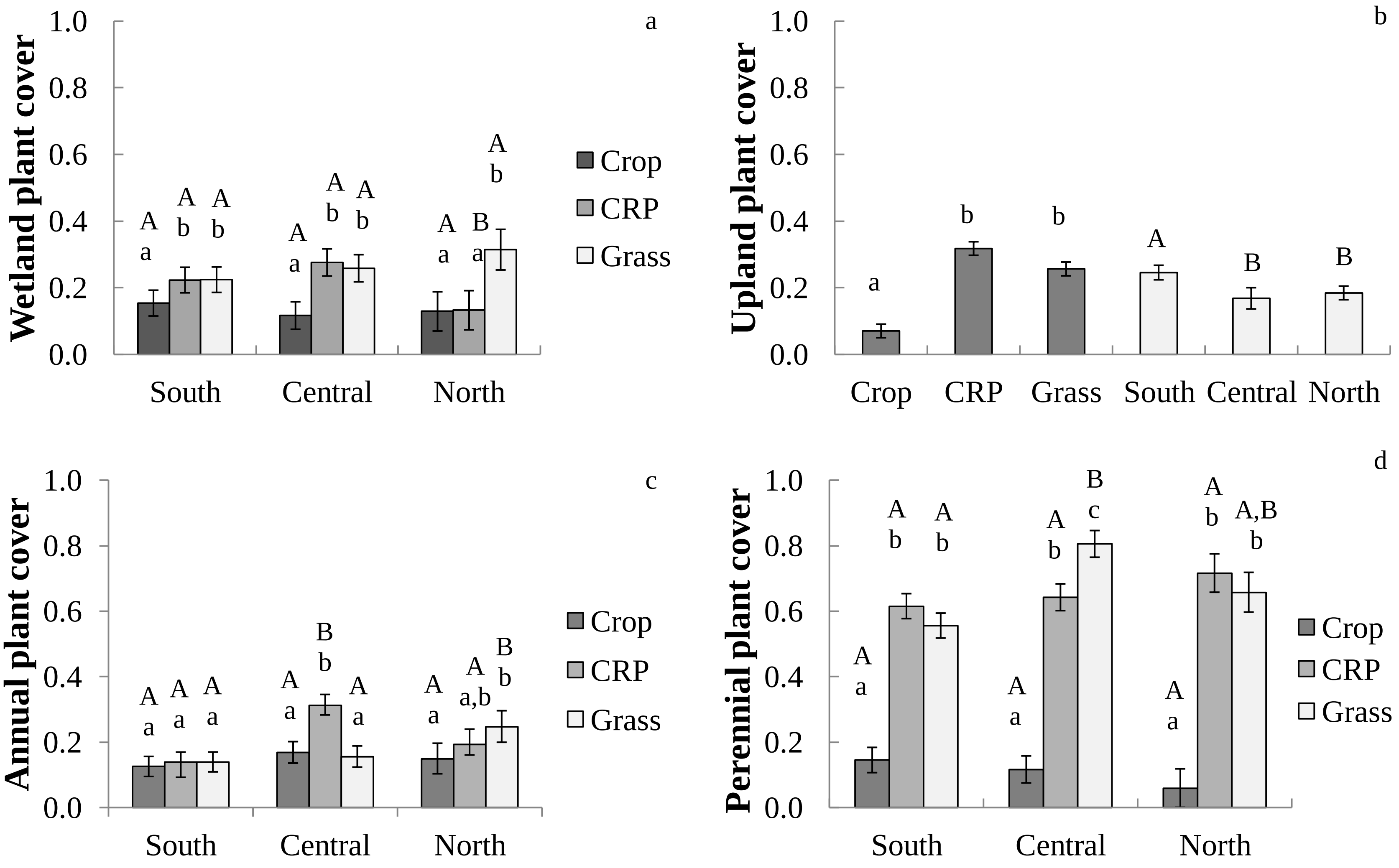


Figure II.2. Mean (± SE) among playas of different land-use and region of a) playa area; b) aboveground biomass. Lower-case letters designate differences among land-use ($P < 0.05$).


a
Wetland plant cover
1.0
0.8
0.6
0.4
0.2
0.0
A a
A b
A b
A a
A b
A b
A a
B a
A b
South
Central
North
Crop
CRP
Grass
b
Upland plant cover
1.0
0.8
0.6
0.4
0.2
0.0
a
b
b
A
B
B
Crop
CRP
Grass
South
Central
North
c
Annual plant cover
1.0
0.8
0.6
0.4
0.2
0.0
A a
A a
A a
A a
B b
A a
A a
A a,b
B b
South
Central
North
Crop
CRP
Grass
d
Perennial plant cover
1.0
0.8
0.6
0.4
0.2
0.0
A a
A b
A b
A a
A b
B c
A a
A b
A,B b
South
Central
North
Crop
CRP
Grass

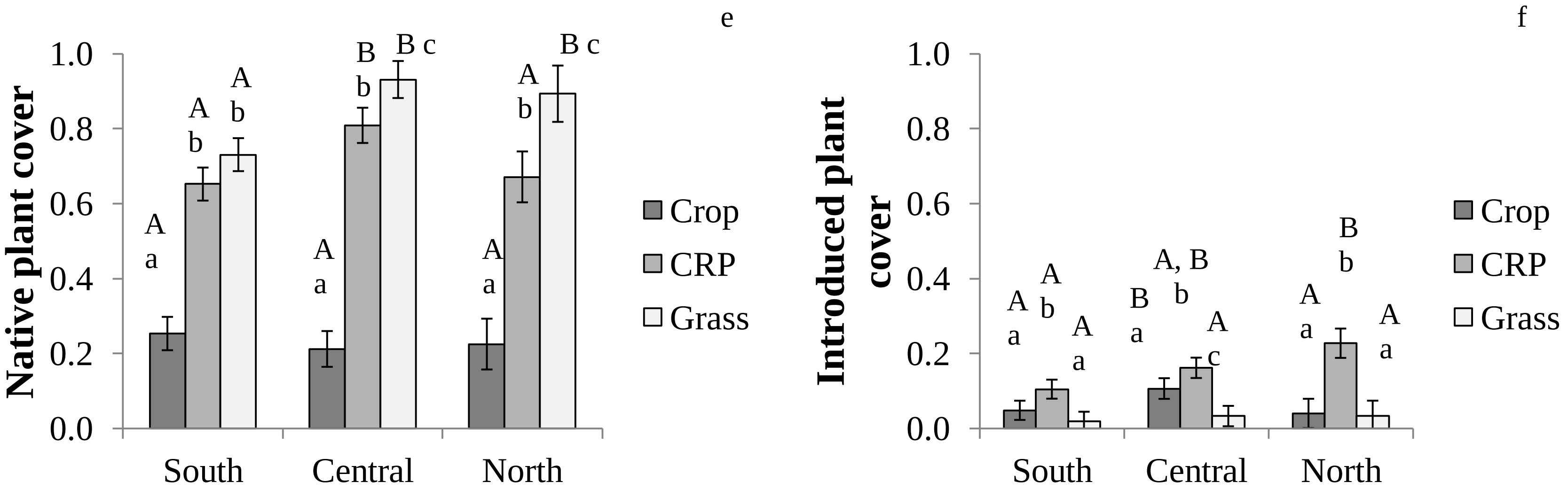


Figure II.3. Significant models for land-use, region, or land-use* region interactions for proportion of cover for a) wetland plants; b) upland plants; c) annual plants; d) perennial plants; e) native plants; f) introduced plants. Upper-case letters designate differences of the same land-use across regions (P < 0.05), whereas lower-case letters designate differences among land-use within regions.

# CHAPTER II

## III. PREDICATING DISPERSAL-LIMITATION IN PLANTS: IMPLICATIONS FOR SELF-DESIGN PLANT COMMUNITY RESTORATION FROM ISOLATED WETLANDS IN PREVIOUS CROPLANDS

### ABSTRACT

Isolated wetlands are globally important, but often degraded by agricultural conversion. Watershed cultivation increases sediment accretion and reduces cover of disturbance-intolerant perennials. Two common opposing restoration practices for wetland plant communities are called self-design vs. intensive revegetation. Self-design restores hydrogeomorphology, but does not inoculate wetland taxa into restoration sites. Self-design may not meet restoration targets if perennial wetland plants are dispersal-limited, preventing plant colonization in restoration sites. However, the alternative practice, intensive revegetation (inoculating wetland taxa into sites following hydrogeomorphic restoration) is costly and time consuming. We investigate whether wetland perennials are dispersal-limited in 309 isolated wetlands among two agricultural landscapes in the U.S. Great Plains (the western High Plains (WHP) and the Rainwater Basin (RWB)) and three land-uses (reference, croplands, and previous croplands) to address the utility of self-design. We also generate analytical tools to predict whether self-design or intensive revegetation will be more successful in isolated wetlands elsewhere. In the WHP and RWB, cover of perennial wetland species were 61% and 31% greater in reference than in cropland and previous cropland wetlands combined. Distance to the nearest reference wetland explained extant wetland plant richness in both regions, and area of surrounding reference wetlands within 15 km also was important in the WHP. Canonical correspondence analysis identified dispersal-limited and cosmopolitan species in reference wetlands, with distance to reference wetlands and area of surrounding reference wetlands important in determining species scores. Further, dispersal-limitation in reference wetlands explained plant cover in clustered and isolated wetlands in previously cropped lands in the WHP and RWB. Plant community patterns in reference systems may predict community composition in previous croplands following restoration. This finding can be used to aid selection of self-design or revegetation as the optimal plant restoration approach in isolated wetlands.

## INTRODUCTION

Loss of wetlands is pervasive in the United States (Dahl 2000) and worldwide (Finlayson et al. 1999). Many remaining wetlands have been impacted by conversion of watersheds from native to agricultural conditions (Brinson and Malvárez 2002). This is particularly true of isolated depressional wetlands worldwide (Brinson and Malvárez 2002). We define isolated wetlands as those in individualized catchments, often containing groundwater connections, but lacking surface water connections to other aquatic areas under normal conditions. Isolated wetlands are estimated to account for approximately 20 % of the numerical total of wetlands in the United States (Tiner et al. 2002); comparable estimates for other parts of the world are lacking. Isolated wetlands are especially vulnerable to agricultural conversion because they often occur in flat, fertile landscapes, allowing them to be easily drained and infilled (Smith et al. 2008). Further, isolated wetlands commonly dry seasonally and are readily cultivated when dry. In this paper, we describe common and opposing practices to restore vegetation associations in isolated wetlands and generate analytical models for predicting the best restoration method.

Isolated wetlands are important because of services they provide common to wetlands in general, including carbon storage capacity, flood water mitigation, habitat for wetland-dependent biota, and purification of surface waters (Tiner 2003, Smith et al. 2008). Further, isolated wetlands maintain stable populations for biota that behave as meta-populations among nearby wetland patches (Hanski 1998, Semlitsch and Bodie 1998, Tiner 2003). Isolated wetlands also provide important stopover sites for migrating wildlife. Thus, loss of these unique habitats is problematic.

Two main philosophies for wetland restoration currently are in practice. The first is based on the concept of self-design (Mitsch et al. 1998). This restoration technique relies on unaugmented colonization by organisms to sites following hydrology and geomorphology restoration. Self-design has also sometimes been called the “Field of Dreams” hypothesis: “If you build it, they will come” (Hilderbrand et al. 2005). This hypothesis suggests that after restoring abiotic processes, organisms self-assemble. For example, in agriculturally modified isolated wetlands, restoration by self-design involves plugging ditches or drainage tiles used to de-water wetlands for cultivation. Removal of upland sediments from wetlands and grading to restore microtopography also are common (Galatowitsch and Van der Valk 1998). Wetland plant communities then are expected to develop from seed banks and dispersal.

However, self-design approaches have been criticized (Streever et al. 2000, Bischoff 2002, Galatowitsch 2006) because dispersal of some plant guilds may be limited by environment and life history traits (van Dorp et al. 1996, Galatowitsch 2006). For example, wetland perennials requiring moist habitats may be dispersal-limited because of intolerance to intervening non-wetland habitat. Further, perennial plants should be more susceptible to landscape isolation than annuals because perennials generally are k-selected whereas annuals are r-selected (Pianka 1970). This previous statement theorizes concerning average plant traits, but we will present analytical tools in this paper for determining traits of individual species. Perennials have been called k-selected because k-selected species are long-lived, slow-growing and competitive in stable environments, but produce few offspring annually (Pianka 1970). R-selected species are short-lived, competitive in fluctuating or disturbed conditions, and produce many offspring in one breeding episode. Species rarely are strictly r- or k-selected, but fall somewhere on the continuum between extremes (Pianka 1970).

As perennials often are k-selected (Pianka 1970), we expect this to limit wetland perennial colonization in disturbed environments such as croplands. Perennial seed sources should also be reduced in agriculturally disturbed seed-banks. We term this model the dispersal-life history wetland plant model. By life history, we mean annual vs. perennial life history strategies. Foundations of this model have been described by others (Godwin 1923, Poschlod and Bonn 1998, Zedler 2000, Ozinga et al. 2005, Galatowitsch 2006, Poschlod et al. 2007). Our model assumes perennials are less effective dispersers than annuals because rates of seed production are less. Therefore, the model predicts, that relative to reference wetlands, perennial wetland plants will be underrepresented and mudflat and shallow water annuals over-represented in agricultural wetlands, or wetlands with a past history of disturbance, such as new restoration sites where agriculture previously occurred.

A wetland restoration approach addressing dispersal-limitation is more time and materials intensive than self-design. The intensive approach involves introducing organisms into restoration sites following restoration of hydrology, usually by seeding or transplanting from nearby reference sites (Streever et al. 2000). Seeding or planting has the advantage of jump-starting plant assembly, potentially reducing establishment of introduced species (Zedler and Kercher 2005). We use “introduced” as defined by the USDA PLANTS database because we used this source to categorize plant species (USDA and NRCS 2010). Thus, here, introduced means plants occurring outside their native range. Disadvantages of the intensive approach include expense, failure of some transplants to establish, and potential failure of restored sites to resemble natural communities. The latter is particularly true if plants are not local genetic varieties or establish disproportionately to native abundance (Zedler and Kercher 2005). Many suggest high initial restoration investments increase restoration success (Klimkowska et al. 2007, Gutrich et al. 2009).

Intensive revegetation and self-design restoration approaches are currently practiced (e.g., Klimkowska et al. 2007, Poschlod et al. 2007, NRCS 2008). Ideally, we would like to predict effective restoration methods to ensure efficient use of time and effort and increase the probability of success. In this paper, we explore the applicability of the dispersal-life history wetland plant model to aid in restoration of isolated wetlands. We investigate this model in two landscapes where isolated wetlands and agriculture occur in high density. We compare effects of landscape isolation on wetland plant communities within major land-use categories to elucidate general principles. We also develop analytical approaches that use extant plant communities in reference wetlands to predict the best restoration practice in regions of interest. Our approach assesses the degree to which landscape isolation limits plant dispersal. Should isolation strongly limit plant dispersal, we suggest revegetation is more likely to establish reference plant communities than self-design. Our approach is powerful because it may identify the best restoration strategy before restoration is initiated.

## METHODS

### *Study area*

We surveyed plants in isolated wetlands, called playas, within two regions of the U.S. Great Plains: the western High Plains (WHP) and the Rainwater Basin (RWB) (Figure III.1). These regions differ in dominant vegetation, land-use history and climate (Smith 2003). Playas in both regions have hydric clay Vertisol soils and are freshwater, recharge wetlands. As such, hydrologic inputs to playas are precipitation and overland sheet flow, while outputs are limited to evapotranspiration and groundwater recharge (Smith 2003). Playas are temporary to seasonal wetlands, remaining wet for periods of weeks to months (Smith 2003). RWB playas are wetter the WHP playas and typically inundate from 1 to several months (Wilson 2010). Individual playas inundate unpredictably and may remain dry for indeterminate periods (Smith 2003, Wilson 2010). Playas in both regions are dominant surface freshwater features because rivers and lakes are rare (Smith 2003, Wilson 2010).

The WHP, a 30 million ha sparsely settled landscape, is a short-grass prairie eco-region encompassing 6 states. Climate in the WHP is semiarid with precipitation varying from 38 cm to 63 cm along a west—east gradient (Smith 2003). Playas average 7 ha (S. McMurry, unpublished data) and are generally round in shape. Up to 60,000 playas occur in the WHP (Playa Lakes Joint Venture, http://pljv.org/). In addition to native short-grass prairie (covering approximately 12 million ha), land-use in the WHP includes croplands (~15 million ha) and United States

Department of Agriculture (USDA) Conservation Reserve Program (CRP) lands (~ 3 million ha) (O'Connell et al. In press). The CRP program was initiated on highly erodible agricultural lands to preserve topsoil by establishing perennial grass cover. This land-use shares features with restoration in that crop production was ceased and the catchment replanted to grass. However, CRP lands rarely resemble short-grass prairie because monocultures of introduced tall-grasses were established in most of the WHP (O'Connell et al. In press) and geomorphology was not restored (e.g., agricultural sediments were not removed). Species richness in CRP playas is greater than in cropland playas and equivalent to grassland playas, but plant composition does not resemble grassland playas (O'Connell et al. In press). True restoration of playas in the WHP is limited to date. However, community composition in CRP playas lends insight into plant assembly after cultivation ceases. We also sampled cropland playas in the WHP, i.e., playas embedded in row-crop agricultural fields and often plowed when dry. We used native, never plowed short-grass playa catchments as our reference condition in the WHP.

The RWB is located in south-central Nebraska (Figure III.1). Climate is more temperate than in the WHP, with greater precipitation, averaging 130 cm yearly (High Plains Regional Climate Center 2011). Playas remaining in the RWB are larger than those in the WHP, averaging 15.6 ha (S. McMurry, unpublished data), and irregularly shaped. The RWB, part of the central plains eco-region, occupies roughly 1.5 million ha, 1.2 million of which has been converted to cropland. Approximately 1800 playas, fewer than 10% of historic playas, remain (Rainwater Basin Joint Venture, www.rwbjv.org). The RWB was originally mixed- to tall-grass prairie, but unlike the WHP, little native prairie is left. Therefore, our reference condition in the RWB is the best available: unplowed playas with some grass buffer between adjacent surrounding croplands. Grass buffers were > 200 m wide and did not cover the majority of the catchment as in the WHP.

We also sampled cropland playas, which in the RWB were those with no buffer between playa boundaries and surrounding cropland, and were often plowed when dry. In addition to reference and agricultural playas, more than 2000 ha of RWB wetlands are in the USDA's Wetland Reserve Program (WRP). WRP restoration in the RWB involved cessation of plowing and removal of eroded agricultural topsoil to restore hydrologic function. Plants then passively recolonized. This represents a self-design restoration technique.

### *Plant composition surveys*

We selected survey playas using GIS databases of probable playa locations (A. Bishop, USFWS, Rainwater Basin Joint Venture, and Playa Lakes Joint Venture). We first randomly selected playas in reference conditions and matched them with nearby playas in other land-uses (cropland and CRP in the WHP, and cropland and WRP in the RWB), generating geographically associated land-use triplets. In the WHP, 261 playas were surveyed (86 each in cropland, CRP and grassland). In the RWB, 48 playas were surveyed (16 each in cropland, grassland and WRP; Figure III.1).

We estimated plant composition and cover using step-point surveys (Evans and Love 1957). Step-point surveys spanned playa diameter along two transects. Surveys involved identification of plants encountered at each step, generating point cover estimates approximately every 1 m. We surveyed playas twice to account for species turnover from cool- (surveyed 10 May – 30 June) to warm-season species (surveyed from 10 July – 31 August) (Smith and Haukos 2002). We collected voucher specimens to verify unknown plants. We recorded whether playas were wet (inundated or surface moist from past inundation) or dry during any field visit.

We list species names as defined in the USDA PLANTS database (USDA and NRCS 2010). USDA PLANTS largely uses taxonomy from the Biota of North America (Kartesz 2011). We used USDA PLANTS to classify plants as annual or perennial and according to water tolerance based on wetland indicator status as described in O'Connell et al. (In press). Biennial species were classified as perennial to simplify analyses. We calculated proportion of wetland cover of all objects encountered (plants, crops, bare ground and water) by adding encounters for each object over both transects and dividing by the total number of steps in both transects.

### *Guild categorization*

We categorized species into guilds incorporating life history traits (annual or perennial), water tolerance and zone of occurrence within wetlands following methods in Galatowitsch (2006). This generates perennial guilds (in order of water tolerance from slightly moist to inundated): wet prairie, sedge meadow, and shallow to deep emergent perennials. Other guilds were (in order of low to high water tolerance): mudflat species (mostly annuals) and shallow emergent annuals. Two perennial species were classified as mudflat species: *Ambrosia grayi* and *Sorghum halepense* because of field observations of habitat. Galatowitsch (2006) also classified some perennial species into a group called "mudflat annuals" based on habitat observations. We follow her methods to enhance comparison between studies, but change the guild name to mudflat species to reflect inclusion of perennials. Species not mentioned in Galatowitsch's study were classified using Stewart and Kantrud (1971), as Galatowitsch did. Species not listed in Stewart and Kantrud (1971) were categorized using field observations, descriptions in Flora of the Great Plains (Great Plains Flora Association 1986), herbarium specimens, and life history designation (annual or perennial) (see Appendix A for categorization of species).

### *Differences in composition, proportion of cover and species richness of perennial guilds among land-use*

To determine if perennial guild composition differed between reference, croplands, and past croplands, we compared plant composition (proportion of total wetland cover for each species) with partial canonical correspondence analysis (pCCA) (CANOCO 4.5, Biometris, Wageningen, The Netherlands). Canonical correspondence analysis (CCA) is a special case of multivariate regression (Palmer 1993), and uses multiple linear least-squares regression to assess relationships of weighted species averages among samples sites along environmental gradients . pCCA is a type of CCA, where variation resulting from co-variables is factored out of species responses, leaving behind variation due to variables of interest (ter Braak 1988). We used survey time (early or late growing season), playa wetness (wet or dry) and latitude and longitude as co-variables, factoring out this variation. This allowed us to determine differences in plant composition among land-use above and beyond that that caused by latitude and longitude, seasonal species turnover, and playa inundation. We used CANOCO to down-weight rare species. This is good general practice because we have incomplete information concerning rare species and must be cautious interpreting relationships for them (ter Braak and Šmilauer 2002). We square-root transformed species cover to reduce influence of outliers. We used CANOCO software to graph species comprising at least 3% of total samples (ter Braak and Šmilauer 2002). A strength of excluding rare species is that conclusions are based on species observed throughout our study areas. For common species, favorable germination conditions were prevalent. Thus, abundances for these species can be modeled more reliably. We used CANOCO to test significance of canonical axes, using Monte Carlo simulation with 999 permutations under the reduced model (Verdonschot and ter Braak 1994). Monte Carlo permutation tests are useful because their only assumption is that data are independent (Verdonschot and ter Braak 1994). We plotted species by guild and visually compared number of species in each guild among land-uses. Species names are shown as the first four letters of the genus and species; see Appendix A for full species names and classification.

We formalized this analysis by comparing cover of wet prairie perennials, sedge meadow perennials, and shallow and deep emergent perennials among land-uses. We used general linear mixed models (GLMMs) with binomial response and logit link between model and response variable (lmer in package lme4 in R, version 2.12.1, the R Foundation for Statistical Computing). A detailed description of GLMMs is provided by Zuur et al. (2009). We accounted for potential spatial correlation in data by designating playa triplets as random variables. For all GLMMs, results were graphed and discussed on the scale of the data for ease of interpretation.

To determine if landscape isolation had significant relationships with richness of wetland perennial guilds in playas (i.e. wet prairie, sedge meadow, shallow and deep emergents), we used ArcGIS to extract distance to nearest reference playa (distance was from the boundary of the surveyed playa to the boundary of the nearest reference playa). Further, we buffered surveyed playas using fine (1 km), medium (5 km), or broad-scale (15 km) radii and extracted area of surrounding reference playas (excluding the surveyed playa) within the buffered region. Dispersal and distance from propagule sources are related (Okubo and Simon 1989, Tilman et al. 1997). Thus, we used regression of species richness on landscape isolation variables to infer dispersal-limitation. We again used GLMMs (Poisson error and log-link between model and response variable, see Zuur et al. (2009)) to compare species richness of wetland plants (facultative wetland through wetland obligates) among land-uses and landscape isolation. The explanatory variables for this analysis were distance to the nearest reference playa, area surveyed within the playa, area surveyed*land-use interaction, playas inundation, area of surrounding playas (within 1, 5, or 15 km) and surrounding playas area*land-use. Over dispersion was investigated and was not evident (Zuur et al. 2009). We used AIC model selection to rank models explaining wetland perennial richness. AIC is mathematically based on log likelihood and is used to rank competing models. We present the highest-ranked model in our results using coefficients averaged among models with $\Delta$ AIC < 4 (Anderson 2008). We also present the proportion of variation explained in wetland plant richness by the best model and a model containing only landscape isolation variables and playa area to assess the degree to which propagule availability explains variation in perennial species richness. We include playa area because area is related to the number of individual plants in wetlands (Rosenzweig 1995), and therefore related to the number of seeds produced *in situ*. Therefore, a model containing wetland area and landscape isolation variables is one that explains the amount of variation in perennial wetland species richness related to the number of propagules produced in the wetland or reaching the wetland. In general linear models, variation explained is determined by deviance (Zuur et al. 2009), where explained data variability is percent explained deviance, e.g., [(null deviance − residual deviance)/null deviance] * 100.

### *Using reference wetlands to predict which plants will have limited presence in previous cropland wetlands because of dispersal-limitation*

We wanted to determine whether plants identified as dispersal-limited in reference conditions had reduced cover in playas where agricultural disturbance has ceased. We compared plants categorized as dispersal-limited or cosmopolitan (e.g., not dispersal-limited) in a pCCA of landscape metrics within reference conditions only. We assumed maximum abundance in isolated wetlands implied species were good dispersers, whereas species maximally abundant in clustered playas should be poor dispersers. Our assumption was based on metapopulation theory, which hypothesizes that populations in small discrete habitat patches, such as isolated wetlands, have higher probability of undergoing local extinction without new colonization events from nearby habitats (Hanski 1998). A justification and a supporting analysis for our assumption can be found in Appendix B.

We used the same covariates, transformations, and inclusion rules as in the pCCA we described earlier in these methods. However, for this model we used manual selection in CANOCO to explore the best landscape metrics to incorporate. If area of surrounding playas was important, we included only the buffered zone explaining the greatest percentage of variation in plant communities in our final model.

This analysis will designate environmental vectors representing degree of landscape isolation: 1) increasing distance from the surveyed playa to the nearest reference playa and 2) increasing area of surrounding playas. Environmental vectors in pCCA point in the direction of strongest correlation between species composition and the depicted variable. The length of the vector increases for stronger correlations. Plant species are plotted as species scores at their centroid of inertia (i.e., where they were maximally abundant). To identify where species load on vectors, one may draw a perpendicular line from species scores to the vector. Species not loading on a vector (on the opposite side of origin) occurred at the lowest values of the variable.

We used the resulting reference playa graph to identify plants common in clustered playas (near to a reference playa and high area of surrounding reference playas). Plants common in clustered playas should load heavily onto the “surrounding playa area” vector and should be on the opposite side of the origin from increasing “distance to reference playa” vector. We categorized these plants as dispersal-limited, regardless of guild. We also identified plants common in isolated playas (far from reference playas and with little area of surrounding reference playas) and categorized these plants as cosmopolitan, meaning they were able to establish in isolated areas.

Next, we identified clustered and dispersed playas in CRP (WHP) or WRP (RWB). To do this, we standardized distance to reference playas and surrounding playa area by converting them to z-scores: *z* = ((observation – mean) ÷ standard deviation). We multiplied z-scores for distance to reference playa by -1 so that increasing (larger) values reflected clustered playas in both metrics. We added the standardized z-scores from both metrics together to generate an overall isolation metric. We then chose the four most isolated and clustered playas by identifying the four lowest and highest scores. We avoided including multiple playas within 20 km of each other in favor of the next most clustered playa, to ensure clustered playas were independent. In the WHP, all of the clustered playas were in Texas. To minimize regional differences when comparing clustered and isolated playas, we limited isolated playas to those in Texas. We again used binomial GLMMs (link = logit) with cover of either dispersal-limited or cosmopolitan plants as the response variable and clustered vs. isolated playa as the predictor. As above, we present variation explained by the model as percent of deviance.

## RESULTS

### *Differences in composition, proportion of cover and species richness of perennial guilds among land-use*

Plant composition differed along all canonical correspondence axes in the WHP (F = 25.58, p = 0.0001) and the RWB (F = 3.32, p = 0.001), suggesting composition differed among land-uses after survey time, location, and playa inundation were taken into account (Figure III.2.a and b).

Fewer species were common in croplands than in reference, WRP, or CRP playas. Plant guild composition also differed by land-use, with wetland perennial guilds under-represented in CRP, WRP, and cropland playas (Figure III.2.a and b). Slightly more mudflat species were maximally abundant in croplands, CRP and WRP than in reference playas.

Cover of wetland perennial guilds was greater in reference and less in CRP or cropland playas in the WHP ($P < 0.001$ for all model effects, Figure III.3a). In the RWB, wet prairie perennials had 20% greater cover in WRP than in reference playas, and 65% greater cover than in croplands. Other perennial guilds in the RWB had greater cover in reference playas than in other land-use ($p < 0.0001$ for all model effects, Figure III.3b). Wet prairie perennials had 34% greater cover in reference than CRP and 93% greater cover than in cropland in the WHP. Sedge meadow perennials were 38% and 66% greater in reference playas than CRP or croplands, respectively in the WHP. In the RWB, sedge meadow perennials were 12% and 70% greater in reference playas than WRP or cropland, respectively. Shallow and deep emergents were 54% and 78% greater in reference playas than in CRP or croplands in the WHP. In the RWB, shallow and deep emergents were 38% and 28% greater in reference playas than in WRP or croplands.

Wetland perennial richness differed by land-use, area surveyed, area surveyed*land-use, and playa inundation in both regions (Table III.1). Further, landscape isolation influenced richness of wetland perennials, with richness of wetland perennials negatively correlated with distance to reference wetlands in both regions (Figure III.4a and b).Surrounding playa area within a 15-km radius corresponded with species richness only in the WHP (Figure III.4a and b). Area of surrounding playas in a 1-km or 5-km radius did not explain variation in species richness in either region, nor did interactions of surrounding playa and land-use within the 1-5 km radius. In the WHP, the final model explaining wetland perennial plant richness accounted for 39% of the variation in the data as indicated by model deviance. A model containing only wetland area, distance to reference and area of surrounding wetlands explained 20% of data variation. In the RWB, the final model explaining wetland perennial plant richness accounted for 45% of the variation in the data. A model containing only wetland area and distance to reference explained 16% of the variation.

### *Using reference wetlands to predict which plants will have limited establishment in previous cropland wetlands because of dispersal-limitation*

Within reference wetlands, species composition varied with all canonical axes, suggesting landscape isolation metrics were correlated with composition in both the WHP and RWB (WHP: F = 3.102, $p < 0.001$; RWB: F = 2.038, $p < 0.001$). In the WHP, distance to reference and area of playas within 15 km were the best predictors of composition (Figure III.5a). Unlike results for perennial species richness in the RWB, both distance to reference and area of playas within 5 km were the best predictors of species composition (Figure III.6a). Dispersal-limited plants had lower cover in isolated CRP or WRP playas and greater cover in clustered playas, while the converse was true for cosmopolitan plants ($p < 0.001$ for all model effects in both regions; Figure III.5b and Figure III.6b; percent deviance explained in the WHP for dispersal limited plants was 35% and was 5% for cosmopolitan species; percent deviance explained in the RWB for dispersal limited plants was 28% and was 10% for cosmopolitan species).

## DISCUSSION

The dispersal-life history wetland plant model was supported by both ordination and GLMM model results suggesting cover of perennial wetland guilds was far less in non-reference land-uses and related to landscape isolation metrics. In the RWB, this was true for guilds with high inundation tolerance, e.g. sedge meadow and shallow and deep emergents, but not for wet prairie perennials, which tolerate somewhat wet to dry conditions. However, precipitation is greater in the RWB than in the WHP. Therefore, the landscape matrix likely was more suitable for wet prairie plants in the RWB than in the WHP, allowing wet prairie perennials to disperse into previous croplands. Perennials requiring inundated conditions to regenerate may have been most dispersal-limited because inundated wetlands were patchier and rarer on the landscape than dry wetlands (O'Connell et al. In press). Thus the conditions for species presence are two-fold. First, propagules for establishment must reach the site (dispersal limitation) or be present in the seed bank (relationship with dispersal discussed below) and conditions for establishment must be present (environmental conditions). Landscape isolation and playa area together explained 16 and 20% of variation in wetland perennial species richness (RWB and WHP respectively) with all land-uses lumped together. Further landscape isolation explained 28% and 35% (RWB and WHP, respectively) of the variation in cover of dispersal limited plants in wetlands with previous agricultural history (CRP and WRP), suggesting that landscape isolation is important for determining cover of some species.

Lack of perennials in playas with cropland watersheds probably was explained by reduced perennial seed banks. Cropland wetlands have shorter hydroperiods than native grassland wetlands and are plowed during dry years (Tsai et al. 2007). Both shorter hydroperiods and plowing may lessen seeds produced by perennials. For example, plowing may remove extant perennials before they re-seed (CH. III). Shorter hydroperiods also may kill perennials intolerant of dry conditions before they re-seed. Some (though not all) perennials produce fewer seeds each season than annuals and are less disturbance tolerant (Shipley and Parent 1991, Kettenring and

Galatowitsch 2011). Therefore, proximity to nearby non-crop playas increases occurrence of perennial wetland species in cropland playas, both in extant vegetation and seed banks.

That croplands may reduce perennial reproduction has been documented by others. For example, a reduced perennial seed bank was documented in agricultural wetlands in prairie potholes (Galatowitsch and van der Valk 1996). Similarly, seed banks in Texas cropland playas also had fewer perennials than annuals and extant vegetation reflected this (Haukos and Smith 1993). In the RWB, both extant vegetation and seeds of perennial species were lower in croplands and WRP than that in reference playas (Beas et al. unpublished data). Thus, lack of dispersal from nearby non-crop wetlands should decrease occurrence of perennial species in both extant vegetation and seed banks. Reduced perennial seed banks lessen perennial cover after cultivation ceases, again, unless perennials recolonize from nearby wetlands.

Additionally, our highest ranked AIC model identified a positive relationship between landscape isolation (distance to nearest reference playas in both regions and area of wetlands in the surrounding landscape in the WHP) and richness of perennial wetland guilds. Importantly, these models incorporated some environmental factors related to germination and disturbance, such as playa inundation and land-use. This means that landscape isolation metrics still explain perennial species richness after accounting for variation due to these factors. Land-use in combination with landscape isolation was not identified as important, suggesting that isolation was important across all land-uses (explained 16-20% of wetland perennial species richness, as mentioned above). In the WHP, both area of surrounding reference wetlands and distance to the nearest reference wetland were important, whereas in the RWB, only distance was important. Playas in the WHP were smaller and drier than those in the RWB (Smith 2003). Thus in the RWB, a nearby reference playa alone may be an adequate source of perennial propagules because playas are large and regularly inundated. In the WHP, a single small nearby reference playa may not be an adequate source because it may often be dry and not contain enough individuals to sustain populations. Haukos and Smith (2004) also demonstrated that species richness increased with surrounding playa numbers in the Southern High Plains. Further cultivation progressively removes cropland playas in WHP because they infill with upland sediments (Luo et al. 1997). Half of the WHP has been converted to cropland, thus likely increasing average dispersal distances between playas.

Other factors may also limit perennial dispersal. Many perennial species reproduce through both seeds and asexual vegetative propagation. When dominant, the latter should further limit long-distance dispersal and representation in seed banks (Takada and Nakajima 1996). Animals also can be important agents of seed dispersal, and tend to disperse seeds of preferred food types (Chang et al. 2005). Sometimes wetland seed dispersal by animals is not as important as dispersal by other means (Chang et al. 2005, Kettenring and Galatowitsch 2011). We do not know whether animal dispersal is important for playa plant communities. We note that eradication of free-roaming buffalo, introduction of cows and farming practices all may have altered dispersal by this means.

Altogether, our results imply many perennial wetland species may be dispersal-limited, even after accounting for variation in land-use and inundation, causing decreased cover of perennials in wetlands where past agriculture reduced perennials from the seed bank. Further, Ozinga et al. (2005) have suggested many plants do not occupy their theoretical niche because of dispersal barriers. Water-dispersed plants, such as many wetland plants, are particularly limited because the movement of water across landscapes is often altered by human development (Ozinga et al. 2009). Prairie pothole researchers also observed wetland perennials were dispersal-limited

(Mulhouse and Galatowitsch 2003, Galatowitsch 2006). Thus, there is growing evidence that dispersal limitation is an important constraint on plant assembly.

Dispersal-limitation observed in reference conditions explained communities in wetlands where agricultural disturbance had ceased, implying reference conditions were good predictors of plant assembly in previous cropland wetlands. Dispersal-limited plants identified in reference playas had greater cover in clustered than isolated WRP or CRP playas, while the converse was true for cosmopolitan plants. Landscape isolation variables explained 28-35% of the variation in cover in isolated playas with previous cultivation history. Therefore, we may be able to predict whether passive recruitment or planting of some species will best meet restoration goals before restoration begins.

We believe these analyses are tools for informing restoration practices in isolated wetlands. For example, our model predicts that in the RWB, isolated unplanted WRP wetlands should develop high cover of *Typha angustifolia* (cattail), *Phalaris arundinacea* (reed-canary grass), *Polygonum pensylvanicum* (pink smartweed), *Echinochloa crus-galli* (barnyard grass), as well as other species encircled by the solid line in Figure III.6a. If wetlands with plant cover dominated by these species meet management goals, then planting is unnecessary. It is worth noting that while not all of these species were annuals, they all were disturbance tolerant and some (e.g., *P. arundinacea*) were nuisance species in the RWB. The spread of nuisance species may be significantly reduced by planting newly restored WRP playas with desirable species when seed sources are available. Others have suggested high species richness can inoculate communities against invasion (Lodge 1993, Tilman 1997). Indeed, *P. arundinacea*, highly invasive in wetlands, sometimes has reduced occurrence in habitats with high species richness (Lavergne and Molofsky 2004). The strength of using ordination techniques to inform restoration decisions is that they depict landscape relationships for individual species. While we argue that perennial wetland plants in general are dispersal-limited, individual species, such as *T. angustifolia*, may differ, with important restoration consequences. Ordination also depicts plant-landscape relationships on the scale of the data used in the region analyzed. Thus, while our study in prairie landscapes with few rivers suggests how plants might behave, the influence of overbank flooding from rivers, or other factors also influence local patterns. These factors can be incorporated into other regional models to inform decisions.

Thus, whether to plant new restorations depends on targeted plant communities and landscape position of restored wetlands. If communities containing mostly cosmopolitan plants as defined by ordination are not acceptable, than the restoration should be planted if it is more than the mean distance away from reference wetlands or has less than average area of reference wetlands in the surrounding landscape. The appropriate metrics determining landscape isolation in plants can be identified using model selection techniques as described in this paper.

Our analysis makes specific restoration recommendations. Lengths of the landscape vectors displayed in pCCA are scaled to the landscape data generating the model. Thus, in the WHP, *Coreopsis tinctoria* (plains coreopsis), *Chenopodium leptophyllum* (narrowleaf goosefoot) and *Polygonum pensylvanicum* (pink smartweed) were more common in clustered wetlands. In the WHP, restored wetlands with > 250 ha of surrounding reference wetlands within 15 km and < 2 km to nearby reference wetlands should not require planting of these species. Similarly, in the RWB, *Alisma trivial* (northern water plantain), *Eleocharis acicularis* (needle spikerush) and *Potamogeton nodosus* (longleaf pondweed) were most abundant in clustered wetlands. In the RWB, clustered wetlands are those with > 1500 ha of reference wetlands within 5 km and < 1.5

km of nearby reference wetlands. Analyses of this kind can be used to make similar recommendations elsewhere.

We hope our model may be generally applicable and can be incorporated into larger restoration efforts. We encourage further analyses in other regions to verify our suggestions. Further, all models have assumptions and limitations. Extant plant composition in reference wetlands is only informative if unmeasured factors were not confounding. Confounding factors may include soil nutrients such as nitrogen and phosphorus, which influence plant colonization and competition. We have data suggesting total soil nitrogen did not differ by land-use in the WHP, though individual nitrogen species may (O'Connell, unpublished data). Preliminary data also suggests phosphorus was similar between reference and cropland playas, but differs for CRP playas (Beas, unpublished data). Similarly, in the RWB, phosphorus was similar in all land-uses, but data on nitrogen were lacking (Beas, unpublished data).

Likewise, hydrology influences wetland plants. Playa inundation was similar among land-use in the RWB (see Appendix D). However, in the WHP, CRP playas inundated less than reference and cropland, probably due to introduced tall-grass cover (Cariveau et al. 2011, O'Connell et al. In press). None of these potential confounding factors varies linearly with patterns in perennial wetland cover and richness. However, it is important to consider confounding factors while planning restoration. While our discussion has concentrated on plant life history and landscape isolation influences on restoration success, we do not suggest these are the only important restoration factors. Rather, we hope these analyses augment toolsets of restoration managers, increasing restoration success and protecting biodiversity.

Table III.1. General linear models of richness of wetland perennial guilds (number of species) in the WHP and the RWB. CI is the parameter 95% confidence interval. Models have Poisson error distribution and log-link between model and response.

| Parameter | Coefficient | Lower CI | Upper CI |
|---|---|---|---|
| Western High Plains | | | |
| Intercept | 2.72E-01 | 1.06E-01 | 4.37E-01 |
| Surveyed area ($m^2$) | 2.04E-06 | 1.67E-06 | 2.42E-06 |
| Distance to reference playa (km) | -2.24E-02 | -3.39E-02 | -1.08E-02 |
| Land-use: CRP | 8.81E-01 | 7.13E-01 | 1.05E+00 |
| Land-use: Reference | 1.10E+00 | 9.38E-01 | 1.26E+00 |
| Playa inundated | 1.80E-01 | 6.59E-02 | 2.95E-01 |
| Playa area (ha) w/in 15 km | 4.40E-04 | 2.99E-08 | 5.81E-08 |
| surveyed area*CRP | -1.39E-06 | -1.87E-06 | -9.20E-07 |
| surveyed area*Reference | -1.76E-06 | -2.19E-06 | -1.34E-06 |
| Rainwater Basin | | | |
| Intercept | 1.29E+00 | 1.01E+00 | 1.56E+00 |
| Surveyed area ($m^2$) | 5.19E-07 | 3.26E-07 | 7.12E-07 |

|  |  |  |  |
|---|---|---|---|
| Distance to reference playa (km) | -1.08E-02 | -2.37E-02 | 2.18E-03 |
| Land-use: Reference | 1.16E+00 | 8.78E-01 | 1.44E+00 |
| Land-use: WRP | 8.91E-01 | 5.91E-01 | 1.19E+00 |
| Playa inundated | 8.73E-02 | -7.63E-02 | 2.51E-01 |
| surveyed area*Reference | -4.79E-07 | -6.77E-07 | -2.82E-07 |
| surveyed area*WRP | -4.09E-07 | -6.26E-07 | -1.93E-07 |

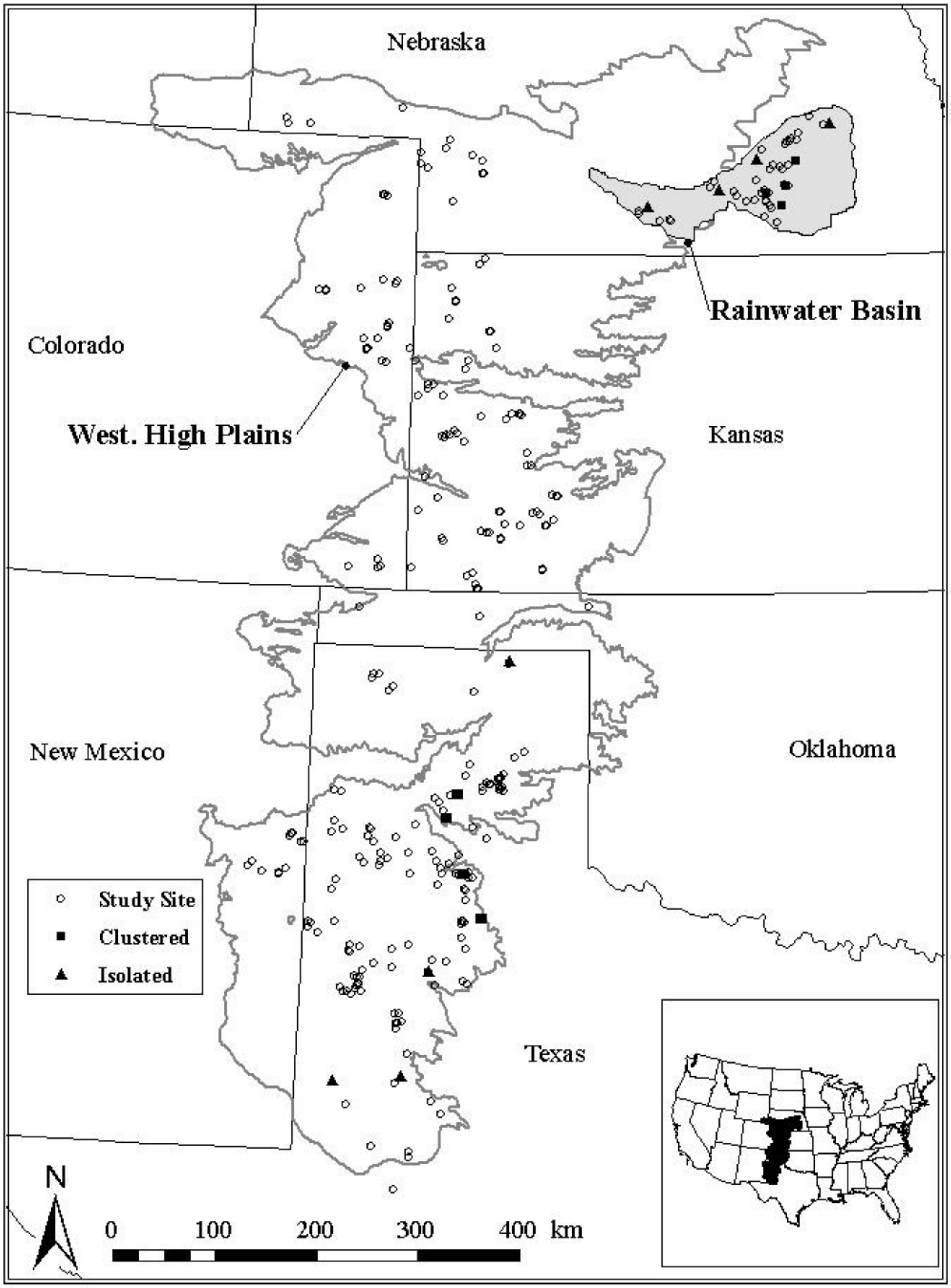


Figure III.1. Locations of study wetlands in the western High Plains and Rainwater Basin, USA. Playas selected for clustered vs. isolated analysis are indicated.

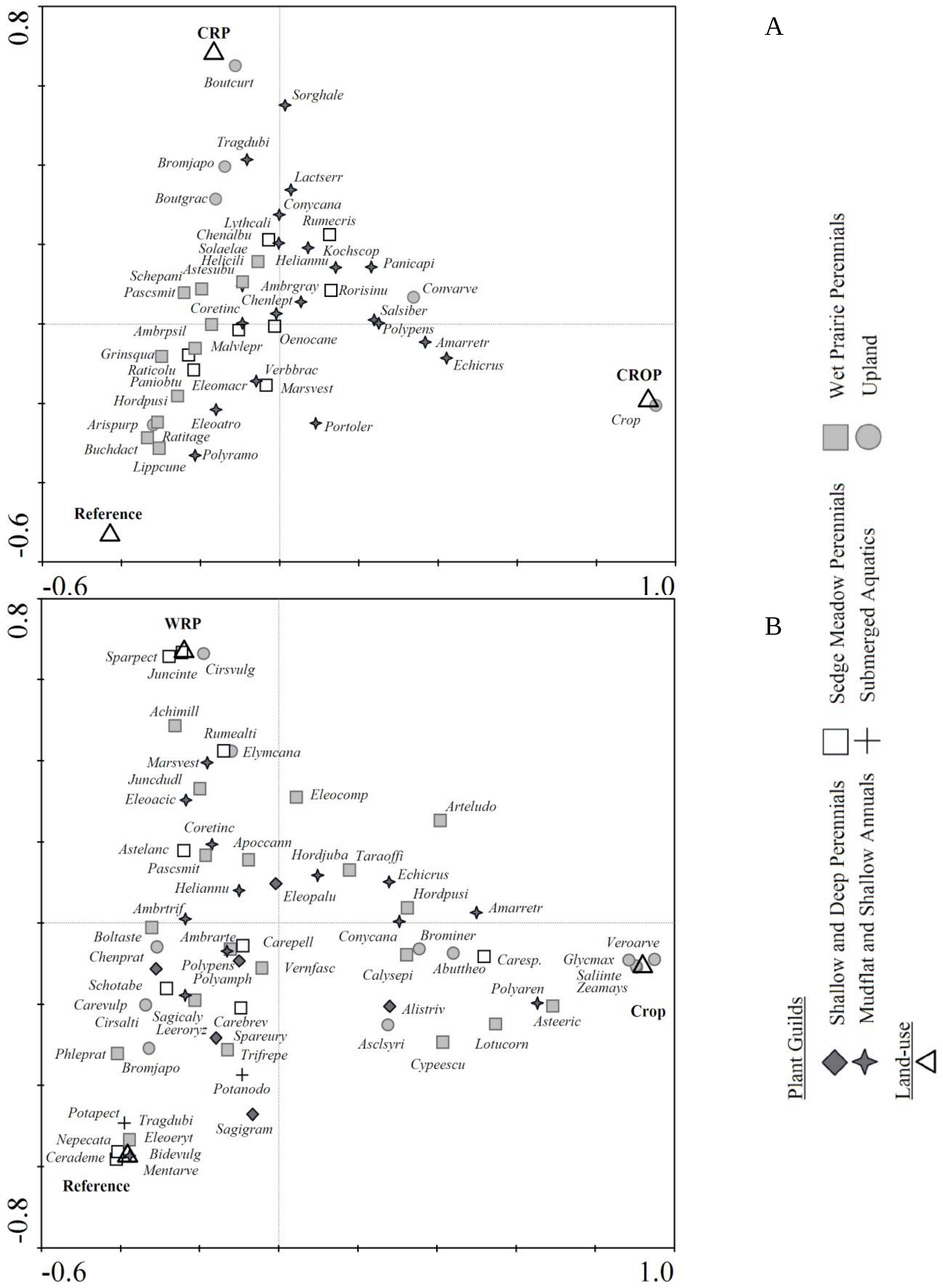


Figure III.2. PCCA of plant community composition (proportion of total cover) among land-use in the WHP (A) and the RWB (B). Species were indicated by the first four letters of the genus and species names. Symbols indicate guild classification.

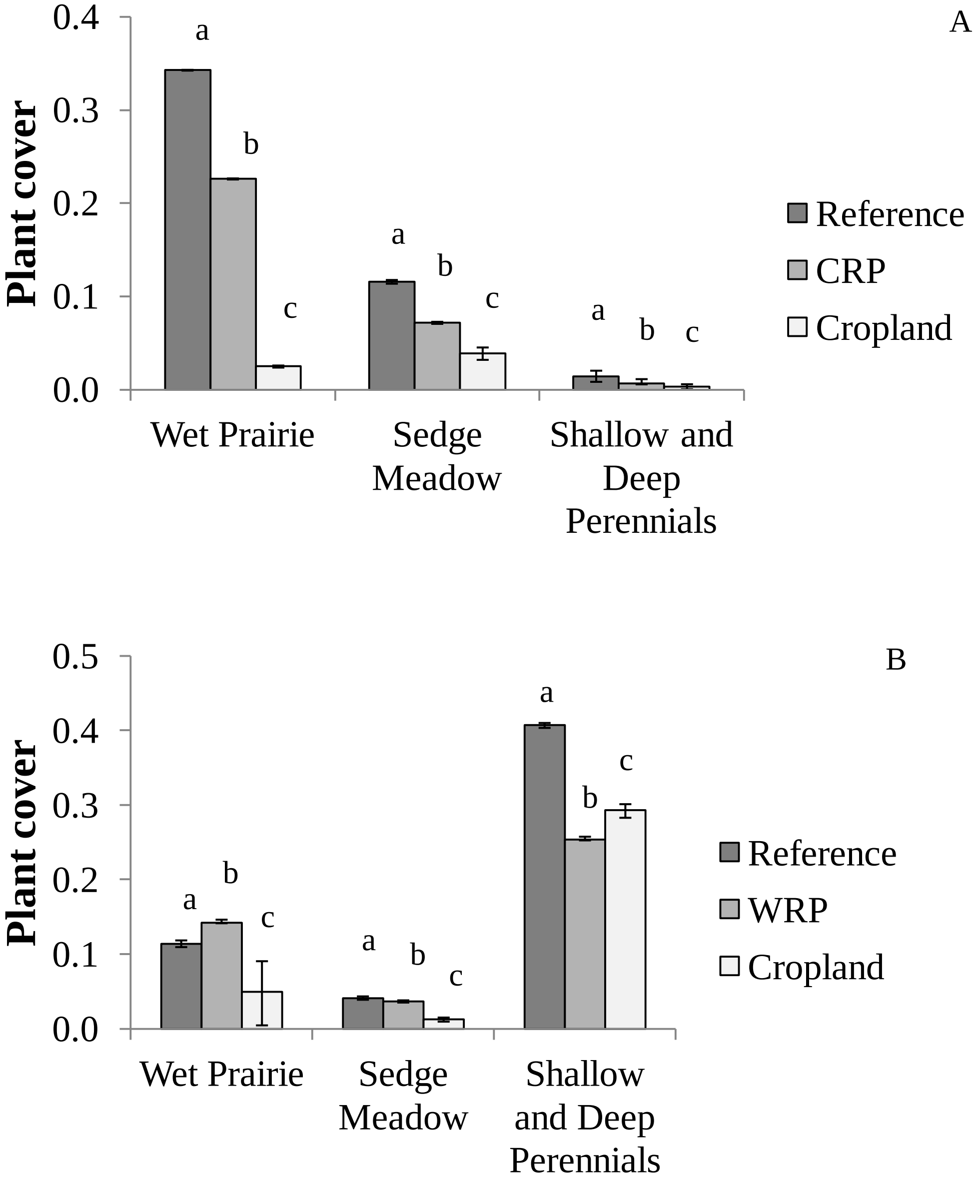
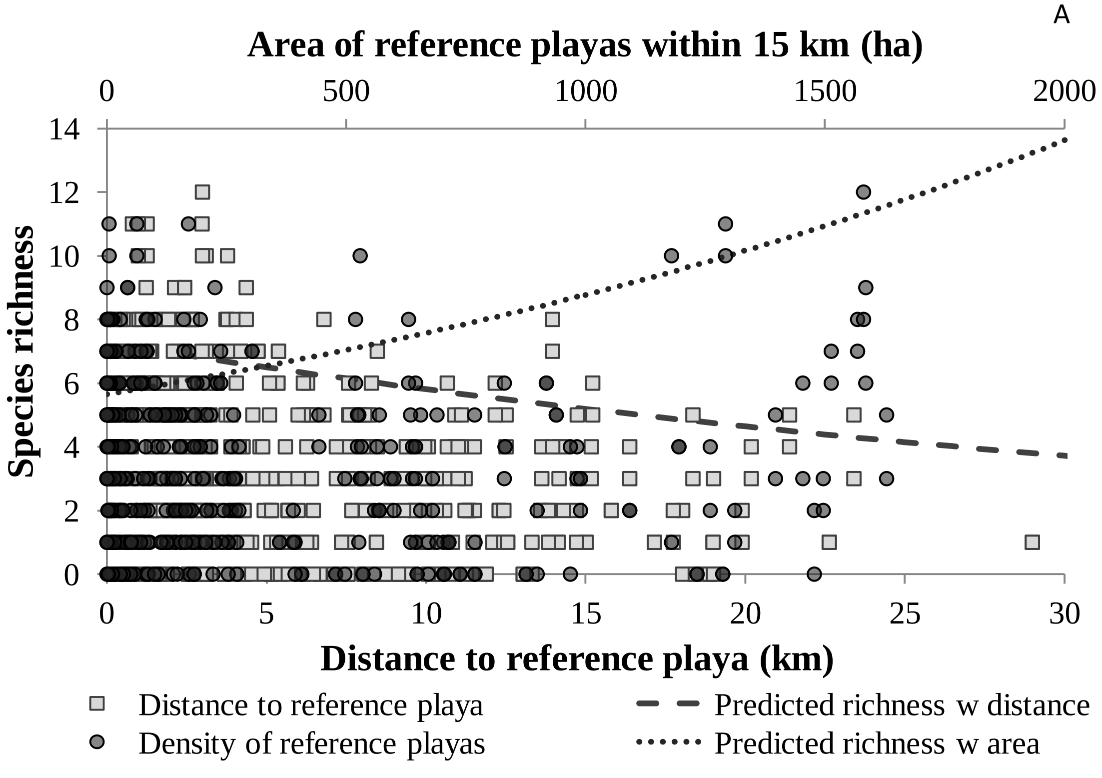


Figure III.3. Wetland perennial guild cover (proportion of total cover) in playas among land-use in the WHP (A) and RWB (B). Lowercase letters indicate significant differences ($P < 0.05$) in plant cover between isolated and clustered playas.



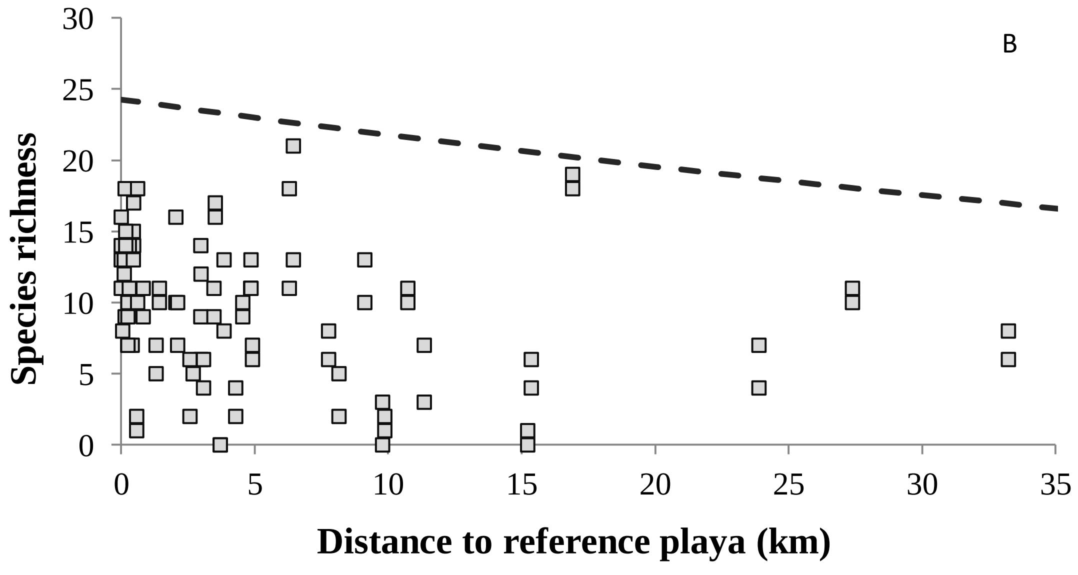


Figure III.4. Richness of wetland perennials (number of species), and landscape isolation metrics in the WHP (A) and RWB (B). Prediction line is in the units of the data and indicates an inundated reference playas with other variables in model (Table III.1) held at their mean.

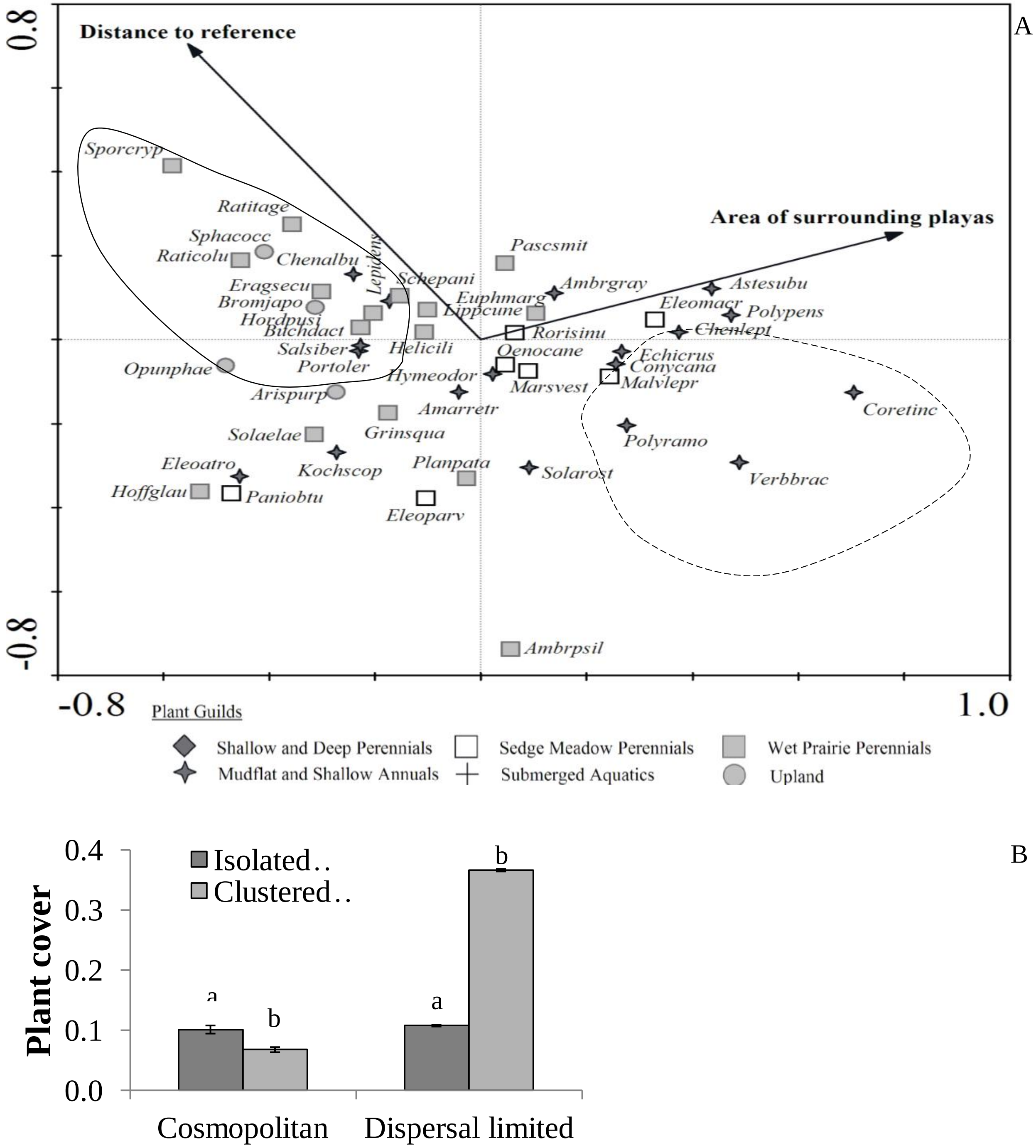


Figure III.5. pCCA of plant composition (proportion of total cover) in reference playas, with distance to reference playa and surrounding playa area within 15 km, in the WHP. Dashed and solid lines encircle dispersal-limited and cosmopolitan species respectively (A). Proportion of total plant cover for cosmopolitan and dispersal-limited plants indentified in (A) found in clustered and isolated CRP playas (B).

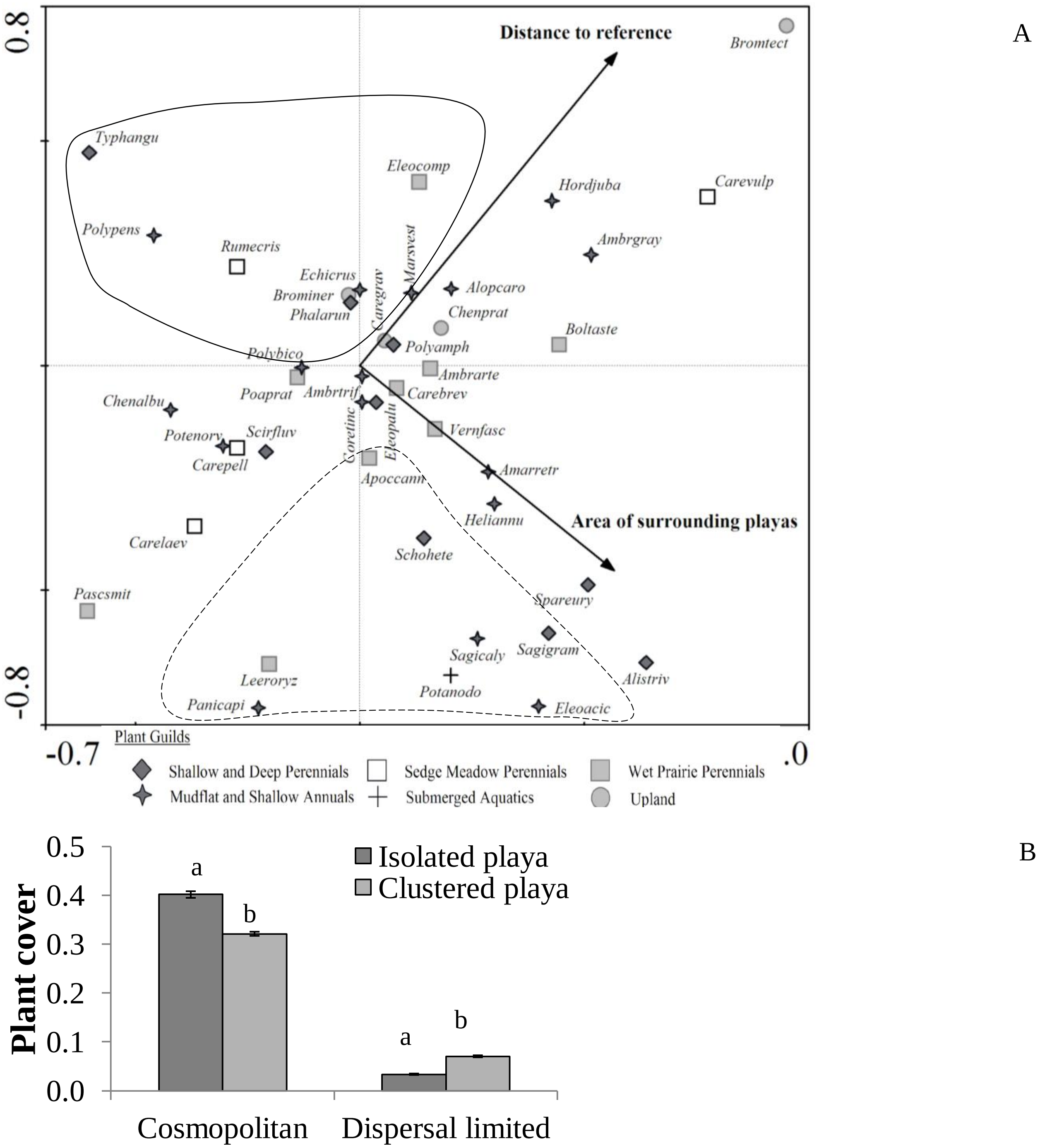


Figure III.6. pCCA of plant community composition (proportion of total cover) in reference playas, with distance to reference playa and area of surrounding playas within 5 km in the RWB (A). Dashed and solid lines encircle dispersal-limited and cosmopolitan species respectively. Proportion of total plant cover of cosmopolitan and dispersal-limited plants indentified in (A) in clustered and isolated WRP playas (B)

# CHAPTER III

# IV. EFFECTS OF SEDIMENT ACCUMULATION ON EMERGENT PLANT COMMUNITIES IN CROPLAND PLAYA WETLANDS OF THE HIGH PLAINS

## ABSTRACT

Identifying community assembly filters is a primary topic in ecology. The High Plains are intensively farmed and these cultivated lands frequently are disturbed. Disturbance includes plowing and eroded topsoil deposition down slope of plowing. These disturbances can influence plant composition in depressional wetlands, such as playas, embedded in cropland catchments. Our objective was to evaluate the influence of sediment deposition and wetland cultivation on wetland plant composition. We surveyed plant communities and measured sediment accretion in cropland playas (46 plowed and 32 unplowed). Sediment accumulation and plowing decreased wetland plant richness, though plowing decreased richness more so. Sediment depth was unrelated to species richness in plowed wetlands, probably because plowing is a stronger disturbance agent. Plowing and sedimentation also influenced species composition. For example, probability of *Eleocharis atropurpurea* increased with sediment depth, while probability of *Panicum*

*capillare* decreased. Unlike richness, species diversity was not related to plowing and sediment depth, perhaps because prevalence of bare ground in cropland wetlands creates sparse but even plant communities. Sedimentation and plowing influences on plant establishment should be considered in playa wetland conservation. As recommended numerous times, conservation practices lessening wetland plant community disturbance should include short-grass buffer strips surrounding wetlands. Further, wetland tillage, allowed under current federal agricultural conservation programs, should be eliminated.

## INTRODUCTION

Playa wetlands are important habitats in the High Plains because they provide sources of water in a semiarid region (Smith 2003). Playas are threatened because short-grass prairies containing playas often were converted to agriculture, altering plant communities and area of inundated habitat (Smith and Haukos 2002, Tsai et al. 2010, O’Connell et al. In press). Further, few regulations protect playas (Haukos and Smith 2003) and restoration of playas has been limited (Smith et al. 2011a). Plant communities in playas provide habitat structure and mediate many ecosystem processes, such as nutrient and water cycling (Smith et al. 2011a). Therefore, determining filters to plant establishment in playa plant communities is important for making conservation recommendations (Funk et al. 2008).

Cultivation of depressional wetland catchments and wetlands is common (Martin and Hartman 1987, Gleason and Euliss 1998, Luo et al. 1999, Brinson and Malvárez 2002, O’Connell et al. In press) and results in alteration of plant communities in embedded wetlands (O’Connell et al. In press). At least two dominant processes likely are responsible for filtering plant occurrence in cropland wetlands. The first is sediment accumulation, a common occurrence in cropland wetlands (Martin and Hartman 1987, Luo et al. 1999, Gleason et al. 2003). Tillage agriculture exposes topsoil and increases sediment loads in overland run-off, depositing upland sediments over wetland soils, decreasing depressional wetland volume (Luo et al. 1997, Gleason et al. 2003). Sediment accumulation also reduces germination of intolerant plant species by burying extant vegetation and seed banks (Gleason and Euliss 1998). Sediment accumulation is important because it may both increase and decrease plant cover and species richness (Wardrop and Brooks 1998, Zobel et al. 2000, Haddad et al. 2008). In non-cropland wetlands, perennial grass cover in the watershed vastly reduces upland sediment accumulation (Luo et al. 1999), eliminating this disturbance on plant communities. Thus, to elucidate effects of sedimentation on emergent depressional wetland plants, we focus on cropland wetlands in this paper.

Croplands also alter embedded wetland plant communities through wetland tillage (O’Connell et al. In press). In croplands, catchment tillage occurs by definition, but wetland basins may or may not be tilled. Tilling playas reduces species richness and plant cover, particularly of perennials (O’Connell et al. In press). Thus, cultivation structures plant communities in wetlands through positive and negative effects on individual species.

In this paper we describe the influence of plowing and sedimentation on cropland playa wetland plant communities. Playas are depressional recharge wetlands, and thus their hydrologic inputs are precipitation and overland run-off, whereas their outputs are groundwater recharge and evapotranspiration (Smith 2003). We refer to playa wetlands, meaning the wetland basins themselves, and catchments, meaning the uplands draining into playas. The influence of eroded upland sediments on playa wetland plant communities has not previously been documented. We hypothesize that sedimentation will reduce species richness because others have suggested that more species are intolerant of sedimentation rates in croplands than tolerant (Jurik et al. 1994, Gleason and Euliss 1998, Gleason et al. 2003). In this paper, we also identify which playa wetland species are most sensitive or tolerant of sediment accumulation. Additionally, we document differences in playa plant communities in plowed and unplowed wetlands. Moreover, we document interactions among sediment accumulation and cultivation because they may yield important conservation information for playa plant communities.

## METHODS

### *Study area*

The High Plains is roughly 30 million ha, and consists largely of flat expanses of short-grass prairie, half of which has been converted to row-crop agriculture (M. McLachlan, PLJV.org, unpublished data). Climate is semiarid and variable, with average yearly precipitation ranging from 38—63 cm along a west to east gradient (Smith 2003).

Playas are round depressions occurring at the lowest elevation in individual catchments. We sampled 78 cropland playas (46 plowed and 32 unplowed playas) from the High Plains, spanning 6 states (Nebraska, Colorado, Kansas, Oklahoma, New Mexico, and Texas) (Figure IV.1). Playas were randomly selected using preexisting GIS databases (see Johnson 2011 for details). Playas were designated as plowed if plow furrows or crops were observed in wetlands during plant surveys.

### *Wetland area and sediment accumulation surveys*

We used GPS (Trimble GeoXT) to survey playa area by delineating playa visual edges. Visual edges were where topography changed from sloped basin edge to flat upland and vegetation changed from hydrophytic to upland plants (Luo et al. 1997). We refined wetland boundary estimates by locating hydric soil edges. To find hydric soils, we cored sediments along transects spanning the visual edge boundary and perpendicular to it. We used two such transects on opposite sides of playa basins. The hydric soil edge was where soil core color and texture changed from wetland soils of heavy clay Vertisols with reduced matrix to coarser, browner upland soils (Schoeneberger et al. 2002, Tsai et al. 2007). See Luo et al. (1997) for a detailed description of distinguishing wetland from upland soil for Randall clay, a common playa soil type in the Southern High Plains.

We also measured depth of upland sediments covering hydric soils by coring to the hydric soil surface in six locations: the center of the playa basin and five equidistant points at approximately one-third the playa radius. To estimate sediment depth, we used the distance (cm) from the soil surface to the depth where cored soils contained greater than 50% hydric soil (Tsai et al. 2007).

### *Wetland plant surveys*

We surveyed plant composition and cover in playas using step-point surveys along two transects spanning playa diameter, following methods in Smith and Haukos (2002). We conducted surveys by walking transects and identifying a single plant species at the toe-tip with each step (Evans and Love 1957). We calculated percent cover for species, bare ground and water by adding both transects together and dividing the number of encounters by the total number of steps. Surveys were conducted twice, once from 10 May – 30 June (cool-season) and once from 10 July – 31 August (warm-season) to capture seasonal species turnover (Smith and Haukos 2002). We also noted whether playas were wet (soils muddy or wetland inundated with standing water) or dry (soil surface dry) during surveys. In croplands, catchments were cultivated by definition, though we did not distinguish fallowed versus cultivated fields.

We classified plants according to wetland indicator status using the USDA PLANTS database (USDA and NRCS 2010). Data collection spanned multiple geographic regions defined by USDA and wetland indicator status differs by region. To be as inclusive as possible, we used the wettest indicator status of sampled regions as our estimate of wetland tolerance. We then limited analyses to plants in facultative minus through wetland obligate categories. We limited our analysis to these wetland plants because upland plants often colonize playas (Smith and Haukos 2002).

### *Statistical analyses*

First, we compared depth of accumulated sediments in plowed and unplowed wetlands using a *t*-test. Next, for plant composition analyses, we used partial canonical correspondence analysis (pCCA) (CANOCO 4.5, Biometris, Wageningen, The Netherlands) to determine effects of sediment accumulation and wetland cultivation on plant communities. Canonical correspondence analysis (CCA) is a form of multivariate regression that uses multiple linear least-squares regression to relate weighted species averages among samples to predictor variables of interest (Palmer 1993). pCCA is a special case of CCA, which partitions variation in species responses into that resulting from co-variables and that due to variables of interest (ter Braak 1988). We used survey time (early or late), playa wetness (wet or dry) and log of playa area as co-variables, factoring out variation from these factors from our results. We used log of playa area because larger wetlands contain more individual plants, influencing species richness (Rosenzweig 1995, O’Connell et al. In press).We log-transformed surveyed wetland area because area is exponentially related to species richness, rather than linearly (Rosenzweig 1995).

For pCCA, we also down-weighted rare species and square-root transformed species cover to reduce influence of outliers (ter Braak and Šmilauer 2002). Down-weighting rare species is good practice because we lack complete information for rarely observed species. Inference based on species with sparse occurrence data may give misleading interpretations. We used 999 Monte Carlo permutations under the reduced model to determine the significance of ordination axes (ter Braak and Šmilauer 2002). We graphed species responses verses ordination axes, and depicted species according to guilds that incorporated water tolerance and perennial or annual life history in graphs. We used wetland plant guilds as defined by (Galatowitsch 2006).Wetland plant guilds observed in cropland playas were mudflat annuals and wet prairie perennials (tolerate moist soils), and sedge meadow perennials and shallow annuals (tolerate shallow water a few centimeters deep). We used wetland indicator status and life history traits listed for species in USDA PLANTS to classify species into guilds. See O'Connell (2011, Chapter II) for further details on guild classification and guild definitions. CANOCO depicts species relationships with environmental variables by graphing them at their centroid of inertia (i.e. where they were maximally abundant) in relation to explanatory variables. Further, we confirmed trends with sediment depth suggested by ordination for selected individual species. For these confirmatory analyses, we used CANOCO to predict selected individual species presence/absence with sediment depth using binomial general linear models (binomial error and logit link between model and response variable). We chose to model *Panicum capillare, Rumex crispus, Eleocharis atropurpurea*, *Lactuca serriola*, and *Amaranthus blitoides* as examples of species responses with sediment depth.

We also evaluated relationships among species richness, species diversity, sediment depth and cultivation via general linear models. We again included log of playa area as a covariate because area sampled influences the number of individual plants observed. Species richness was the number of wetland species observed. We used Simpsons diversity index as our estimate of species diversity, because it provides an unbiased estimate as long as the number of individuals is >2 (Hurlbert 1971), as was the case for our samples. We used the vegan package in R to calculate Simpson indices for all samples (R, version 2.12.1, the R Foundation for Statistical Computing). To model species richness, we used a Poisson error distribution and log-link between model and the response variable. To model species diversity, we used binomial error and logit link between the model and response variable (Zuur et al. 2009).

Our analysis assumes sedimentation is a periodic, reoccurring disturbance experienced by plants. Thus, we supposed that the depth of accumulated upland sediments was a good approximation of the intensity of sediment disturbance experienced by extant plants in playas. Conversely, if sedimentation does not occur regularly, sediment depth may reflect a past disturbance rather than one experienced by plants we surveyed. However sediments are likely to be annually deposited in cropland playas where bare ground in upland catchments is common (O’Connell et al. In press) and catchment plowing occurs annually. Precipitation runoff of these bare fields is the main agent of sediment import into playas (Smith 2003).

## RESULTS

Sediment depth was different in plowed and unplowed wetlands ($F_{1, 154}$ = 3.11, $P$ = 0.08; mean plowed = 34 cm ± 2.5 cm, mean unplowed = 29 cm ± 3.1 cm). However, ordination supported that species composition in playas differed in plowed and unplowed wetlands and along a sediment depth gradient after wetland area, survey time and inundation were accounted for (significance of first axis $F$ = 3.68, $P$ = 0.001, significance of all canonical axes $F$ = 2.76, $P$ =

0.001) (Figure IV.2). Sediment depth increased likelihood of encountering some species while it decreased others (Figure IV.2, Table IV.1). For example, *Rumex crispus* and *Eleocharis atropurpurea* were found more often in sediment depths > 50 cm, *Lactuca serriola* had little relationship with sediment depth and *Panicum capillare* and *Amaranthus blitoides* were less likely to be found as sediment depth increased (Table IV.1, Figure IV.3).

Further, our general linear models suggest plowing and sediment depth significantly explained species richness of wetland plants (Table IV.2, Figure IV.4, percent deviance explained = 44%). Unplowed wetlands had 70% greater richness than plowed (10 vs 3,Table IV.2). Interactions among wetland area and sediment depth were not significant ($P = 0.37$). Interactions among sediment depth and wetland plowing also were not significant ($P = 0.15$). Species diversity did not vary with sediment depth, wetland area or wetland cultivation ($F_{3,152} = 1.153$, $P = 0.33$, mean = 0.53, Figure IV.5).

## DISCUSSION

Plowing and upland sediment accumulation influenced plant composition and species richness. Plowing reduced presence of some plant species. We previously demonstrated that plowing was destructive of wetland plant communities (O'Connell et al. In press). In this study, we saw that perennial wetland species particularly were reduced. Perennial adult plants require multiple seasons to generate new individuals through seed or propagules. Plowing seasonally destroys adult plants, preventing most perennial reproduction. Thus perennials should not be represented without dispersal from nearby wetlands. Further, perennial wetland species often are dispersal limited (Galatowitsch 2006). Thus, reduced cover of perennial wetland species in plowed playas was expected.

Sediment depth also was associated with decreased species richness, and is a consequence of tilling wetland catchments (Luo et al. 1999). Sediment depth was negatively associated with species richness in unplowed playas, whereas species richness was relatively constant with sediment depth in plowed wetlands. In plowed wetlands, sediment depth likely was unrelated to species richness because plowing is a far greater disturbance than sediment accumulation. Interestingly, species diversity, rather than richness, was not influenced by sediment accumulation and plowing, probably because plant cover was generally reduced in cropland playas (O'Connell et al. In press), while bare ground increased, resulting in even, but sparse, plant communities. Thus, sediment accumulation and plowing were associated with plant community composition differences in embedded wetlands.

As predicted, sediment accumulation increased the likelihood of encountering some species. Species associated with deeper sediments were those plotted in Figure IV.2 in the quadrant of the graph where the sediment depth vector is increasing. For example *Eleocharis atropurpurea* was observed only in cropland wetlands with >50 cm sediment depth. Conversely, sediment accumulation reduced cover of some species, e.g., those on the opposite side of the origin from the increasing sediment depth vector in Figure IV.2. For example, *Panicum capillare* had reduced probability of occurrence in wetlands with deep sediments. Figure IV.2 may be a useful predictive tool for those managing for target wetland communities because it illustrates relationships with sediment depth and wetland cultivation.

Others also have demonstrated that sediment depth and plant communties were related. Even slight sediment accumulation strongly reduces seedling emergence, e.g., 0.25 cm (Jurik et al. 1994), 0.5 cm (Dittmar and Neely 1999, Gleason et al. 2003). In our study the lowest sediment depth observed in cropland wetlands was 7 cm, suggesting plant communities we observed already were a subset of those with some sedimentation tolerance. Others have suggested large seeded plants generally are less affected by sediment than smaller seeds (Jurik et al. 1994, Dittmar and Neely 1999), perhaps because larger seeds have greater nutrient reserves, allowing seedlings to push through deep sediments to the soil surface. We did not measure seed mass in this study, but Flora of the Great Plains reports seed length, a proxy for seed mass (Great Plains Flora Association 1986). Patterns among seed length and relationships with sediment depth were not apparent in this study (Table IV.1). Similarly to Dittmar and Neely (1999), we observed few patterns with perennial and annual life history and resilience to sediment accumulation (e.g. Figure IV.2), though plowing was strongly associated with annual species as mentioned above.

Croplands, wetland cultivation and sedimentation probably were not randomly distributed across the High Plains, and we should consider the influence this may have on results. For example, we note there were regional differences in the percentage of plowed and unplowed wetlands (Oklahoma and further north $N_{\text{unplowed}} = 8$ and $N_{\text{plowed}} = 25$; south of Oklahoma $N_{\text{unplowed}} = 23$ and $N_{\text{plowed}} = 21$). Therefore, differences among regions, such as climate could be confounding. However, average monthly precipitation during surveyed months was similar among High Plains' states (NOAA 2011). Further, the main action of wetland cultivation was to reduce plant communities to mainly annual species. We did not observe differences in the cover of annual species in cropland wetlands among northern and southern states (O'Connell et al. In press). Thus, regional differences in plant cover among northern and southern wetlands do not explain conclusions concerning wetland cultivation. Additionally, sediment depths were not similar between northern and southern wetlands (Oklahoma and further north $_{\text{unplowed}} = 19.2$ cm and $_{\text{plowed}} = 13.3$ cm; south of Oklahoma $_{\text{unplowed}} = 38.5$ cm and $_{\text{plowed}} = 41.6$ cm). Perhaps deeper sediments were observed in southern cropland playas because of longer cultivation history there

(Smith et al. 2011b). Thus, probably fewer sediment intolerant species were observed in southern cropland playas.

Plant communities in crop playas may more closely resemble those in non-crop catchments by minimizing wetland tillage and reducing sediment accumulation. To achieve this, conservation programs within the United States Department of Agriculture (USDA) should be promoted. These conservation programs provide landowner incentives to reduce sediment loads and plowing. For example, short-grass buffer strips of native prairie species can be planted surrounding wetlands to catch sediments in overland run-off (Skagen et al. 2008). The USDA also has the Wetland Reserve Program for wetland enhancement, restoration and protection. Such programs should be promoted in the High Plains, as in other regions, to help protect playa communities (Smith et al. 2011a). Finally, there are the Highly Erodible Land Conservation and Wetland Conservation Compliance provisions, which have been termed “Swampbuster”. Swampbuster provisions deny USDA benefits to producers who farm wetlands after 1990, but allows crop production on wetlands dry through natural conditions (Glaser 1985). Seasonal wetlands such as playas are commonly dry, and therefore Swampbuster is not an effective deterrent to playa tillage. For example, 59% of the wetlands we surveyed were plowed. Our data suggest that plowing wetlands reduces plant cover and species richness, alters community composition and removes perennial wetland species. Swampbuster would be more effective if it were modified to prevent plowing of wetlands with hydric soils (i.e, those likely to become wet when climate allows). Row crop agriculture covers 15.6 million ha in the High Plains. Our pre-existing GIS database (described in methods) suggest that 39,000 ha of cropland playas occur in High Plains croplands. If we extrapolate parameter estimates from this study, plowing occurs in 60% of crop playas (23,400 ha), reducing plant species richness to an average total of 3 species and plant cover to an average total of 5% (O’Connell et al. In press). Therefore, plowed wetlands reduce plant structure for wildlife habitat and wetland functions that rely on plants across the High Plains. These trends can be remediated by farmer education and more effective enforcement of Swampbuster provisions, integrating agriculture with functioning wetland ecosystems.

Table IV.1. General linear models explaining presence of selected species in High Plains cropland playas from Figure IV.2. Models have binomial error distribution with logit link between model and predictor variables. For reference, seed lengths also are provided (Great Plains Flora Association 1986).

| Species | Seed length (mm) | Intercept | Sediment | F | P |
|---|---|---|---|---|---|
| *Amaranthus blitoides* | 1.5-2 | -1.23 | -0.028 | 3.11 | 0.080 |
| *Eleocharis atropurpurea* | 0.5-0.6 | -7.53 | 0.102 | 89.95 | < 0.001 |
| *Lactuca serriola* | 2-3 | -1.28 | -0.001 | 3.10 | 0.082 |
| *Panicum capillare* | 1.5 | -0.09 | -0.054 | 9.20 | 0.003 |
| *Rumex crispus* | 2 | -2.56 | 0.021 | 2.80 | 0.096 |

Table IV.2. General linear model explaining species richness of wetland plants in High Plains cropland playas. Model has Poisson error distribution with log link between model and predictor variables.

| Factor | Estimate | SE | Z | P |
|---|---|---|---|---|
| Intercept | 2.019 | 0.095 | 20.69 | < 0.001 |
| Sediment depth (cm) | -0.004 | 0.002 | -2.15 | 0.031 |
| Log of surveyed wetland area (ha) | 0.624 | 0.133 | 4.92 | < 0.001 |
| Playa plowed | -1.226 | 0.075 | -15.95 | < 0.001 |

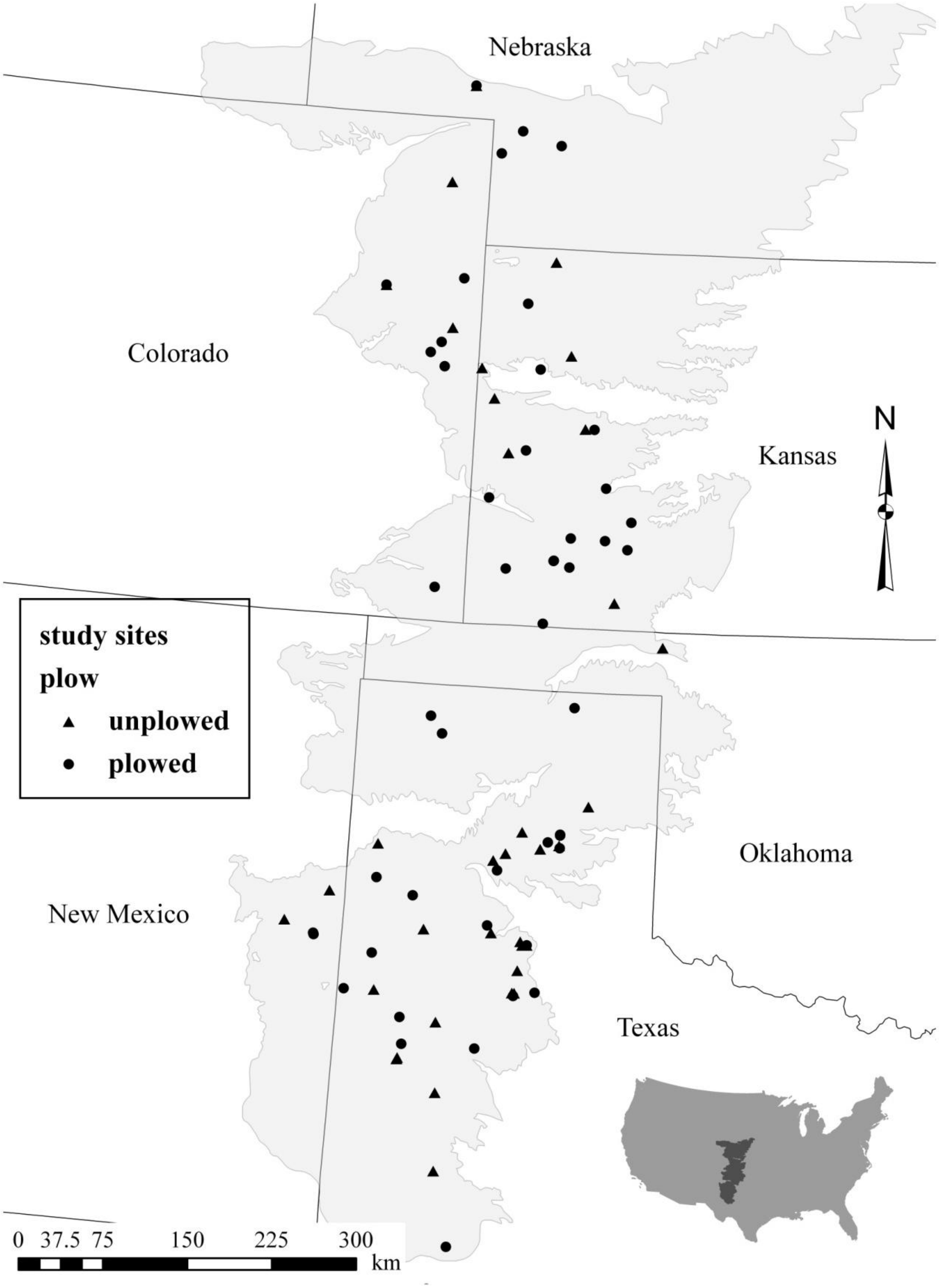


Figure IV.1 Locations of study wetlands in the High Plains, USA. Cultivated and uncultivated wetlands are indicated. The extent of the High Plains is shaded.

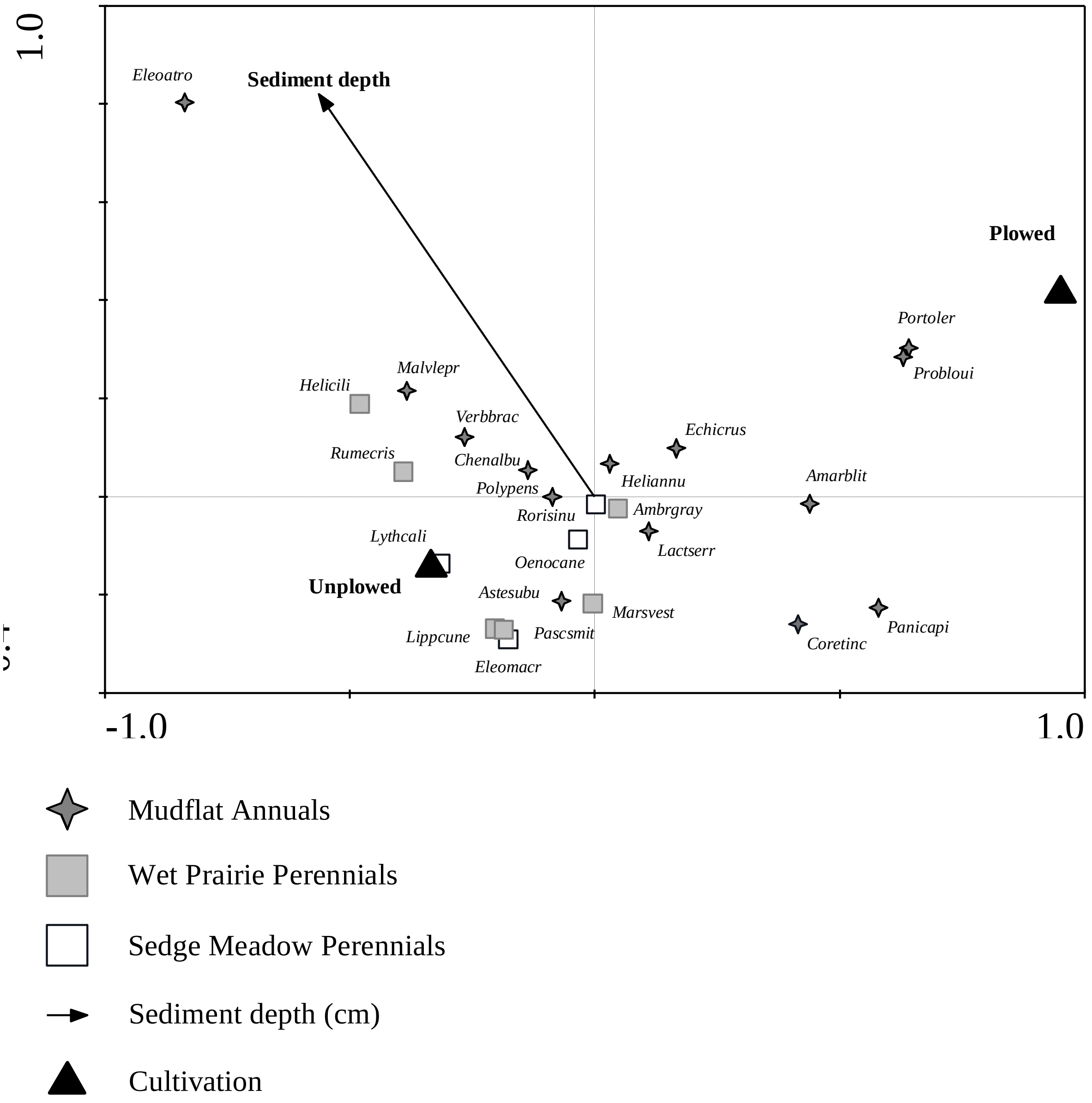


Figure IV.2 First and second canonical correspondence axes (graphed on x and y axes respectively) relating species composition with plowing and sediment import (depth in cm). Species are shown as the first four letters of the genus and species names. See Appendix A for full names.

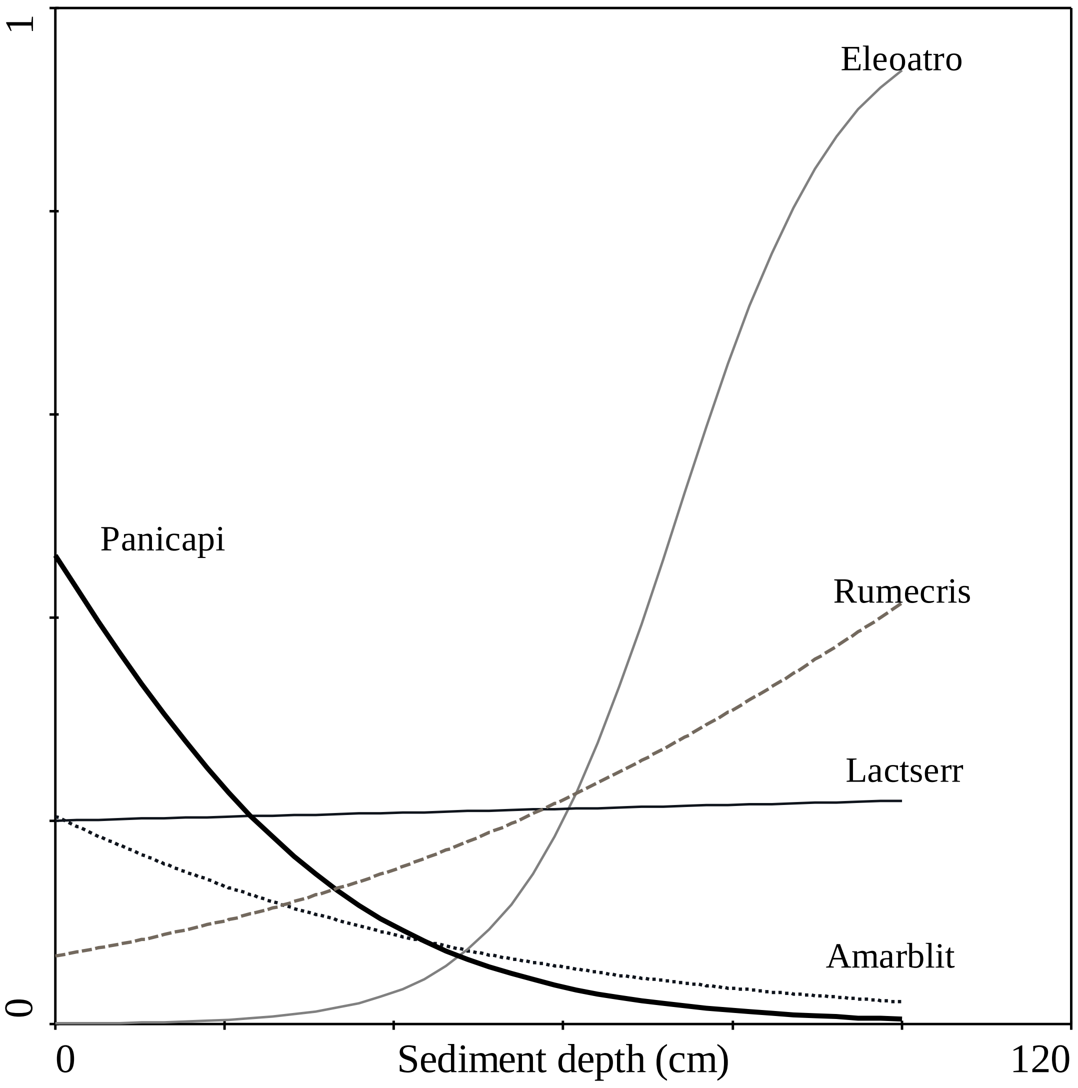


Figure IV.3. Probability of presence with increasing sediment depth for selected species depicted in Figure IV.2. General linear model equations and full species names are listed in Table IV.1. These models have binomial error distribution and logit link between the model and response variable.

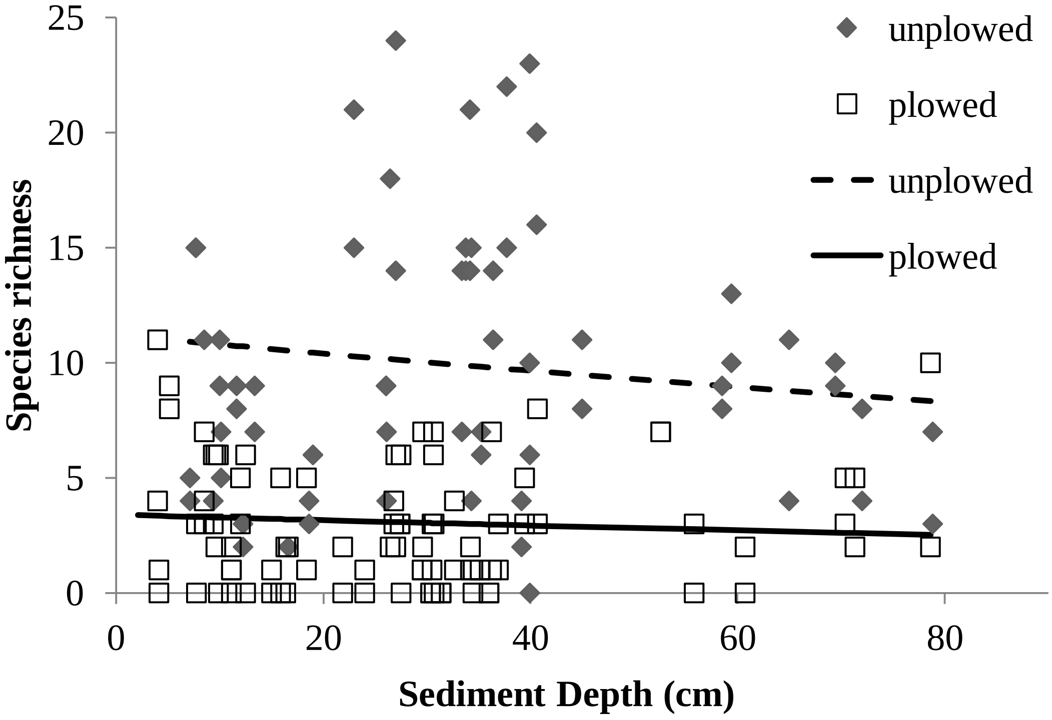


Figure IV.4. Predicted species richness of wetland plants from a general linear model (graphed in the units of surveyed species richness) in cultivated and uncultivated playas. Model has Poisson error distribution and log-link between model and response variable.

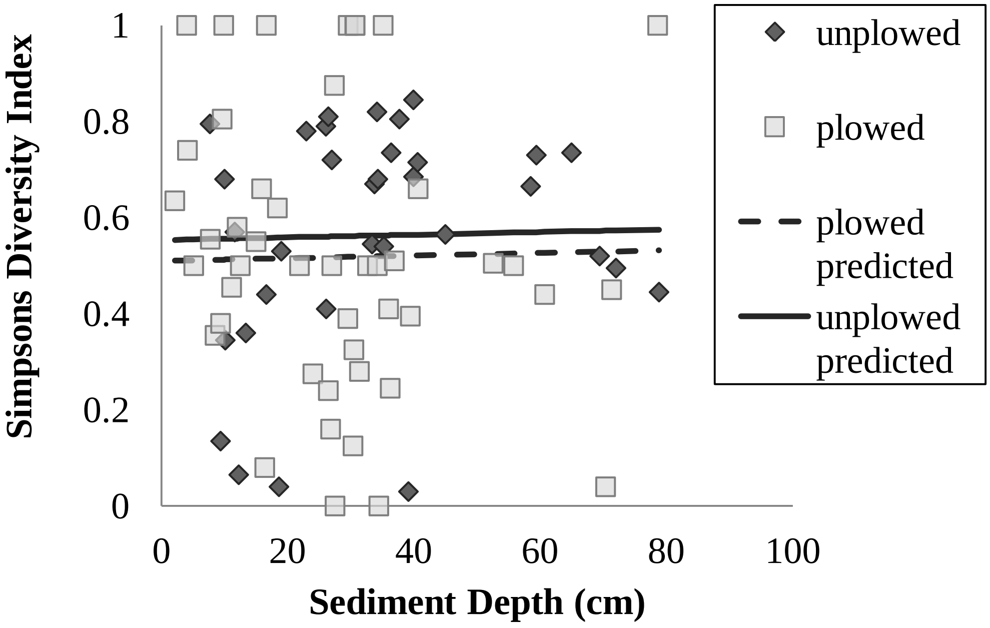


Figure IV.5. Predicted Simpson's species diversity index for wetland plants in cultivated and uncultivated playas of the High Plains, USA with log of wetland area as a covariate. We observed no significant differences for relationships among Simpson's Index and sediment depth and wetland cultivation.

# CHAPTER IV

## V. EFFECTS OF LAND USE AND CONSERVATION PROGRAMS ON SOIL ORGANIC CARBON SEQUESTRATION IN PLAYAS, ADJACENT PRAIRIES AND CROPLAND OF THE HIGH PLAINS

### ABSTRACT

Soil organic carbon (SOC) is an important carbon reservoir. Some land practices may promote SOC storage and lessen atmospheric $CO_2$ (associated with climate warming). SOC estimates are lacking for some habitats, including High Plains playa wetlands. Therefore, we examined SOC within playa catchments (wetlands plus watershed) among common land-uses (55, 55, and 56 in native grassland, Conservation Reserve Program (CRP) lands, and cropland, respectively). We hypothesized SOC differed among land-uses, habitats (wetland and upland) and that wetlands and uplands might interact, influencing SOC. We estimated SOC (kg $m^{-2}$) to a depth of 50 cm from 4 soil cores/catchment (playa centers, and 10, 40 and 100 m outside playas). In 17 catchments/land-use, we estimated SOC to 100 cm to identify deeper SOC patterns. For each core, we also estimated plant species richness, belowground biomass and soil moisture to determine relationships with SOC. In playas, SOC to 50 cm depth was 15%

greater in CRP than croplands, but was not different from grassland SOC. To 100 cm, SOC was 24% greater in grassland and CRP playas than cropland. In uplands, SOC averaged 28% greater in grassland than cropland to 50 cm and was 24% greater than cropland and CRP to 100 cm. We estimate 30-100 years are required for CRP uplands to resemble native grassland SOC. SOC increased with species richness in grassland and cropland catchments, but decreased with increasing richness in CRP, suggesting species composition influenced SOC. SOC increased with playa area at all CRP and grasslands points, suggesting playas and uplands interact, influencing SOC. Playa area was not related to SOC in croplands, perhaps because cropland playas were smaller. In croplands, playa tillage reduced total catchment SOC by 10%. High Plains playas store 7.1 Tg C and conversion to cropland caused loss of 1Tg C. To promote SOC, we should conserve large playas and species rich native grasslands, refrain from tilling cropland playas and maintain CRP enrollments in native grass mixtures over long timescales.

## INTRODUCTION

Soil organic carbon (SOC) represents more than two-thirds of global terrestrial organic carbon stores, and significantly more than carbon in terrestrial vegetation (Post et al. 1982). SOC therefore is an important global carbon reservoir, and residence times of some soil carbon exceeds 1000s of years (Post et al. 1982). Organic carbon does not accumulate indefinitely in most soils, but equilibrates at some level determined by soil parent material, climate, biota (vegetation and soil fauna), topography, and time since soil development (Sumner 2000). SOC therefore varies considerably across landscapes and land management exerts significant influence on stocks (Post and Kwon 2000, Sumner 2000). Therefore, quantifying SOC and identifying management promoting SOC sequestration may help mitigate global climate change (Flatch et al. 1997, Rees et al. 2005).

SOC inputs are plant root exudates, microbial biomass, and root decomposition, while plant litter contributes a minor fraction to total SOC (Rasse et al. 2005). All SOC does not cycle through soils at the same rate (Post and Kwon 2000, Paul et al. 2006). Turnover rates differ because organic carbon is either labile and rapidly cycled or stable and incorporated into soil organic matter by physical and chemical encapsulation within soil aggregates (Six et al. 2002). Stable SOC accumulates gradually and decomposes slowly. Chemical stabilization involves binding of carbon with clay and silt, and smaller soil particles have greater binding surface area available. Thus, soils with more clay and silt have greater SOC than coarser soils, other factors being equal . SOC also may be physically protected by encapsulation of soil particles in micro-aggregate soil structures, making them physically unavailable for digestion by soil organisms (Sumner 2000). Consequently, soils with more intact aggregate structure, such as lands without tillage agriculture, may have more SOC (Sumner 2000). Soils with biochemically complex organic matter also have greater SOC. For example, root turnover contributes to long-term SOC because roots have greater structural complexity than root exudates and microbial mass (Rees et al. 2005). Accordingly, plant communities with extensive root structure, such as grasslands, will have greater SOC than plant communities with sparser roots, assuming climate is equivalent (Jackson et al. 2002).

Further, wetlands may store more SOC than some habitats because standing deep water causes anaerobic conditions, retarding decomposition of organic matter (Raich and Schlesinger 1992, Trumbore 1997). Draining and developing wetlands often results in $CO_2$ export to the atmosphere (Trumbore 1997). Conversely, wetland conservation may help mitigate global climate change (Euliss et al. 2006). Playas are depressional, recharge wetlands common in short-grass prairies of the central United States High Plains (Smith 2003). Playas are important in this semiarid region because they provide biodiversity refugia for plants and animals, alleviation of flooding, water filtration and storage, and aquifer recharge in a landscape where precipitation is variable and scarce (Smith et al. 2011a). Throughout this paper we refer to playas (wetland basins themselves), uplands (non-wetland higher elevation areas surrounding playas), and catchments (playas combined with the uplands that drain into them).

Land-use alterations are known to alter SOC (Sumner 2000, Lal et al. 2001) and common surrounding High Plains playas (Luo et al. 1999, O'Connell et al. In press). Alterations in the High Plains landscape include two main types. The first is grassland conversion for crop cultivation, such as wheat, corn and cotton. Crop agriculture increases cover of introduced weeds and bare ground and also results in upland sediment accumulation in wetland basins (Luo et al. 1999, O'Connell et al. In press). Excessive sediment accumulation reduces playa volume, increases inundated surface area, increases evaporation losses and reduces playa hydroperiods (Tsai et al. 2007). Upland sediment accumulation in playas also buries playa hydric soils, possibly altering relationships of SOC with depth in playas. Conversion of grassland to cropland can result in 20-30% losses of SOC, depending on soils and original land-use (West and Post 2002).

A second common land-use alteration in the High Plains is the United States Department of Agriculture (USDA) Conservation Reserve Program (CRP) lands (Smith et al. 2011a). In the High Plains, CRP removes highly erodible croplands from production by planting perennial grass cover. CRP covers approximately 15% of the High Plains landscape and thus is a common land cover category (O'Connell et al. In press). Unfortunately, grasses used in most of the High Plains were introduced tall-grasses (O'Connell et al. In press). These grasses provide barriers to overland sheet flow in catchments, reducing erosion, but also reducing inundation frequency in wetlands (Detenbeck et al. 2002, van der Kamp et al. 2003, Cariveau et al. 2011, O’Connell et al. In press). Altered inundation frequency will likely alter soil moisture. Soil moisture increases SOC, therefore altered inundation frequency may influence SOC in the High Plains. Further, SOC generally has been shown to increase in CRP over the croplands they replace, but rates of accumulation vary with climate and other factors (Post and Kwon 2000). Previous studies have not evaluated how playas, CRP, and grasslands influence SOC in the High Plains. Both croplands and CRP lands change vegetation communities and water cycling within embedded wetlands and may be important for altering SOC stores.

Further, SOC may vary within playa catchments because soil moisture and texture may vary with distance from playas. Moist and finer-textured soils generally increase SOC (Jobbágy and Jackson 2000, Jackson et al. 2002). Moisture increases SOC partially because very dry soils retard microbial activity (Sumner 2000). Additionally, clay content increases SOC as mentioned previously because clay has high surface area for binding organic matter into stable complexes (Hassink et al. 1997, Jobbágy and Jackson 2000). Particle size and soil moisture are influenced by slope, with finer particles, moister soils and higher SOC found at slope bottoms (Sumner 2000). Playas drain gently sloping catchments (e.g. are at the lowest catchment elevation), and thus, there are gradients in soil texture (Luo et al. 1999), but likely in soil moisture, and SOC as well along the catchment slope.

Finally, recent soil carbon research suggests SOC increases with plant species richness (Tilman et al. 2006, Steinbeiss et al. 2008). Species richness sometimes increases plant productivity because of more complete soil nutrient exploitation, possibly resulting in higher plant-derived carbon inputs into soils (Tilman et al. 1996, Wilsey and Potvin 2000, Balvanera et al. 2006), although this explanation has never been fully investigated. Plant composition, richness and aboveground biomass differs among land-use type in High Plains playas (Smith and Haukos 2002, O'Connell et al. In press). Thus we expect relationships in SOC with plant species richness to explain some land-use SOC differences.

In this paper, we quantify SOC in playas and surrounding uplands among land-uses (native grassland, cropland, and CRP lands) to identify land management promoting SOC sequestration in the High Plains. Further, we hypothesize that playas and surrounding uplands may interact. Specifically, we suggest SOC may decrease with distance from playas within uplands because of gradients in soil moisture and texture. Our objectives are 1) to compare SOC between playas and uplands among land-use types and 2) to compare SOC within a land-use type between playas and surrounding uplands and with increasing distance from playas within uplands. We compare SOC over several depth intervals to elucidate patterns in High Plains SOC with soil depth. We further compare SOC with patterns in belowground biomass, soil moisture and plant species richness to elucidate potential drivers of SOC sequestration in the High Plains. Modeling such data can be used to inform land management decisions and maximize soil carbon sequestration in the High Plains. Our approach is novel because we analyze SOC across a broad geographical region where data are lacking and also model the influence of many variables associated with SOC.

## METHODS

We sampled playa catchments from the short-grass prairie eco-region called the High Plains, covering six states from western Nebraska and eastern Colorado, south to eastern New Mexico and western Texas (Figure V.1). Playas here are in high density, with up to 60,000 individual wetlands occurring (Playa Lakes Joint Venture, www.pljv.org). The High Plains is short-to mixed grass prairie with a semiarid climate. Precipitation ranges from 38-63 cm along a west—

east gradient (Smith 2003). Evapotranspiration ranges from 280-165 cm along a south—north gradient (Smith 2003). Agricultural cultivation has increased since the 1940s and wheat, cotton, corn, and sorghum are common crops (Bolen et al. 1989). Remaining prairie is generally uniformly grazed by domestic livestock (Samson et al. 2004).

Soils throughout the Great Plains are most often Mollisols, Alfisols, and Entisols (USDA-NRCS 2006). Playas have hydric, clay Vertisol soils, of Randall, Lipan, Ness, Lofton, Stegall, Pleasant, and Scott clays (Smith 2003, Soil Survey Staff 2011). Playas average 7 ha (S. McMurry, unpublished data) and are generally round in shape.

We sampled 165 catchments (55 in native grassland, 55 in CRP, and 56 in cropland) to 50 cm depth, in a random design stratified by playa density/region and county. Of these, we sampled to 100 cm 17, 15, and 17 catchments each in grassland, CRP, and cropland, respectively (Figure V.1). To select sample sites, we initially chose catchments in native grasslands because native range is most limited, and then paired these with nearby catchments in the other land-uses.

We sampled catchments for SOC during the growing season in 2009. To sample catchments, we first surveyed playa area with a GPS (Trimble GeoXT) by walking playa visual edges. We delineated playa visual edges by noting changes in vegetation from hydrophytic to upland plants and changes in topography from sloped basin edge to flat upland (Luo et al. 1997). We refined our playa boundary estimates by coring to locate hydric soil edges. We cored along transects perpendicular to the visual edge boundary and used two such transects on opposite sides of the playa basin (Tsai et al. 2007). The hydric soil edge was where soil color and texture changed from wetland soils of heavy clay Vertisols with matrix chroma < 3 to coarser, browner upland soils (Luo et al. 1997, Tsai et al. 2007). We used Muncell soil color charts to confirm hydric and upland soil classifications (Schoeneberger et al. 2002). See Luo et al. (1997) for distinct chromas distinguishing Randall clay playa wetland soil series from upland soils. A similar process was followed for other wetland soils.

To elucidate patterns in SOC with soil depth, we took intact soil cores from playas at multiple depth intervals within the soil profile: 0-5 cm, 5-25 cm and 25-50 cm. At the above mentioned playa subsets, we additionally collected 50–75 cm and 75–100 cm depth intervals. We used soil cores, slide hammers and augers to sample soils (AMS Inc., American Falls, ID, USA). We used a 5.08-cm soil core and a slide hammer to collect the 1-5 cm depth interval. For other depths, we used a 3.81-cm soil core and slide hammer. To minimize compaction, we collected each depth interval separately, extracted it, and then used a 7.62 cm soil auger to excavate a wider pit down to the next depth interval surface. This minimized friction and suction on the soil core, as well as compaction of collected soil. Some compaction did occur, but to account for this we used the internal volume of the core, rather than of the retained soil as our soil volume estimate (Bronson et al. 2004).

In a similar manner, we collected soil samples along a transect extending from the playa visual edge southwest into the upland at 10 m, 40 m and 100 m from the playa. Some playas have lunettes (small ridges or dunes) on their southeast side (generally windward of playas) with soils differing from surrounding uplands (Smith 2003, Bowen and Johnson 2011). We chose to always extend transects southwest to avoid lunettes and ensure sampling consistency. At playa subsets in the upland, 50–75 cm and 75–100 cm depth intervals were collected, but only at the 40 m point. At the time of soil collection, we recorded all plant species growing within a 0.5 m radius of sampling points. Soil samples were placed in sealed plastic freezer bags, stored on ice in the field and chilled to 4˚ C in the lab until analysis (USDA-NRCS 2004).

In the lab, soils were oven dried at 105˚ C until constant weight achieved. We ground soils to pass through a 2-mm sieve. Rock and other fragments > 2 mm were rare, but when present were weighed. Volume of > 2 mm fragments was estimated using fluid displacement within a 50-ml graduated cylinder. Soil bulk density (g dry soil /$cm^3$) was calculated as: soil bulk density ($d_b$) = (weight of oven dry soil < 2mm) ÷ (volume of soil + pores), where volume was the internal volume of the soil core for that depth interval minus the volume of fragments > 2 mm (Lal et al. 2001).

To elucidate relationships among SOC and moisture, we calculated percent soil moisture (g $H_2O$/100 g dry soil) as percent water on a dry-mass basis, using the formula: percent soil moisture = 100 * (soil wet-mass – soil dry-mass) ÷ soil dry-mass (Sumner 2000). We weighed some soil samples soon after collection in the field to determine wet mass. We compared this mass over time and thus verified that soils stored in sealed plastic freezer bags retained field moisture indefinitely when bags were sealed. Therefore, we measured wet weight of the majority of samples in the lab before drying.

To estimate variation in SOC with variation in root biomass, we removed, weighed and recorded coarse root biomass > 2 mm from dried soil samples. We estimated percent dry weight of coarse belowground biomass as: percent belowground biomass = 100 * dry belowground biomass ÷ soil dry-mass (Sumner 2000).

Percent total soil carbon by weight was measured using LECO TruSpec carbon and nitrogen analyzers (LECO Corporation, St. Joseph, MI, USA). Soils in the semiarid High Plains often contain inorganic carbonates ($CaCO_3$) (Reeves 1970). We tested for inorganic carbonates by reacting soil subsamples with 2 m HCl (Schumacher 2002). When present, we measured percent inorganic carbon using a modified pressure calciminer method (Sherrod et al. 2002). We calculated percent soil organic carbon (pSOC) as percent total carbon minus percent inorganic carbon in soils. We converted pSOC to areal soil organic carbon (SOC) (kg $m^{-2}$) using: SOC = [ (pSOC x $d_b$ x $l_1$) + (pSOC x $d_b$ x $l_2$) +. . . (pSOC x $d_b$ x $l_n$)]/ 10,where l is the thickness of each sampled layer in cm. Dividing by 10 is needed to convert from g $cm^{-3}$ to kg $m^{-2}$ (Lal et al. 2001). Similarly, we estimated areal soil moisture (kg $m^{-2}$) and belowground biomass (kg $m^{-2}$) by substituting percent soil moisture and percent dry root biomass for pSOC in the above equation. All subsequent analyses use these areal measurements for SOC, soil moisture, and root biomass.

We compared SOC among land-use and sampling points (playa and 10, 40, or 100 m into the upland) using linear models in program R (version 2.12.1, the R Foundation for Statistical Computing). Model residuals were not normal, so we log transformed SOC, resulting in models with reduced heterogeneity of variances and normal residuals. We present untransformed means in the results for ease of interpretation. We analyzed SOC separately over intervals from the surface to 5 cm depth, surface to 50 cm depth, and surface to 100 cm depth.

Finally, to explain potential differences among playas, uplands and land-use, we used AIC model selection procedures (R package MuMIn, Burnham and Anderson 2002). To select the highest ranked model explaining SOC in playas and uplands, we modeled the 50 cm depth. We modeled each land-use separately and used species richness of plants, sampling point (playa or 10, 40 and 100 m from playa visual edge), playa area (ha), sampling point*playa area interactions, root biomass, soil moisture, latitude, and longitude as potential explanatory variables. In croplands, we also added whether playa basins themselves were plowed, or only surrounding uplands, and also sampling point*plowing interactions. We averaged model coefficients over all models with $\Delta$ AIC < 4 for each land-use (Burnham and Anderson 2002). We present variables selected in greater than 50% of these models as important for explaining SOC in that land-use. To evaluate model selection output, we plotted species richness and soil moisture with other selected model variables within land-use and visually examined correlations (see Appendix C for variable plots). We did this because species richness and soil moisture may help explain observed trends.

## RESULTS

### *SOC differences among land-use types*

In playas, SOC to 5 cm depth was not different among land-uses ($F_{2,170}$ = 0.66, P = 0.51; Fig.2a). SOC was 15% less in croplands than CRP from the soil surface to 50 cm depth ($F_{2,169}$ = 3.337, P = 0.038; Fig.2b), and was 20% greater in native grasslands and CRP than in cropland when compared from the soil surface to 100 cm ($F_{2,44}$ = 2.07, P = 0.08 and P = 0.09 respectively; Fig.2c).

In uplands, SOC to 5 cm or 50 cm depths was not different among land-use at the 10 m sampling point ($F_{2,167}$ = 1.06, P = 0.35, and $F_{2,164}$ = 0.83,p = 0.44, respectively; Figure V.2 a and b). At the 5 cm depth and 40 m sampling point, SOC was 25% less in cropland than in grassland and CRP ($F_{2,170}$ = 2.57, P = 0.08; Figure V.2a), though it was not different in any land-use at the 100 m point (P = 0.20; Figure V.2a). When compared over a depth of 50 cm, SOC was 31% and 24% greater in grasslands than croplands at 40 and 100 m from playa edges ($F_{2,168}$ = 5.79, P = 0.004 and $F_{2,166}$ = 2.593, P = 0.02, respectively; Figure V.2b), though CRP was not different from cropland or grassland at either point (P = 0.17 and 0.21, respectively; Figure V.2b). However, SOC to a 100 cm depth at 40 m from playas was 24% greater in grasslands than CRP and cropland ($F_{2,45}$ = 2.38, P = 0.1; Figure V.2c).

### *Comparing playa and upland SOC and comparing SOC with increasing distance to playas within a land-use*

To depths of 5 and 50 cm in uplands, SOC had no relationship with distance to playas in any land-use (P = 0.18 or greater; Figure V.2a and b). However, over a 50 cm depth in native grasslands, SOC at only the 40 m point was higher than in playas themselves ($F_{3,221}$ = 2.32, P = 0.08; Figure V.2b), though SOC did not differ among the 40 m and other upland points (P = 0.21 or greater). Compared over a depth of 100 cm, playa and upland points only differed in CRP, where they were 21% higher in playas ($F_{1,28}$ = 3.5, P = 0.07; Figure V.2c).

Species richness was related to SOC in all land-use catchments (Table V.1, Figure V.3), but increased with SOC in grasslands and croplands and decreased with SOC in CRP. In grassland and CRP catchments, area had a positive relationship with SOC (kg $m^{-2}$) in both playa and uplands. Playa area interactions with sampling point were not important (Table V.1). Latitude and longitude also influenced SOC. SOC increased along a northerly gradient in cropland and grassland catchments, and along an easterly gradient in CRP and cropland catchments. Some factors only were important in a single land-use. For example, soil moisture in playa and upland points was associated with decreased SOC in CRP, but was not important elsewhere. In croplands, plowing wetlands decreased SOC in both playa and upland points and interactions among wetland and upland sampling points were not important (Table V.1).

## DISCUSSION

### *Differences among land-use in playas and uplands*

SOC in playas was generally less in croplands than other land uses to a depth of 100 cm. Further, SOC was generally less in cropland uplands than in other land-uses over most depths and sampling points. SOC within CRP uplands was less than native grassland and similar to cropland when compared over 100 cm depths, though CRP was similar to grasslands near the soil surface. Thus, grassland uplands possess SOC stores at depth not accounted for by shallower estimates.CRP fields in contrast accumulate SOC near the surface but were not equivalent with grasslands at depth, perhaps because roots are sparser deeper in the soil profile, slowing SOC accumulation. Bronson et al. (2004), in their study of cropland, native grassland, and CRP in 3 sites within the Southern High Plains observed similar trends among land-use, though they made observations only down to 30 cm. They attributed lower SOC accumulation in CRP to semiarid climate, which might cause rapid soil matter oxidation.

Post and Kwan (2000) reviewed studies of SOC in CRP lands and found that arid climates and low productivity generally retard SOC accumulation to rates of 0.1 - 0.03 kg C $m^{-2}$ $yr^{-1}$ in re-established grasslands. In our study, CRP uplands were 3 kg C $m^{-2}$ less than the SOC in native grassland to a 1 m depth. If we assume Post and Kwan's (2000) accumulation rates apply here, an additional 30-100 years should be necessary for CRP SOC to resemble SOC in native grasslands. Croplands planted to grass sometimes have higher SOC than nearby croplands (Potter et al. 1999), but often do not approach SOC in native prairies (Huggins et al. 1997, Purakayastha et al. 2008), even after 60 years since planting (Potter et al. 1999), but see Reeder et al. (1998) for an exception. Potter et al. (1999) suggested that 160 years would be necessary for the central Texas restored grassland they studied to equilibrate with native prairie.

Wetland SOC did not differ from uplands over a 100 cm depth, except in CRP, where playas had 21% greater SOC than uplands. In a previous study, we observed that CRP playas were drier than grassland or cropland playas and dominated by CRP grasses rather than wetland vegetation (O'Connell et al. In press). The combination of CRP grasses and wetland species may allow CRP playas to accumulate SOC at faster rates than surrounding CRP uplands. The relationship of SOC with specific plant species should be explored in future studies. Further, decomposition rates may be less in playas than in uplands, allowing CRP playas to accumulate SOC faster. Decomposition has not been measured in playas and surrounding uplands as of yet.

In general, playas may not accumulate SOC as much as other wetlands because constantly fluctuating hydrology may promote rapid decomposition (Anderson and Smith 2002) rather than anaerobic soils and SOC accumulation. Playas are temporary to seasonal wetlands (pond water from a few weeks to several months during a year) (Smith 2003). For comparison, prairie potholes, depressional wetlands common to northern prairies where climate is cooler and wetter, sequester 10 kg C $^{m-2}$ to a depth of 30 cm in reference conditions (Euliss et al. 2006). Playas sequester approximately 6.5 kg C $^{m-2}$ to a depth of 50 cm in grasslands. However, we do not suggest that playas are unimportant for sequestering SOC. Playas in grasslands had 20% greater SOC than those in cropland to a 100 cm depth. Our pre-existing databases described in our methods suggest there are 73,000 ha of playas within the High Plains (27,000 ha in grassland, 6,000 ha in CRP and in 39,000 ha cropland). We can combine these figures with SOC estimates to generate total SOC lost by conversion of playas to cropland. If we simplify calculations by ignoring potential losses in playa area due to sediment accumulation in croplands, we multiply average SOC to 100 cm by hectares of playas in each land-use. Thus, currently playas store 7.1 Tg C. Conversion of grassland playas to cropland conservatively caused 1 Tg C loss. Conversion of all playa wetlands to cropland wetlands would result in an additional 0.5 Tg C loss. Losses of C in uplands by converting native prairie to cropland would add to this loss. For example, Burke et al. (1989) estimated that 0.8-2 kg C m$^{-2}$ was lost in the top 20 cm of soil by conversion of native grassland to cropland in the Northern High Plains

(Colorado, Nebraska, and Kansas) and that > 50 years are required for organic matter recovery in abandoned High Plains croplands (Burke et al. 1995, Fuhlendorf et al. 2002). Thus, preservation of intact playas in native grasslands will help mitigate global climate change.

### *Interactions in SOC between playas and uplands in the High Plains*

Our hypothesis that SOC would decrease with distance from playas was not supported. Soil moisture only decreased with distance from playas in CRP and grassland, and had no relationship in croplands. However, soil moisture was not related to SOC as expected. Rather, in grasslands, soil moisture had no relationship with SOC and in CRP, soil moisture decreased with increasing SOC. This does not mean that soil moisture does not influence SOC, but rather suggests that other processes were more important in this system.

To determine what did relate to SOC, we considered variables selected as important in all land-uses to be most important. Species richness was highly important. Recently, others also found that SOC increased with increasing plant diversity in planted grasslands (Tilman et al. 2006, Fornara and Tilman 2008, Steinbeiss et al. 2008). Perhaps diverse plant communities produced greater biomass, resulting in more complete utilization of soil nutrients and higher plant-derived carbon inputs into soil, causing increased SOC (Tilman et al. 1996, Wilsey and Potvin 2000, Balvanera et al. 2006). Alternatively, diversity in plant functional traits may be more important than productivity *per se* (Fornara and Tilman 2008, Steinbeiss et al. 2008). Similarly, in our study, species richness and belowground biomass also were not positively related within any land-use (see Appendix C). However, in the High Plains, species richness had a positive relationship with SOC in cropland and grassland but a negative relationship in CRP. This suggests species identity may be as important as richness. For example, some species may increase SOC more than others (Vinton and Burke 1995). Further, microbial communities differ with plant composition (Vinton and Burke 1995). Recent findings have documented that soil faunal diversity is associated with increased SOC (Nielsen et al. 2011). Thus relationships between plants and soil nutrient status may be complex because of interactions among plants, soil, and soil fauna.

Other important variables relating to SOC were playa area, latitude and longitude, which all were selected in 2 out of 3 land-uses. In croplands, playa area likely was not important because playas there were generally small (O'Connell et al. In press). Interestingly, in grassland and CRP, where playa area was important, sampling point interactions with playa area were not. Thus, uplands in catchments with large playas have more SOC than catchments with small playas. This relationship of playa area with SOC was not a result of larger playas having moister soils or greater species richness in uplands (See Appendix C). However, species composition still may differ among catchments with different playa areas. For example, we documented that species composition within playas changes with playa area (Ch. II). Large playa catchments also may be compositionally different than small playa catchments. For example, playa species often establish in uplands during wet conditions and thus species in playas influence upland species composition. However, other factors than species composition could be important. Elevation and soil texture gradients may vary with playa area in uplands. For example, larger catchments may have steeper slopes than smaller ones. We cannot unambiguously state why playa area and upland SOC were related. However, the evidence suggests playas and uplands interact in some manner, and that playa conservation, particularly of large playas, is important for promoting SOC sequestration in the High Plains.

Latitude and longitude also were selected as important for explaining SOC, probably because they influence community composition and climate. For example, Haukos and Smith documented species composition differences with the spatial location of playas by state and county in the Southern Great Plains (Haukos and Smith 2004). Similarly, in our study, plant species richness had a positive relationship with longitude in CRP and cropland and with latitude in grasslands. Soil moisture increased with latitude in all land-uses and additionally with longitude in CRP (See Appendix C). Thus, differences in soil moisture and species composition along geographical gradients probably influenced relationships of latitude and longitude with SOC.

Interestingly, in CRP catchments, soil moisture was negatively associated with SOC. Yet, past studies have demonstrated that soil moisture should increase SOC, when temperature, soil texture and land-use are equivalent (Post et al. 1982, Jobbágy and Jackson 2000). We hypothesize that the influence of species composition was more important for promoting SOC sequestration in CRP and overrode effects of soil moisture. Identification of species associated with increased SOC should allow targeted land management promoting SOC storage.

Finally, in croplands, whether playas themselves had been tilled was an important SOC determinant. Plowing playas reduces species richness and plant cover vs. unplowed cropland playas (O'Connell et al. In press). Given the importance of species richness in our analyses, the effect of plowing on plant communities was probably strongly influential. Plowing also causes erosion by exposing bare ground. These soils accumulate in cropland playas, reducing playa area and burying hydric soils (Luo et al. 1999), to an average depth of 27 cm in High Plains (S. McMurry, unpublished data). Thus, we may have detected less SOC in cropland playas because sediments buried surface hydric soils richer in SOC. We do not have strong evidence of carbon rich soils buried at depth in cropland playas (Figure V.4a). For example, SOC deep in the soil profile in cropland playas is equal to or less than that measured in cropland uplands over the same depth interval. It also is always less than that observed in grassland playas for the same depth interval, though standard errors often overlapped. Thus, we cannot completely discount the possibility of carbon rich buried soils in crop playas because our sampling depth intervals may have been too coarse to detect important trends. However, cultivation decreases SOC in its own right (Burke et al. 1995). For example, tillage mixes topsoil, exposing previously protected organic matter to oxygen, increasing decomposition rates and contributing to SOC losses (Sumner 2000). In our study, tilled playas averaged 10% less SOC than untilled crop playas. We do not know if this was because of declines in species richness, hydric soil burial, topsoil mixing or some combination. We conclude that wetlands should not be tilled to help promote SOC sequestration in the High Plains.

In summary, we suggest native grassland catchment conservation should promote SOC sequestration in the High Plains. Further maintenance of high species diversity within a land-use also is positively associated with SOC, though identification of specific species that increase SOC would help specifically target land management. Playas in croplands should not be tilled to help reduce losses of SOC. Untilled playas also have concomitant benefits for plant communities (O’Connell et al. In press). Current USDA conservation programs (e.g. Swampbuster Provisions, as in the 1985 Farm Bill (Glaser 1985)) allow plowing of depressional wetlands dry through natural conditions. We suggest these Swampbuster provisions should be modified to limit plowing of depressional wetlands in order to enhance carbon sequestration in cropland wetlands. Eastern and northern playas had greater SOC than southwestern ones. Thus conservation should be targeted there if resources are limited and SOC sequestration is a management goal. Finally, catchments with larger playas have greater SOC per unit area than those with small playas and should be preserved to promote SOC in the High Plains.

Table V.1. Best models explaining SOC in playas and uplands within a land-use. Coeffecients were averaged over models with Δ AIC < 4. Importance is the proportion of models in which the variable was selected. Only variables with importance > 0.5 are presented.

| Parameter | Coefficient | SE | Importance |
|---|---|---|---|
| Grass | | | |
| Intercept | 3.35 | 4.56 | |
| Playa area (ha) | 0.014 | 0.005 | 1 |
| Species richness | 0.005 | 0.015 | 1 |
| Latitude | 0.032 | 0.025 | 0.77 |
| CRP | | | |
| Intercept | 13.1 | 4.1 | |
| Species richness | -0.019 | 0.014 | 1 |
| Soil moisture | -0.011 | 0.01 | 1 |
| Longitude | 0.111 | 0.04 | 1 |
| Playa area (ha) | 0.015 | 0.007 | 0.83 |
| Cropland | | | |

| | | | |
|---|---|---|---|
| Intercept | 6.14 | 4.18 | |
| Species richness | 0.0168 | 0.0165 | 1 |
| Playa basin plowed | -0.115 | 0.0603 | 0.94 |
| Longitude | 0.049 | 0.0403 | 0.77 |
| Latitude | 0.016 | 0.0144 | 0.73 |

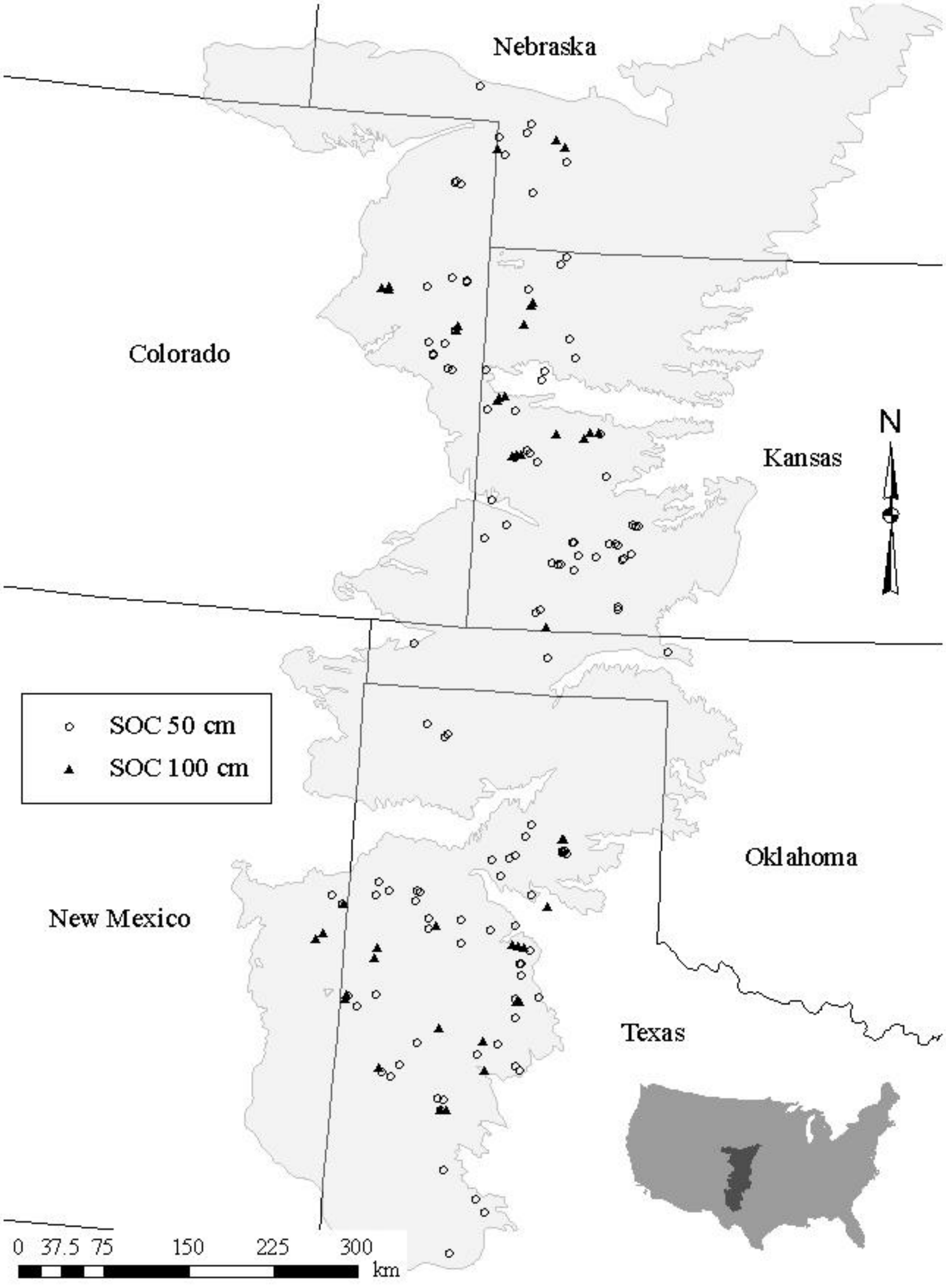


Figure V.1. Sites where SOC was sampled to either 50 cm or 100 cm in playas and uplands in the High Plains, USA. The border of the High Plains is shaded.

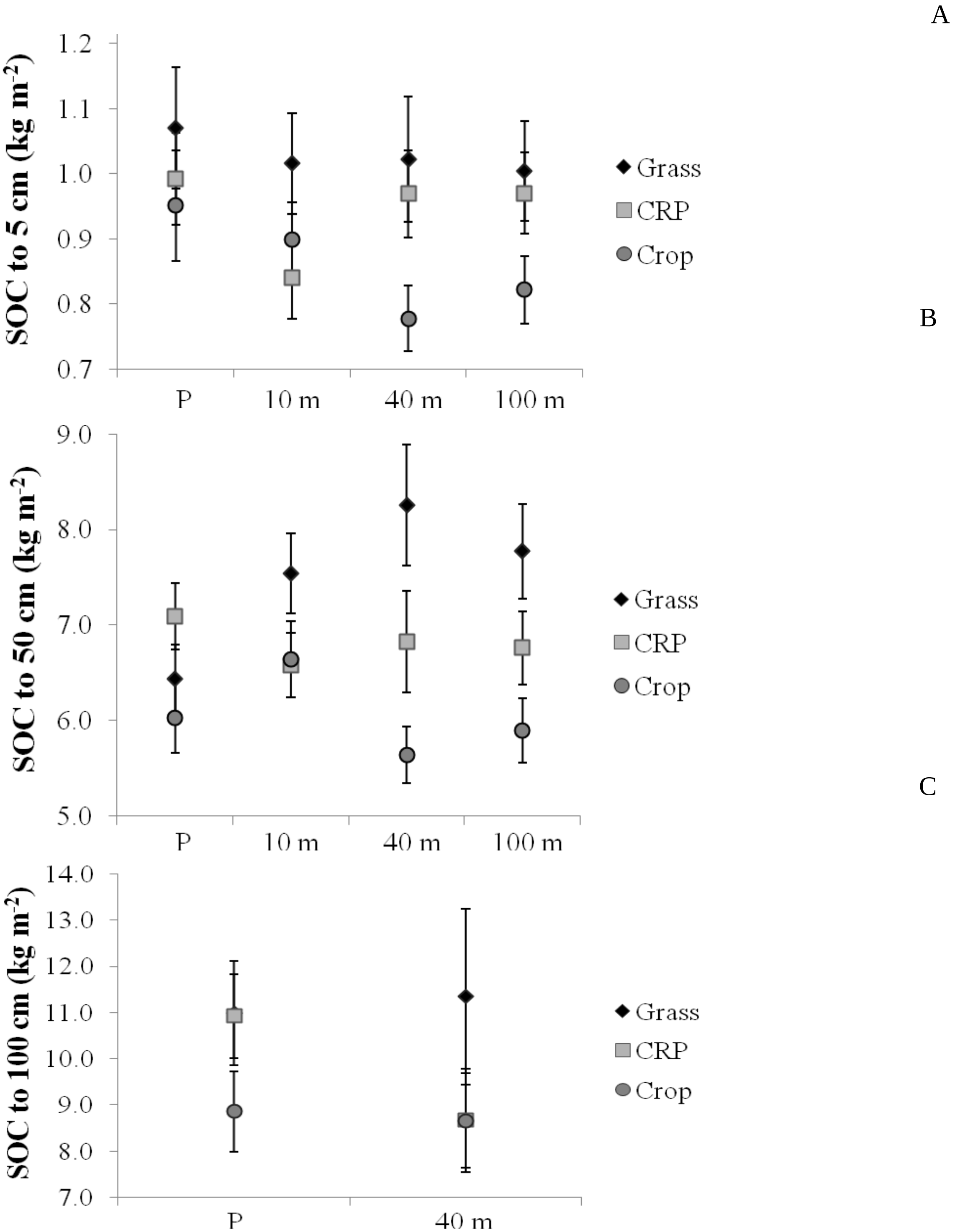


Figure V.2. SOC (kg m-2) within the High Plains, USA, from the soil surface to (A) 5 cm, (B) 50 cm, and (C) 100 cm. P = playa center, and 10 m, 40 m and 100 m are samples taken at these distances from the playa visual edge along a transect heading southwest.

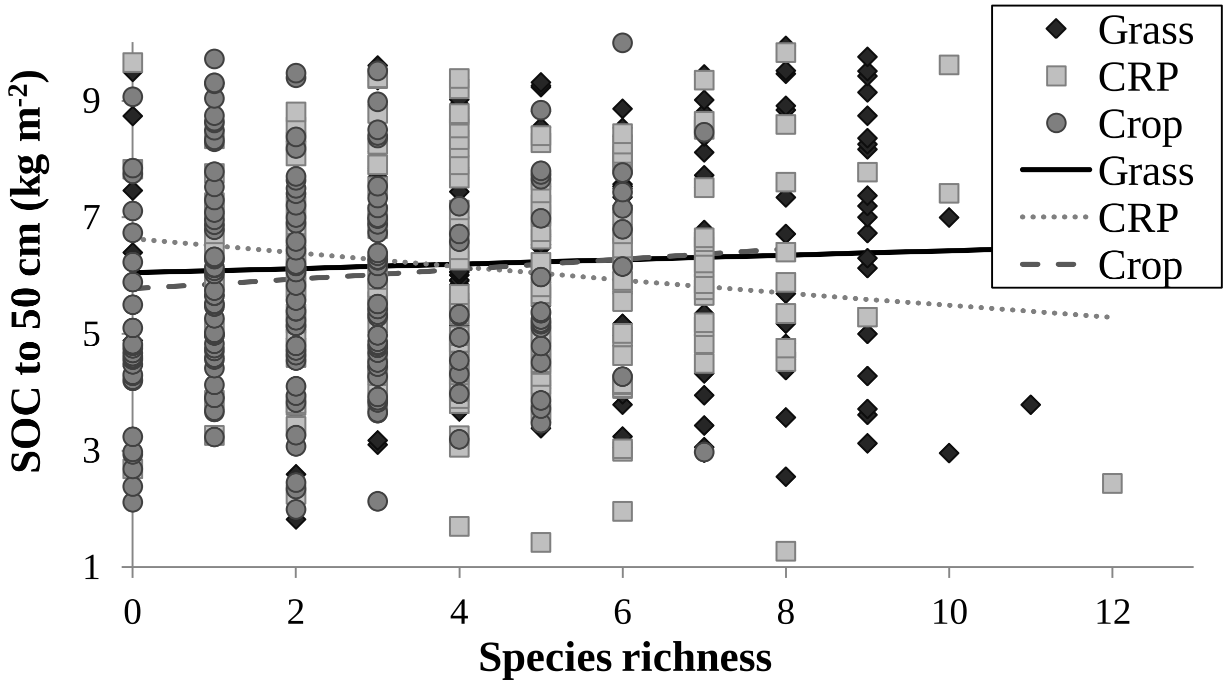


Figure V.3. Species richness in playa catchments among land-use and relationships with SOC to 50 cm depth. Prediction lines are for models listed in Table V.1, and have variables other than species richness held at their mean values.

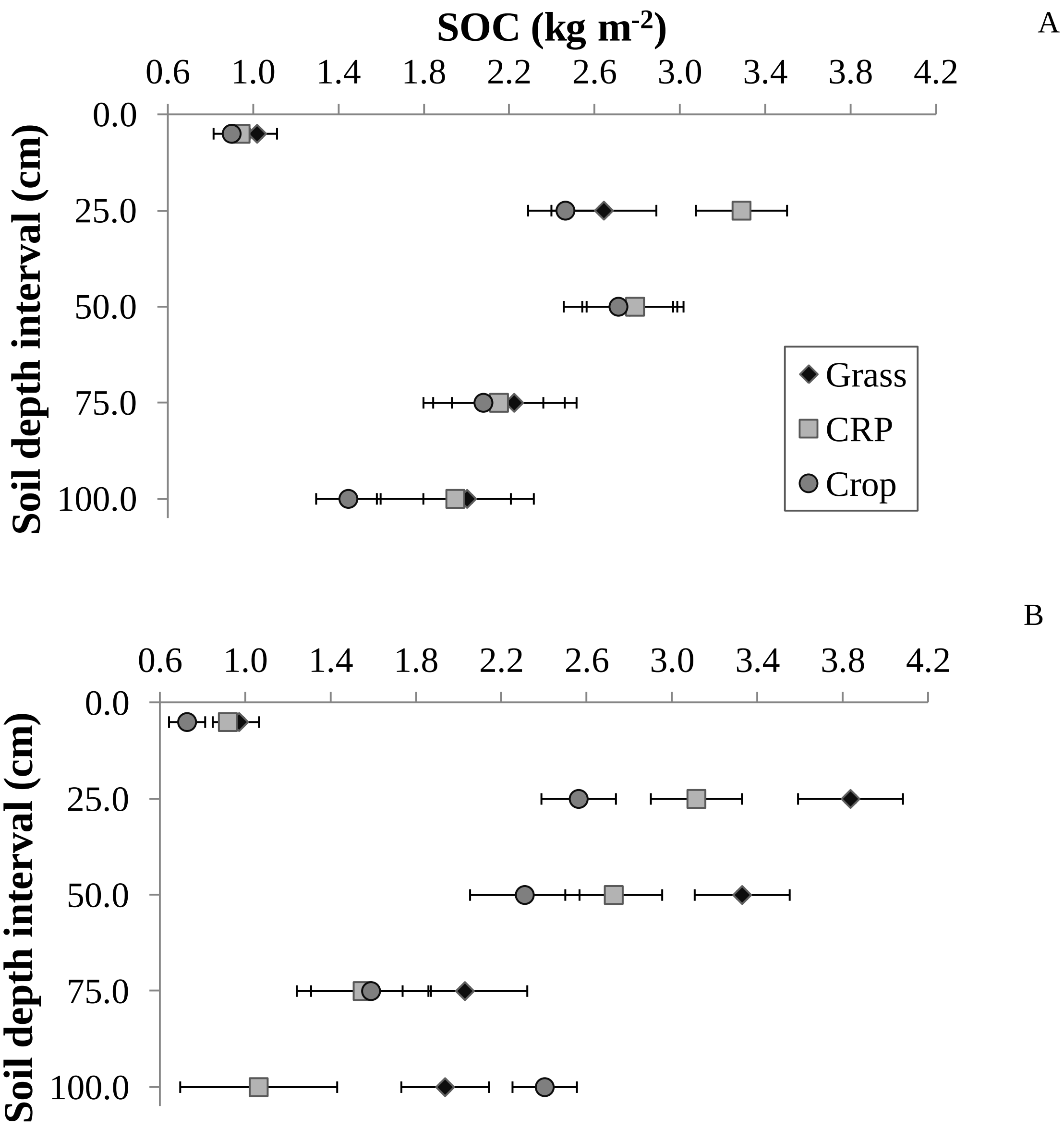


Figure V.4. SOC (kg m-2) in the High Plains USA among land-use by depth interval (0-5, 5-25, 25-50, 50-75, and 75-100 cm) in (A) playas and (B) 40 m from playas in uplands. SOC is symbolized at the bottom of the depth interval depicted.

# APPPENDICES

## A. PLANT GUILDS AND SCIENTIFIC NAMES FOR SPECIES IN THE WESTERN HIGH PLAINS AND RAINWATER BASIN

Table A. 1 Guilds and scientific names for common species observed in western High Plains playas. See methods in Ch. II for a detailed description of how guilds were classified.

| Scientific Name | Guild |
|---|---|
| *Amaranthus blitoides* | Mudflat |
| *Amaranthus retroflexus* | Mudflat |
| *Ambrosia grayi* | Mudflat |
| *Aster subulatus* | Mudflat |
| *Chenopodium album* | Mudflat |
| *Chenopodium leptophyllum* | Mudflat |
| *Conyza canadensis* | Mudflat |
| *Coreopsis tinctoria* | Mudflat |
| *Echinochloa crus-galli* | Mudflat |
| *Eleocharis atropurpurea* | Mudflat |
| *Helianthus annuus* | Mudflat |
| *Hymenoxys odorata* | Mudflat |
| *Kochia scoparia* | Mudflat |

| Scientific Name | Guild |
|---|---|
| *Lactuca serriola* | Mudflat |
| *Melilotus officinalis* | Mudflat |
| *Panicum capillare* | Mudflat |
| *Polygonum pensylvanicum* | Mudflat |
| *Polygonum ramosissimum* | Mudflat |
| *Portulaca oleracea* | Mudflat |
| *Salsola iberica* | Mudflat |
| *Solanum rostratum* | Mudflat |
| *Sorghum halepense* | Mudflat |
| *Tragopogon dubius* | Mudflat |
| *Verbena bracteata* | Mudflat |
| *Eleocharis macrostachya* | Sedge Meadow Perennial |
| *Eleocharis parvula* | Sedge Meadow Perennial |
| *Lythrum californicum* | Sedge Meadow Perennial |
| *Malvella leprosa* | Sedge Meadow Perennial |
| *Oenothera canescens* | Sedge Meadow Perennial |
| *Panicum obtusum* | Sedge Meadow Perennial |
| *Rorippa sinuate* | Sedge Meadow Perennial |
| *Rumex crispus* | Sedge Meadow Perennial |
| *Polygonum amphibium* | Shallow Emergent Perennial |
| *Marsilea vestita* | Shallow Emergent Annual |
| *Aristida purpurea* | Upland |

| | |
|---|---|
| *Baptisia australis* | Upland |
| *Bothriochloa ischaemum* | Upland |
| *Bouteloua curtipendula* | Upland |
| *Bouteloua gracilis* | Upland |
| *Bromus japonicas* | Upland |
| *Convolvulus arvensis* | Upland |
| *Eragrostis curvula* | Upland |
| *Euphorbia albomarginata* | Upland |
| *Ambrosia psilostachya* | Wet Prairie Perennial |
| *Buchloe dactyloides* | Wet Prairie Perennial |
| *Chloris verticillata* | Wet Prairie Perennial |
| *Cuscuta squamata* | Wet Prairie Perennial |
| *Cynodon dactylon* | Wet Prairie Perennial |
| *Grindelia squarrosa* | Wet Prairie Perennial |
| *Helianthus ciliaris* | Wet Prairie Perennial |
| *Hoffmannseggia glauca* | Wet Prairie Perennial |
| *Hordeum pusillum* | Wet Prairie Perennial |
| *Lippia cuneifolia* | Wet Prairie Perennial |
| *Panicum virgatum* | Wet Prairie Perennial |
| *Pascopyrum smithii* | Wet Prairie Perennial |
| *Plantago patagonica* | Wet Prairie Perennial |
| *Ratibida columnifera* | Wet Prairie Perennial |
| *Ratibida tagetes* | Wet Prairie Perennial |

|  |  |
|---|---|
| *Schedonnadrus paniculatus* | Wet Prairie Perennial |
| *Sitanion hystrix* | Wet Prairie Perennial |
| *Solanum elaeagnifolium* | Wet Prairie Perennial |
| *Sporobolus cryptandrus* | Wet Prairie Perennial |
| *Thinopyrum ponticum* | Wet Prairie Perennial |

Table A. 2. Guilds and scientific names for common species found in Rainwater Basin playas. See methods in Ch. II for a description of how guilds were classified.

| Scientific Name | Guild |
|---|---|
| *Schoenoplectus heterochaetus* | Deep Emergent Perennial |
| *Typha angustifolia* | Deep Emergent Perennial |
| *Alopecurus carolinianus* | Mudflat |
| *Amaranthus retroflexus* | Mudflat |
| *Ambrosia grayi* | Mudflat |
| *Ambrosia trifida* | Mudflat |
| *Ammannia robusta* | Mudflat |
| *Bacopa rotundifolia* | Mudflat |
| *Chenopodium album* | Mudflat |
| *Conyza canadensis* | Mudflat |
| *Coreopsis tinctoria* | Mudflat |
| *Echinochloa crus-galli* | Mudflat |

| | |
|---|---|
| *Eleocharis acicularis* | Mudflat |
| *Helianthus annuus* | Mudflat |
| *Hordeum jubatum* | Mudflat |
| *Lepidium densiflorum* | Mudflat |
| *Melilotus officinalis* | Mudflat |
| *Mollugo verticillata* | Mudflat |
| *Panicum capillare* | Mudflat |
| *Polygonum bicorne* | Mudflat |
| *Polygonum pensylvanicum* | Mudflat |
| *Polygonum ramosissimum* | Mudflat |
| *Potentilla norvegica* | Mudflat |
| *Rorippa palustris* | Mudflat |
| *Sagittaria calycina* | Mudflat |
| *Setaria pumila* | Mudflat |
| *Aster lanceolatus* | Sedge Meadow Perennial |
| *Carex laeviconica* | Sedge Meadow Perennial |
| *Carex pellita* | Sedge Meadow Perennial |
| *Carex vulpinoidea* | Sedge Meadow Perennial |
| *Rorippa sinuata* | Sedge Meadow Perennial |
| *Rumex crispus* | Sedge Meadow Perennial |
| *Sagittaria brevirostra* | Sedge Meadow Perennial |
| *Alisma triviale* | Shallow Emergent Perennial |
| *Eleocharis palustris* | Shallow Emergent Perennial |

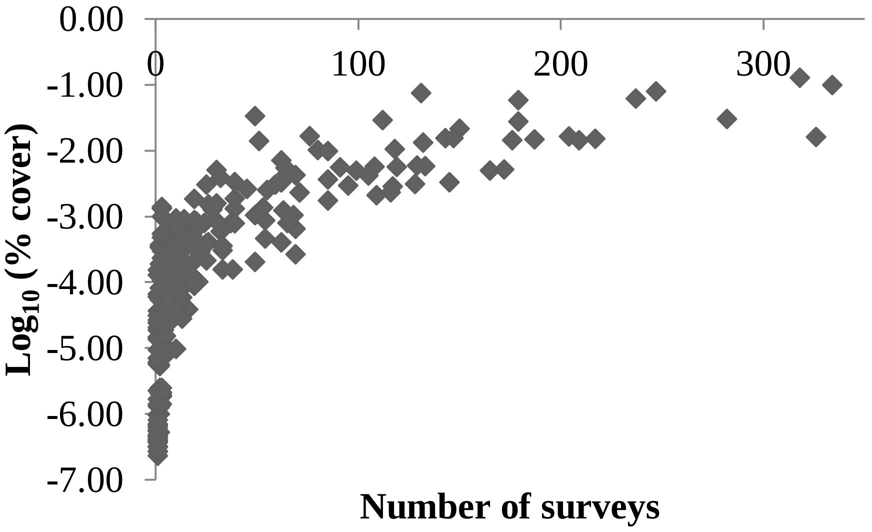
| | |
|---|---|
| *Phalaris arundinacea* | Shallow Emergent Perennial |
| *Polygonum amphibium* | Shallow Emergent Perennial |
| *Sagittaria graminea* | Shallow Emergent Perennial |
| *Scirpus fluviatilis* | Shallow Emergent Perennial |
| *Sparganium eurycarpum* | Shallow Emergent Perennial |
| *Leptochloa fascicularis* | Shallow Emergent Annual |
| *Marsilea vestita* | Shallow Emergent Annual |
| *Potamogeton nodosus* | Submerged Aquatic |
| *Potamogeton pectinatus* | Submerged Aquatic |
| *Abutilon theophrasti* | Upland |
| *Asclepias syriaca* | Upland |
| *Bromus inermis* | Upland |
| *Bromus japonicus* | Upland |
| *Bromus tectorum* | Upland |
| *Carex gravida* | Upland |
| *Chenopodium pratericola* | Upland |
| *Cuscuta campestris* | Upland |
| *Medicago sativa* | Upland |
| *Solidago missouriensis* | Upland |
| *Sorghum bicolor* | Upland |
| *Thlaspi arvense* | Upland |
| *Veronica arvensis* | Upland |
| *Zea mays* | Upland |

| | |
|---|---|
| *Ambrosia artemisiifolia* | Wet Prairie Perennial |
| *Apocynum cannabinum* | Wet Prairie Perennial |
| *Boltonia asteroides* | Wet Prairie Perennial |
| *Calystegia sepium* | Wet Prairie Perennial |
| *Carex brevior* | Wet Prairie Perennial |
| *Cyperus esculentus* | Wet Prairie Perennial |
| *Elymus canadensis* | Wet Prairie Perennial |
| *Galium aparine* | Wet Prairie Perennial |
| *Helianthus maximilianii* | Wet Prairie Perennial |
| *Hordeum pusillum* | Wet Prairie Perennial |
| *Juncus dudleyi* | Wet Prairie Perennial |
| *Leersia oryzoides* | Wet Prairie Perennial |
| *Lotus corniculatus* | Wet Prairie Perennial |
| *Oxalis stricta* | Wet Prairie Perennial |
| *Pascopyrum smithii* | Wet Prairie Perennial |
| *Poa pratensis* | Wet Prairie Perennial |
| *Rumex altissimus* | Wet Prairie Perennial |
| *Taraxacum officinale* | Wet Prairie Perennial |
| *Trifolium repens* | Wet Prairie Perennial |
| *Vernonia fasciculata* | Wet Prairie Perennial |

# B. ANALYTICAL SUPPORT FOR PLAYA PLANT COMMUNITIES AS METAPOPULATIONS

In Chapter II, we assumed that playa wetland plants may act as metapopulations. This assumption supposes that plants are seed limited, as has been demonstrated in many habitats (Turnbull et al. 2000). The applicability of metapopulation theory to plants with persistent seed banks has been discussed (Perry and Gonzalez-Andujar 1993, Eriksson 1996, Husband and Barrett 1996). Viable seeds persisting in seed banks potentially decrease both the probability of extinction and the importance of propagule rain from external habitats (Husband and Barrett 1996). If nearby patches experience similar environmental conditions, extinction still may be high without dispersal from external habitats (Husband and Barrett 1996)., Propagule rain increases richness in seed banks as well as in extant vegetation. Further, in habitats with significant temporal heterogeneity, such as prairies where wet, dry, hot and cold extremes are frequent, dispersal from external patches is more likely to be necessary to prevent local extinction (Perry and Gonzalez-Andujar 1993). Data from both the WHP and the RWB show a strong positive correlation between species abundance (log percent cover) and the number of surveys in which the species was encountered, as predicted by metapopulation theory (Figure B. 1a and b) (Gotelli and Simberloff 1987). We used log of percent cover to be consistent with Gotelli and Simberloff (1987), to aid comparison with their results. Percent cover is a proportion, thus log of cover results in negative numbers in the resulting graph. Thus, in summary, we feel there is support for employing a metapopulation model in depressional wetland plant communities.

A



B

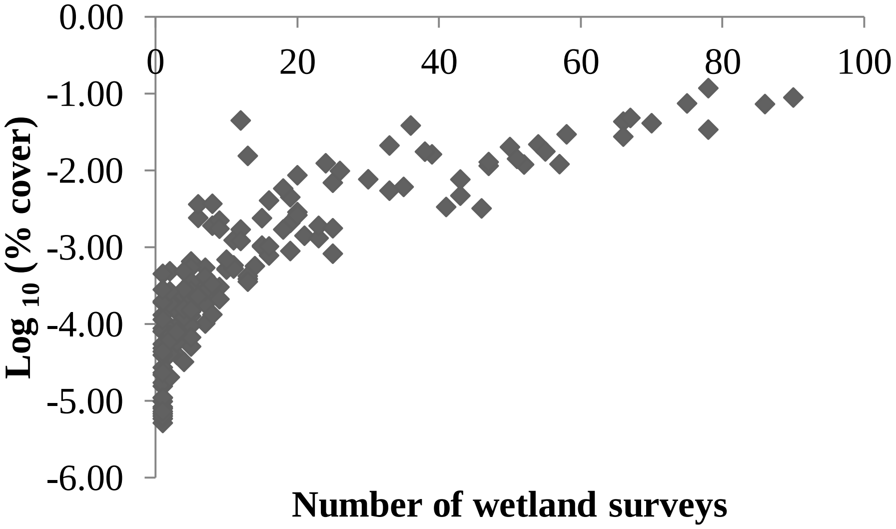


Figure B. 1. Percent cover and number of wetland surveys in which a species was encountered in A) the High Plains and B) the Rainwater Basin. A positive correlation suggests wetland playa plants meet some aspects of metapopulation predications (Gotelli and Simberloff 1987).

## C. RELATIONSHIPS AMONG ADDITIONNAL VARIABLES MENTIONED IN CH. IV (SOIL MOISTURE, BELOWGROUND BIOMASS, LATITUDE, LONGITUDE, SPECIES RICHNESS)

In this appendix we present plots for variables mentioned in Ch. IV, but that were not formally statistically analyzed. We did not statistically analyze these variables because this did not meet the objectives of CH IV and doing so would increase type II error rate. However, visual inspection of correlation among variables may help some readers understand trends in our data. Therefore we present these plots for variables and trends mentioned in Ch. IV.

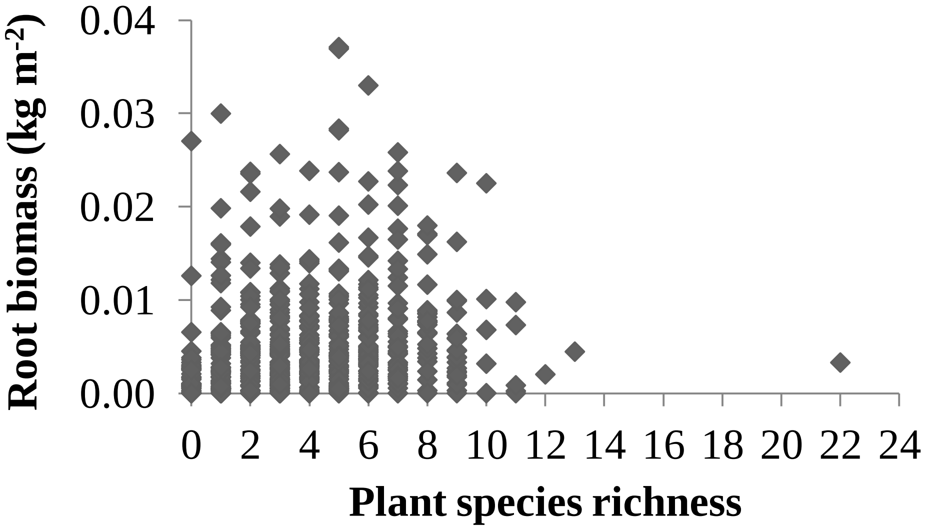


Figure C. 1. Plant species richness and belowground biomass for all catchment sampling points in all land-uses to 50 cm depth.

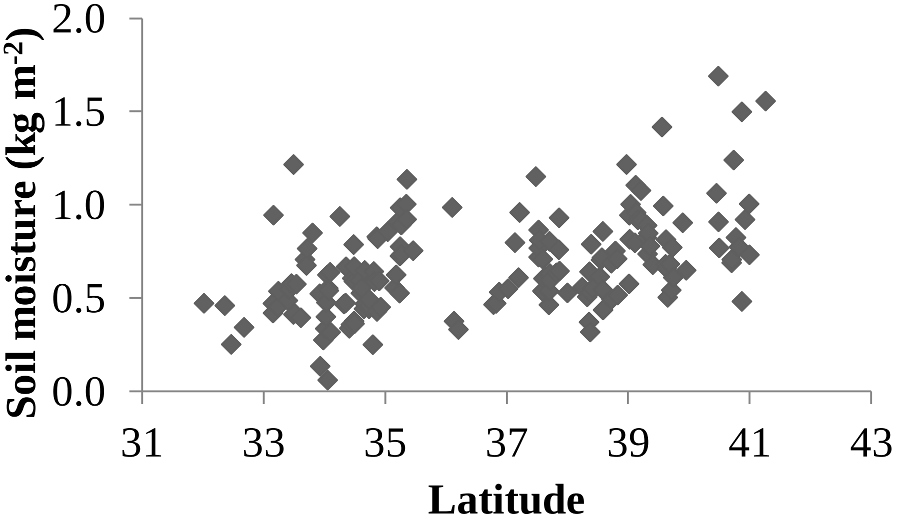


Figure C. 2. Soil moisture (kg m-$^{2}$) to 50 cm depth vs. latitude in all playa catchments (native grassland, cropland, and CRP).

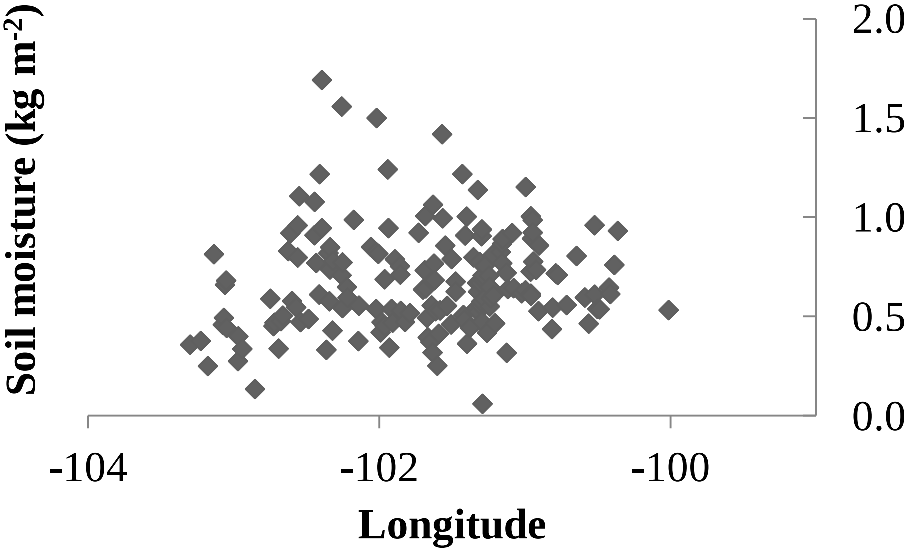


Figure C. 3.Soil moisture (kg m$^{-2}$) to 50 cm depth vs. longitude in all playa catchments (native grassland, cropland, and CRP).

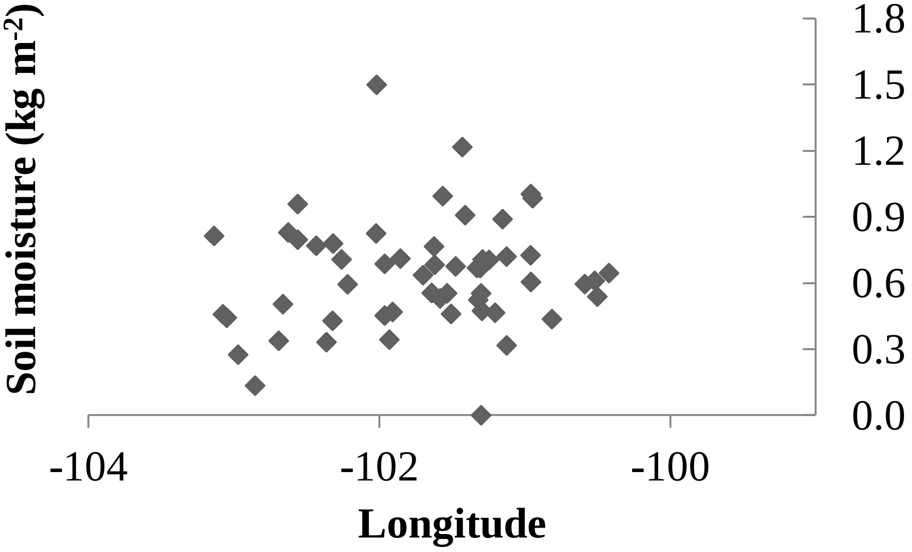


Figure C. 4. Soil moisture (kg m$^{-2}$) to 50 cm depth vs. longitude in CRP catchments only.

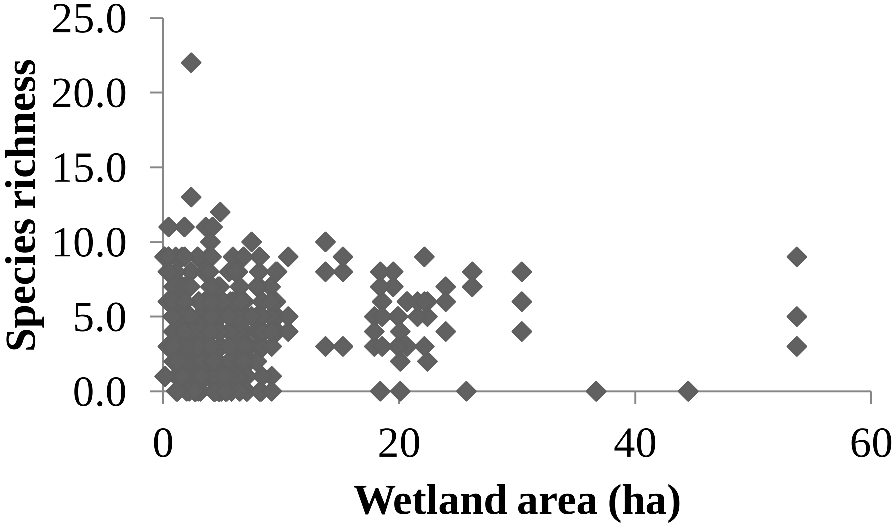


Figure C. 5. Species richness in upland sampling points (10, 40, 0r 100 m away from playa visual edge) in playa catchments vs. wetland area (ha) in all land-uses.

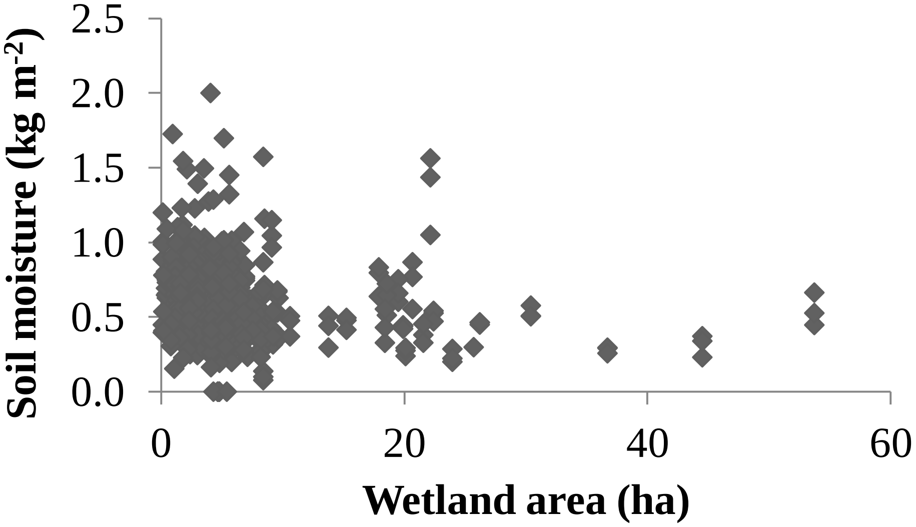


Figure C. 6. Species richness in upland sampling points (10, 40, 0r 100 m away from playa visual edge) in playa catchments vs. wetland area (ha) in all land-uses.

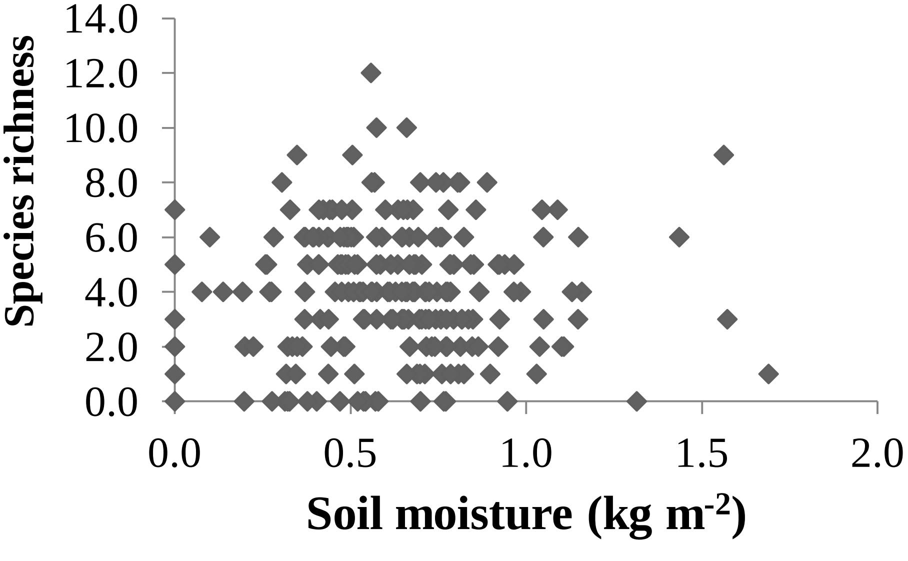


Figure C. 7. Plant species richness vs. soil moisture (kg m$^{-2}$) to 50 cm depth vs. in CRP catchments only.

# D. EFFECTS OF LAND-USE ON PLANT COMMUNITIES IN THE RAINWATER BASIN

## OBJECTIVE

We examined plant community characteristics among land-use in the Rainwater Basin (RWB) as we did in Chapter I for the western High Plains. Objectives are similar to those described in that chapter. These data were reported to our funders, USDA and the NRCS-CEAP WETLANDS program in quarterly reports. We present them here so that they also are publically available.

## METHODS

These methods follow those in Chapter I, except sub-regions were not analyzed because the RWB is a smaller area. See Chapter II for a description of the RWB, land-use types, and a map of study sites. Briefly, we surveyed plant community composition in 48 playas (16 each in reference, wetland reserve program lands (WRP), and croplands) and recorded whether playas were wet or dry at the time of survey. We used USDA PLANTS (USDA and NRCS 2010) to categorize plants as annual, perennial, native, introduced, upland, or wetland. We compared species richness of plants among land-use using the species richness area curve (log *Species richness* = *z*log *Area* +log *c*) as we did described in Chapter I (Rosenzweig 1995). We compared plant categories and number of inundated playas among land-use, also as described in Chapter I.

## RESULTS

Slopes among species richness area relationships (z-values) were equal in all land uses (Table D. 1, $F_{5,90} = 11.86$, $P < 0.001$, $R^2 = 0.40$). However, the intercept (c-value) was less in cropland playas than in reference or WRP.

Table D. 1. Log-log relationship of plant species richness with playa area (ha) among different land uses in the Rainwater Basin (N = 32 surveys, 2 surveys/playa). Uppercase letters indicate significant differences across land uses (P < 0.05).

| Land use | Slope (z) | 95 % CI of slope | Intercept (c) | 95 % CI of intercept |
|---|---|---|---|---|
| Reference | 0.12 A | 0.04 – 0.19 | 3.29 A | 2.77 – 3.81 |
| WRP | 0.12 A | 0.04 – 0.19 | 3.29 A | 2.77 – 3.81 |
| Cropland | 0.12 A | 0.04 – 0.19 | 2.61 B | 2.44 – 2.78 |

We observed 144 plant species in playa basins in the Rainwater Basin. Playas with cropland catchments had more upland plants and less wetland plants than playas in the other two land use types ($F_{2,78} = 12.55$, $P < 0.001$ and $F_{2,78} = 12.69$, $P < 0.001$, respectively, Figure D. 1b). Cover of annual plants was 37% greater in cropland playas than the other two land use types ($F_{2,78} = 4.88$, $P = 0.01$, Figure D. 1c). Conversely, perennial plants in reference and WRP playas were more than double that in croplands ($F_{2,78} = 10.62$, $P < 0.001$, Figure D. 1c). Native plants had 50% less cover in cropland playas than in WRP and reference playas. Introduced plants had more than 300% greater cover in croplands than in other catchments ($F_{2,78} = 23.22$, $P < 0.001$ and $F_{2,78} = 21.76$, $P < 0.001$, respectively, Figure D. 1d).

We detected no difference in frequency of inundated playas encountered among land use types ($N_{reference} = 16$; $N_{crop} = 13$; $N_{WRP} = 16$; $\chi 2 = 0.75$, df = 2, $P = 0.69$, Figure D. 1a). Average number of wet playas was 11.7 (out of 32 surveys) per land-use.

## DISCUSSION

In the RWB, reference playas were dominated by native wetland perennials and had greater species richness of plants (i.e., c values) than observed in the western High Plains. RWB playas have more heterogeneity in elevation than western High Plains playas, likely creating more hydric zones and increasing diversity (Smith 2003). Playas in the RWB also likely are wetter on average than those in the western High Plains because annual rainfall is greater in the RWB. In addition, many wetlands are provided supplemental water in the RWB. State and federal conservation agencies actively pump water into playas to provide waterfowl and shorebird habitat during spring migration. Cropland playas in the RWB were dominated by annuals with roughly equal proportions of native and introduced plants and slightly more wetland than upland plants. The high percentage of upland annuals rather than upland perennials resulted from a predominance of annual crops in these playas. Similarly to western High Plains cropland playas, plant cover was less than in other catchments while bare soil was higher in RWB cropland playas. Species richness also was less than observed in RWB reference playas. Low species richness and high annual plant covers suggests disturbance from plowing, planting, and harvesting prevents establishment of perennial playa plants and encourages encroachment by introduced species.

WRP playas, like reference playas, were dominated by wetland perennial natives and had similar species richness relationships to grassland playas. Thus WRP playas may be approaching reference condition biodiversity. However, multivariate community analyses presented in Chapter II demonstrate that these communities contain different species sets. In particular certain plant guilds were under-represented in WRP sites. These results mirror those of Galatowitsch (2006) in prairie potholes. She found that prairie pothole sedge-meadow species, several of which we also observed in the Rainwater basin, such as *Leersia oryzoides*, *Carex vulpinoidea*, and *Helianthus grosseserratus* were dispersal limited and do not readily colonize restoration sites by natural means. We see similar patterns in the RWB, where the above three species are present in reference sites, but not in WRP sites.

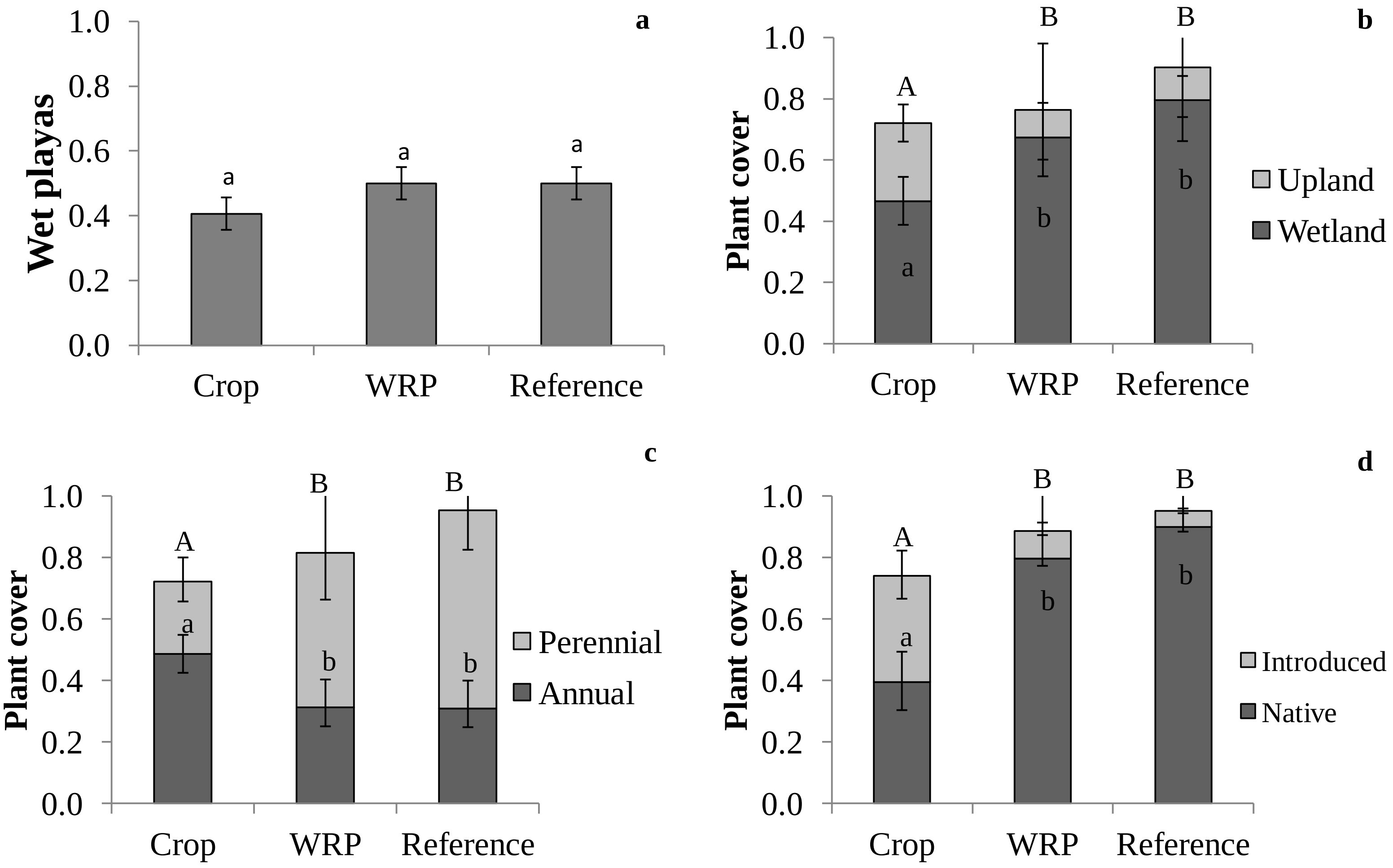


Figure D. 1. Proportion of wet playas a) and proportion of plant cover in the Rainwater Basin among playas of different land use of b) wetland and upland plants; c) annual and perennial plants; and d) native and introduced plants. Similar means are marked with the same letter ($P > 0.05$).

# LITERATURE CITED

Anderson , D. R. 2008. Model based inference in the life sciences: A primer on evidence. Springer, New York, NY, USA.

Anderson, J. T. and L. M. Smith. 2002. The effect of flooding regimes on decomposition of Polygonum pensylvanicum in playa wetlands (Southern Great Plains, USA). Aquatic Botany **74**:97-108.

Balvanera, P., A. B. Pfisterer, N. Buchmann, J.-S. He, T. Nakashizuka, D. Raffaelli, and B. Schmid. 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. Ecology Letters **9**:1146-1156.

Beas, B. J., L. M. Smith, K. R. Hickman, T. G. LaGrange, and R. Stutheit. unpublished data. Seed bank responses to wetland restoration: do restored wetlands resemble reference conditions following sediment removal? Aquatic Botany **In review**.

Bischoff, A. 2002. Dispersal and establishment of floodplain grassland species as limiting factors in restoration. Biological Conservation **104**:25-33.

Bolen, E. G., L. M. Smith, and H. L. Schramm, Jr. 1989. Playa lakes: prairie wetlands of the Southern High Plains. BioScience **39**:615-623.

Bowen, M. W. and W. C. Johnson. 2011. Late Quaternary environmental reconstructions of playa-lunette system evolution on the central High Plains of Kansas, United States. Geological Society of America Bulletin.

Brinson, M. M. and A. I. Malvárez. 2002. Temperate freshwater wetlands: types, status, and threats. Environmental Conservation **29**:115-133.

Bronson, K. F., T. M. Zobeck, T. T. Chua, V. Acosta-Martinez, R. S. v. Pelt, and J. D. Booker. 2004. Carbon and nitrogen pools of Southern High Plains cropland and grassland soils. Soil Science Society of America Journal **68**:1695-1704.

Burke, I. C., W. K. Lauenroth, and D. P. Coffin. 1995. Soil organic matter recovery in semiarid grasslands: Implications for the Conservation Reserve Program. Ecological Applications **5**:793-801.

Burke, I. C., C. M. Yonker, W. J. Parton, C. V. Cole, K. Flach, and D. S. Schimel. 1989. Texture, climate, and cultivation effects on soil organic-matter content in US grassland soils. Soil Science Society of America Journal **53**:800-805.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd edition. Springer, New York, NY, USA.

Cariveau, A., D. Pavlacky, A. Bishop, and T. LaGrange. 2011. Effects of surrounding land use on playa inundation following intense rainfall. Wetlands **31**:65-73.

Chang, E. R., E. L. Zozaya, D. P. J. Kuijper, and J. P. Bakker. 2005. Seed dispersal by small herbivores and tidal water: are they important filters in the assembly of salt-marsh communities? Functional Ecology **19**:665-673.

D'Antonio, C. M. and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics **23**:63-87.

Dahl, T. E. 2000. Status and trends of wetlands in the conterminous United States 1986 to 1997. U.S. Department of the Interior and U.S. Fish and Wildlife Service, Washington, DC.

de Bello, F., J. Lepš, and M.-T. Sebastià. 2007. Grazing effects on the species-area relationship: Variation along a climatic gradient in NE Spain. Journal of Vegetation Science **18**:25-34.

Detenbeck, N. E., C. M. Elonen, D. L. Taylor, A. M. Cotter, F. A. Puglisi, and W. D. Sanville. 2002. Effects of agricultural activities and best management practices on water quality of seasonal prairie pothole wetlands. Wetlands Ecology and Management **10**:335-354.

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

Ehrenfeld, J. G. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. Ecosystems **6**:503-523.

Eriksson, O. 1996. Regional dynamics of plants: A review of evidence for remnant, source-sink and metapopulations. Oikos **77**:248-258.

Euliss, N. H., Jr., R. A. Gleason, A. Olness, R. L. McDougal, H. R. Murkin, R. D. Robarts, R. A. Bourbonniere, and B. G. Warner. 2006. North American prairie wetlands are important nonforested land-based carbon storage sites. Science of The Total Environment **361**:179-188.

Evans, R. A. and R. M. Love. 1957. The step-point method of sampling: a practical tool in range research. Journal of Range Management **10**:208-212.

Farm Service Agency. 2010. The Conservation Reserve Program: 39th Signup Results. United States Department of Agriculture, Washington, D.C., USA.

Finlayson, C. M., N. C. Davidson, A. G. Spiers, and N. J. Stevenson. 1999. Global wetland inventory – current status and future priorities. Marine and Freshwater Research **50**:717-727.

Flatch, K. W., T. O. Barnwell, Jr., and P. Crosson. 1997. Impacts of agriculture on carbon dioxide. Pages 1-13 *in* E. A. Paul, K. Plaustian, E. T. Elliot, and C. V. Cole, editors. Soil organic matter in temperate agroecosystems: long-term experiments in North America. CRC Press, Boca Raton, FL USA.

Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, M. T. Coe, G. C. Daily, H. K. Gibbs, J. H. Helkowski, T. Holloway, E. A. Howard, C. J. Kucharik, C. Monfreda, J. A. Patz, I. C. Prentice, N. Ramankutty, and P. K. Snyder. 2005. Global consequences of land use. Science **309**:570-574.

Fornara, D. A. and D. Tilman. 2008. Plant functional composition influences rates of soil carbon and nitrogen accumulation. Journal of Ecology **96**:314-322.

Fuhlendorf, S. D., H. Zhang, T. R. Tunnell, D. M. Engle, and A. F. Cross. 2002. Effects of grazing on restoration of southern mixed prairie soils. Restoration Ecology **10**:401-407.

Funk, J. L., E. E. Cleland, K. N. Suding, and E. S. Zavaleta. 2008. Restoration through reassembly: plant traits and invasion resistance. Trends in Ecology &amp; Evolution **23**:695-703.

Galatowitsch, S. M. 2006. Restoring prairie pothole wetlands: does the species pool concept offer decision-making guidance for re-vegetation? Applied Vegetation Science **9**:261-270.

Galatowitsch, S. M. and A. G. van der Valk. 1996. Vegetation and environmental conditions in recently restored wetlands in the Prairie Pothole region of the USA. Vegetatio **126**:89-99.

Galatowitsch, S. M. and A. G. Van der Valk. 1998. Restoring prairie wetlands: an ecological approach. Iowa State Pr.

Ganesan, G. 2010. Estimating recharge through playa lakes to the Southern High Plains Aquifer. Master's thesis. Texas Tech University, Lubbock, TX, USA.

Glaser, L. K. 1985. Provisions of the Food Security Act of 1985. United States Department of Agriculture, Washington, D.C., USA.

Gleason, R., N. Euliss, D. Hubbard, and W. Duffy. 2003. Effects of sediment load on emergence of aquatic invertebrates and plants from wetland soil egg and seed banks. Wetlands **23**:26-34.

Gleason, R. A. and N. H. Euliss, Jr. 1998. Sedimentation of prairie wetlands. Great Plains Research **8**:97-112.

Godwin, H. 1923. Dispersal of pond floras. Journal of Ecology **11**:160-164.

Gotelli, N. J. and D. Simberloff. 1987. The distribution and abundance of tallgrass prairie plants: A test of the core-satellite hypothesis. The American Naturalist **130**:18-35.

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

Gurdak, J. J. and C. D. Roe. 2009. Recharge rates and chemistry beneath playas of the High Plains aquifer—A literature review and synthesis. U.S. Geological Survey, Playa Lakes Joint Venture, Reston, VA, USA.

Gurevitch, J. and D. K. Padilla. 2004. Are invasive species a major cause of extinctions? Trends in Ecology & Evolution **19**:470-474.

Guthery, F. S. and F. C. Bryant. 1982. Status of playas in the Southern Great Plains. Wildlife Society Bulletin **10**:309-317.

Gutrich, J. J., K. J. Taylor, and M. S. Fennessy. 2009. Restoration of vegetation communities of created depressional marshes in Ohio and Colorado (USA): The importance of initial effort for mitigation success. Ecological Engineering **35**:351-368.

Haddad, N. M., M. Holyoak, T. M. Mata, K. F. Davies, B. A. Melbourne, and K. Preston. 2008. Species' traits predict the effects of disturbance and productivity on diversity. Ecology Letters **11**:348-356.

Hanski, I. 1998. Metapopulation dynamics. Nature **396**:41-49.

. 1997. Size and density fractionation of soil organic matter and the physical capacity of soils to protect organic matter. European Journal of Agronomy **7**:189-199.

Haukos, D. and L. Smith. 1993. Seed-bank composition and predictive ability of field vegetation in playa lakes. Wetlands **13**:32-40.

Haukos, D. A. and L. M. Smith. 2003. Past and future impacts of weltand regulations on playa ecology in the southern Great Plains. Wetlands **23**:577-589.

Haukos, D. A. and L. M. Smith. 2004. Plant communties of playa wetlands in the Southern Great Plains. Museum of Texas Tech University **Special publication 47**:1-63.

Hickman, K. R., G. H. Farley, R. Channell, J. E. Steier, and C. Lauver. 2009. Effects of old world bluestem (*Bothriochloa ischaemum*) on food availability and avian community composition within the mixed-grass prairie. The Southwestern Naturalist **51**:524-530.

High Plains Regional Climate Center. 2011. Historical Climate Data Summaries. Lincoln, NE, USA.

Hilderbrand, R. H., A. C. Watts, and A. M. Randle. 2005. The myths of restoration ecology. Ecology and Society **10**:19.

Holm, S. 1979. A simple sequentially rejective multiple test procedure. Scandinavian Journal of Statistics **6**:65-70.

Huberty, C. J. and J. D. Morris. 1989. Multivariate analysis versus multiple univariate analyses. Psychological Bulletin **105**:302-308.

Huggins, D. R., D. L. Allen, J. C. Gardner, D. L. Karlen, D. F. Bezdicek, M. J. Rosek, M. J. Alms, M. Flock, B. S. Miller, and M. L. Staben. 1997. Enhancing carbon sequestration in CRP-managed land. Pages 323-334 *in* R. Lal, J. M. Kimble, R. F. Follett, and B. A. Stewart, editors. Management of carbon sequestration in soil. CRC Press, Baco Ratan, FL, USA.

Hurlbert, S. H. 1971. The nonconcept of species diversity: a critique and alternative parameters. Ecology **52**:577-586.

Husband, B. C. and S. C. H. Barrett. 1996. A metapopulation perspective in plant population biology. Journal of Ecology **84**:461-469.

Jaccard, J. and V. Guilamo-Ramos. 2002. Analysis of variance frameworks in clinical child and adolescent psychology: issues and recommendations. Journal of Clinical Child & Adolescent Psychology **31**:130 - 146.

Jackson, R. B., J. L. Banner, E. G. Jobbagy, W. T. Pockman, and D. H. Wall. 2002. Ecosystem carbon loss with woody plant invasion of grasslands. Nature **418**:623-626.

Jobbágy, E. G. and R. B. Jackson. 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. Ecological Applications **10**:423-436.

Johnson, L. A. 2011. Occurrence, function, and conservation of playa wetlands: the key to biodiversity of the southern Great Plains. PhD dissertation. Texas Tech University, Lubbock, TX, USA.

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

Kartesz, J. T. 2011. North American Plant Atlas  The Biota of North America Program (BONAP), Chapel Hill, N.C.http://www.bonap.org/MapSwitchboard.html

Kettenring, K. M. and S. M. Galatowitsch. 2011. Seed rain of restored and natural prairie wetlands. Wetlands **31**:1-12.

Klimkowska, A., R. Van Diggelen, J. P. Bakker, and A. P. Grootjans. 2007. Wet meadow restoration in Western Europe: A quantitative assessment of the effectiveness of several techniques. Biological Conservation **140**:318-328.

Lal, R., J. M. Kimble, R. F. Follett, and B. A. Stewart, editors. 2001. Assessment methods for soil carbon. CRC Press, Boca Raton, FL, USA.

Lavergne, S. and J. Molofsky. 2004. Reed canary grass (Phalaris arundinacea) as a biological model in the study of plant invasions. Critical Reviews in Plant Sciences **23**:415-429.

Lodge, D. M. 1993. Biological invasions: Lessons for ecology. Trends in Ecology & Evolution **8**:133-137.

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

Luo, H. R., L. M. Smith, D. A. Haukos, and B. L. Allen. 1999. Sources of recently deposited sediments in playa wetlands. Wetlands **19**:176-181.

MacArthur, R. and E. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, NJ, USA.

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

Millennium Ecosystem Assessment. 2005. Ecosystems and human well-being: Wetlands and water synthesis. Island Press, Washington, D.C., USA.

Mitsch, W. J. and J. G. Gosselink. 2007. Wetlands. Fourth edition. John Wiley & Sons, Hoboken, NJ, USA

Mitsch, W. J., X. Wu, R. W. Nairn, P. E. Weihe, N. Wang, R. Deal, and C. E. Boucher. 1998. Creating and restoring wetlands. BioScience **48**:1019-1030.

Mulhouse, J. M. and S. M. Galatowitsch. 2003. Revegetation of prairie pothole wetlands in the mid-continental US: twelve years post-reflooding. Vegetatio **169**:143-159.

Nielsen, U. N., E. Ayres, D. H. Wall, and R. D. Bardgett. 2011. Soil biodiversity and carbon cycling: a review and synthesis of studies examining diversity–function relationships. European Journal of Soil Science **62**:105-116.

NOAA. 2011. National Climatic Data Center. U.S. Department of Commerce.www.ncdc.noaa.gov

NRCS. 2008. Wetland restoration, enhancement, or creation. United States Department of Agriculture, Natural Resources Conservation Service, and U.S. Fish and Wildlife Service Part 650 Engineering Field Handbook, United States Department of Agriculture, Natural Resources Conservation Service, U.S. Fish and Wildlife Service, Washington D.C., USA.

O'Connell, J. L., L. A. Johnson, L. M. Smith, S. T. McMurry, and D. A. Haukos. In press. Influence of land-use and conservation programs on wetland plant communities of the semi-arid United States Great Plains. Biological Conservation **In press**.

Okubo, A. and A. L. Simon. 1989. A theoretical framework for data analysis of wind dispersal of seeds and pollen. Ecology **70**:329-338.

Ozinga, W. A., C. Römermann, R. M. Bekker, A. Prinzing, W. L. M. Tamis, J. H. J. Schaminée, S. M. Hennekens, K. Thompson, P. Poschlod, M. Kleyer, J. P. Bakker, and J. M. Van Groenendael. 2009. Dispersal failure contributes to plant losses in NW Europe. Ecology Letters **12**:66-74.

Ozinga, W. A., J. H. J. Schaminée, R. M. Bekker, S. Bonn, P. Poschlod, O. Tackenberg, J. Bakker, and J. M. Groenendael. 2005. Predictability of plant species composition from environmental conditions is constrained by dispersal limitation. Oikos **108**:555-561.

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

Paul, E. A., S. J. Morris, R. T. Conant, and A. F. Plante. 2006. Does the acid hydrolysis–incubation method measure meaningful soil organic carbon pools? Soil Science Society of America **70**:1023-1035.

Perry, J. N. and J. L. Gonzalez-Andujar. 1993. Dispersal in a metapopulation neighbourhood model of an annual plant with a seedbank. Journal of Ecology **81**:453-463.

Pianka, E. R. 1970. On r-and k-selection. The American Naturalist **104**:592-597.

Poschlod, P. and S. Bonn. 1998. Changing dispersal processes in the central European landscape since the last ice age: An explanation for the actual decrease of plant species richness in different habitats? Acta Botanica Neerlandica **47**:27-44.

Poschlod, P., C. Meindl, J. Sliva, U. Herkommer, M. Jäger, U. Schuckert, A. Seemann, A. Ullmann, and T. Wallner. 2007. Natural revegetation and restoration of drained and cut-over raised bogs in southern Germany — a comparative analysis of four long-term monitoring studies. Global Environmental Research **11**:205-216.

Post, W. M., W. R. Emanuel, P. J. Zinke, and A. G. Stangenberger. 1982. Soil carbon pools and world life zones. Nature **298**:156-159.

Post, W. M. and K. C. Kwon. 2000. Soil carbon sequestration and land-use change: processes and potential. Global Change Biology **6**:317-327.

Potter, K. N., H. A. Torbert, H. B. Johnson, and C. R. Tischler. 1999. Carbon storage after long-term grass establishment on degraded soils. Soil Science **164**:718-725.

Purakayastha, T., D. Huggins, and J. Smith. 2008. Carbon sequestration in native prairie, perennial grass, no-till, and cultivated Palouse silt loam. Soil Science Society of America Journal **72**:534-540.

Raich, J. W. and W. H. Schlesinger. 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. Tellus B **44**:81-99.

Rasse, D. P., C. Rumpel, and M.-F. Dignac. 2005. Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation. Plant and Soil **269**:341-356.

Reeder, J. D., G. E. Schuman, and R. A. Bowman. 1998. Soil C and N changes on conservation reserve program lands in the Central Great Plains. Soil and Tillage Research **47**:339-349.

Rees, R. M., I. J. Bingham, J. A. Baddeley, and C. A. Watson. 2005. The role of plants and land management in sequestering soil carbon in temperate arable and grassland ecosystems. Geoderma **128**:130-154.

Reeves, C. C., Jr. 1970. Origin, classification, and geologic history of caliche on the southern High Plains, Texas and eastern New Mexico. The Journal of Geology:352-362.

Robel, R. J., J. P. Hughes, S. D. Hull, K. E. Kemp, and D. S. Klute. 1998. Spring burning: resulting avian abundance and nesting in Kansas CRP. Journal of Range Management **51**:132-138.

Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press, Cambridge, UK.

Ryder, P. D. 1996. Groundwater atlas of the United States: High Plains Aquifer. United States Geologic Survey, Reston, VA, USA.

Samson, F. and F. Knopf. 1994. Prairie conservation in North America. BioScience **44**:418-421.

Samson, F. B., F. L. Knopf, and W. R. Ostlie. 2004. Great Plains ecosystems: past, present, and future. Wildlife Society Bulletin **32**:6-15.

Schoeneberger, P., D. Wysocki, E. Benham, and W. Broderson. 2002. Field book for describing and sampling soils, Version 2. National Soil Survey Center, Natural Resources Conservation Service, and U.S. Department of Agriculture, NRCS, USDA, Lincoln, Nebraska.

Schumacher, B. A. 2002. Methods for the determination of total organic carbon (TOC) in soils and sediments. United States Environmental Protection Agency, U.S. EPA, Las Vegas, NV, USA.

Semlitsch, R. D. and J. R. Bodie. 1998. Are small, isolated wetlands expendable? Conservation Biology **12**:1129-1133.

Sherrod, L. A., G. Dunn, G. A. Peterson, and R. L. Kolberg. 2002. Inorganic carbon analysis by modified pressure-calcimeter method. Soil Science Society of America Journal **66**:299-305.

Shipley, B. and M. Parent. 1991. Germination responses of 64 wetland species in relation to seed size, minimum time to reproduction and seedling relative growth rate. Functional Ecology **5**:111-118.

Six, J., R. T. Conant, E. A. Paul, and K. Paustian. 2002. Stabilization mechanisms of soil organic matter: Implications for C-saturation of soils. Plant and Soil **241**:155-176.

Skagen, S. K., C. P. Melcher, and D. A. Haukos. 2008. Reducing sedimentation of depressional wetlands in agricultural landscapes. Wetlands **28**:594-604.

Smith, L., N. Euliss, D. Wilcox, and M. Brinson. 2008. Application of a geomorphic and temporal perspective to wetland management in North America. Wetlands **28**:563-577.

Smith, L. M. 2003. Playas of the Great Plains. University of Texas Press, Austin, TX, USA.

Smith, L. M. and D. A. Haukos. 2002. Floral diversity in relation to playa wetland area and watershed disturbance. Conservation Biology **16**:964-974.

Smith, L. M., D. A. Haukos, S. T. McMurry, T. LaGrange, and D. Willis. 2011a. Ecosystem services provided by playa wetlands in the High Plains: potential influences of USDA conservation proprams and practices. Ecological Applications **21**:S82–S92

Smith, L. M., S. T. McMurry, J. L. O'Connell, and D. A. Haukos. 2011b. Influence of U. S. Department of Agriculture Programs and conservation practices on ecological services provided by playa wetlands in the High Plains. Department of Zoology; U. S. Fish and Wildlife Service, Oklahoma State University; Texas Tech University; CEAP Wetlands DRAFT FINAL Report, Stillwater, OK; Lubbock, TX.

Soil Survey Staff. 2011. Official soil series descriptions. Natural Resources Conservation Service, United States Department of Agriculture.http://soils.usda.gov/technical/classification/osd/index.html

Steinbeiss, S., H. BeßLer, C. Engels, V. M. Temperton, N. Buchmann, C. Roscher, Y. Kreutziger, J. Baade, M. Habekost, and G. Gleixner. 2008. Plant diversity positively affects short-term soil carbon storage in experimental grasslands. Global Change Biology **14**:2937-2949.

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, U.S. Fish and Wildlife Service, Northern Prairie Wildlife Research Center Online, Washington, D.C, Jamestown, ND, USA.

Streever, B., J. Zedler, W. J. Mitsch, X. Ben Wu, R. W. Nairn, and N. Wang. 2000. To plant or not to plant. BioScience **50**:188-190.

Sumner, M. E. 2000. Handbook of soil science. CRC Press, Boca Raton, FL, USA.

Takada, T. and H. Nakajima. 1996. The optimal allocation for seed reproduction and vegetative reproduction in perennial plants: An application to the density-dependent transition matrix model. Journal of Theoretical Biology **182**:179-191.

ter Braak, C. J. F. 1988. Partial canonical correspondence analysis. Pages 551-558 *in* H. H. Bock, editor. Classification and related methods of data analysis. North-Holland, Amsterdam, The Netherlands.

ter Braak, C. J. F. and P. Šmilauer. 2002. CANOCO reference manual and CanoDraw for Windows user's guide: Software for canonical community ordination (version 4.5). Microcomputer Power, Ithaca NY, USA.

Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. Ecology **78**:81–92.

Tilman, D., L. CL, and K. P. 1997. Population dynamics in spatial habitats. Page 368 *in* T. D and K. P, editors. Spatial ecology: the role of space in population dynamics and interspecific interactions. Princeton University Press, Princeton Princeton, NJ, USA.

Tilman, D., J. Hill, and C. Lehman. 2006. Carbon-negative biofuels from low-input high-diversity grassland biomass. Science **314**:1598-1600.

Tilman, D., D. Wedin, and J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature **379**:718-720.

Tiner, R. W. 2003. Geographically isolated wetlands of the United States. Wetlands **23**:494-516.

Tiner, R. W., H. C. Bergquist, G. P. DeAlessio, and M. J. Starr. 2002. Geographically isolated wetlands: a preliminary assessment of their characteristics and status in selected areas of the United States. U.S. Department of the Interior, Fish and Wildlife Service, Northeast Region, Hadley, MA, USA.

Trumbore, S. E. 1997. Potential responses of soil organic carbon to global environmental change. Proceedings of the National Academy of Sciences **94**:8284-8291.

Tsai, J.-S., L. S. Venne, S. T. McMurry, and L. M. Smith. 2010. Vegetation and land use impact on water loss rate in playas of the southern High Plains, USA. Wetlands **30**:1107-1116.

Tsai, J. S., L. S. Venne, S. T. McMurry, and L. M. Smith. 2007. Influences of land use and wetland characteristics on water loss rates and hydroperiods of playas in the Southern High Plains, USA. Wetlands **27**:683-692.

Turnbull, L. A., M. J. Crawley, and M. Rees. 2000. Are plant populations seed-limited? A review of seed sowing experiments. Oikos **88**:225-238.

USDA-NRCS. 2004. Soil survey laboratory methods manual.*in* R. Burt, editor. U. S. Department of Agriculture, Natural Resources Conservation Service, Lincoln, Nebraska, Soil Survey Investigations Report No. 42.

USDA-NRCS. 2006. Land resource regions and major land resource areas of the United States, the Caribbean, and the Pacific Basin. U.S. Department of Agriculture Handbook 296, Washington D.C., USA.

USDA. 2003. National Planning Procedures Handbook, Amendment 4. United States Department of Agriculture and National Resources Conservation Service, Beltsville, MD, USA.

USDA. 2011. FY 2012: Budget summary and annual performance plan, http://www.obpa.usda.gov/budsum/FY12budsum.pdf. U.S. Department of Agriculture, Washington D.C., USA.

USDA and NRCS. 2010. The PLANTS Database. National Plant Data Center, Baton Rouge, LA, USA.http://plants.usda.gov

van der Kamp, G., M. Hayashi, and D. Gallén. 2003. Comparing the hydrology of grassed and cultivated catchments in the semi-arid Canadian prairies. Hydrological Processes **17**:559-575.

van Dorp, D., W. P. M. van den Hoek, and C. Daleboudt. 1996. Seed dispersal capacity of six perennial grassland species measured in a wind tunnel at varying wind speed and height. Canadian Journal of Botany **74**:1956-1963.

Verdonschot, P. F. M. and C. J. F. ter Braak. 1994. An experimental manipulation of oligochaete communities in mesocosms treated with chlorpyrifos or nutrient additions: multivariate analyses with Monte Carlo permutation tests. Hydrobiologia **278**:251-266.

Vinton, M. A. and I. C. Burke. 1995. Interactions between individual plant species and soil nutrient status in shortgrass steppe. Ecology **76**:1116-1133.

Wardrop, D. H. and R. P. Brooks. 1998. The occurrence and impact of sedimentation in central Pennsylvania wetlands. Environmental Monitoring and Assessment **51**:119-130.

West, T. O. and W. M. Post. 2002. Soil organic carbon sequestration rates by tillage and crop rotation. Soil Sci. Soc. Am. J. **66**:1930-1946.

Wilsey, B. J. and C. Potvin. 2000. Biodiversity and ecosystem functioning: importance of species evenness in an old field. Ecology **81**:887-892.

Wilson, R. D. 2010. Evaluating hydroperiod response in the Rainwater Basin wetlands of South-Central Nebraska. Masters of science thesis. University of Nebraska - Lincoln, Lincoln, NE, USA.

Zedler, J. B. 2000. Progress in wetland restoration ecology. Nature **15**:402–407.

Zedler, J. B. and S. Kercher. 2005. Wetland resources: Status, trends, ecosystem services, and restorability. Annual Review of Environment and Resources **30**:39-74.

Zobel, M., M. Otsus, J. Liira, M. Moora, and T. Möls. 2000. Is small-scale species richness limited by seed availability or microsite availability? Ecology **81**:3274-3282.

Zuur, A., E. Ieno, N. Walker, A. Saveliev, and G. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, NY, USA.

VITA

Jessica L. O'Connell

Candidate for the Degree of

Doctor of Philosophy

Thesis: INFLUENCES ON PLANT SPECIES DISTRIBUTIONS AND SOIL ORGANIC CARBON IN PLAYA CATCHMENTS OF THE HIGH PLAINS

Education:

- Completed the requirements for the Doctor of Philosophy at Oklahoma State University, Stillwater, Oklahoma in May, 2012.
- Completed the requirements for the Master of Science at Louisiana State University, Baton Rouge, LA in 2006.
- Completed the requirements for the Bachelor of Arts at Sonoma State University, Cotati, CA in 2003.

Experience:

- Teaching Assistant, Guest Lecturer, Research Assistant, Oklahoma State University, 2008-2011
- Teaching Assistant, Guest Lecturer, Tulane University, 2007
- Avian Research Technician, Arkansas State University, 2007
- Research Associate, Louisiana State University, 2004-2006
- Wetland Research Technician, Louisiana State University, 2004
- Staff Biologist, PRBO Conservation Science 2003-2004

Professional Memberships:

- Society for Wetland Scientists
- American Association for the Advancement of Science
- Ecological Society of America

Name: Jessica L. O'Connell Date of Degree: May, 2012

Institution: Oklahoma State University Location: Stillwater, Oklahoma

Title of Study: INFLUENCES ON PLANT SPECIES DISTRIBUTIONS AND SOIL ORGANIC CARBON IN PLAYA CATCHMENTS OF THE HIGH PLAINS

Pages in Study: 142 Candidate for the Degree of Doctor of Philosophy

Major Field: Zoology

Scope and Method of Study: Depressional wetlands are threatened globally by conversion to agriculture, altering wetland processes and degrading societal services. We elucidated effects of land management and conservation programs on plant species distributions and soil organic carbon (SOC) in prairies and wetlands of the United States Great Plains. Plant composition mediates many wetland processes and information concerning plant distributions aids wetland and prairie conservation, maximizing management goals. We surveyed 309 wetlands (261 in the western High Plains (WHP), 48 in the Rainwater Basin (RWB)) and surrounding uplands (WHP only) in 3 land-use types: Reference (i.e. native prairie in the WHP and best available in the RWB), United States Department of Agriculture conservation programs (Conservation Reserve Program (CRP) lands in the WHP, Wetland Reserve Program lands (WRP) in the RWB), and cropland. We quantified plant composition, inundation probability, above and belowground biomass, wetland area, wetland sediment accumulation, soil moisture, and SOC. We identified influences on plant distributions, including land management, dispersal limitation, and disturbance processes. We provide restoration models and suggestions for remediation of plant communities where appropriate.

Findings and Conclusions: Plant communities interact with abiotic wetland processes and plant conservation maintains wetland services. Croplands and CRP influenced inundation probability in WHP wetlands. Introduced high-biomass tall-grasses planted in CRP reduced overland runoff, while exposed soil in croplands increased sediment erosion into wetlands. Reduction of playa inundation reduces water available for people and wildlife in the WHP, a semiarid landscape with limited surface water. Plowing and sediment accretion in cropland playas also reduced plant species richness and plowing reduced wetland perennial species. Further, many wetland perennials observed were dispersal-limited and did not quickly return to wetlands, even after plowing ceased. These perennial wetland species probably must be inoculated into previously cultivated wetlands before they will be represented in plant communities. Additionally, SOC was higher in grasslands than cropland and CRP and plant species richness was an important determinant of SOC in playas and uplands. Thus, plant species distributions are critical for enhancing SOC and water availability in playas. Conservation programs containing provisions to protect playa plants, including planting common native species and using grass buffers to control erosion into wetlands, should be promoted over long timescales.

ADVISER'S APPROVAL: Loren Smith :