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Influence of land-use and conservation programs on wetland plant communities of the semiarid United States Great Plains

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ABSTRACT

Depressional wetlands are predominant surface hydrological features providing critical societal ecosystem services in the semiarid United States High Plains. Critical wetland properties 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 six states within three 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 should not be planted 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.

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1. Introduction

Wetlands are globally recognized as 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., 2011). 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 land practices intended to conserve playas. Such suggestions should inform

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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 and shortens hydroperiods (Luo et al., 1997; Tsai et al., 2007). Shortened hydroperiods influence all other playa ecosystem properties (Smith et al., 2011). Upland sediments in playas are naturally removed only by wind because playas have no overland water outputs. Sediment removal by wind is far slower than sediment accumulation in croplands (Luo et al., 1999). 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 average $97 million annually (Farm Service Agency, 2010). Most CRP plantings in the High Plains were introduced perennial grasses (e.g., those occurring outside of their historical range as defined by USDA and NRCS (2010)). Thus, CRP playas are previously cultivated wetlands that now are often planted with extensive introduced grass cover. Introduced grasses in CRP plantings may alter water cycling, belowground nutrients 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 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 management practices vary in both croplands and CRP and these practices may influence wetland plant communities. In CRP two main land management practices occur: planting native grasses vs. introduced grasses. In High Plains CRP lands, introduced grasses mostly were planted. The exception was Kansas, where native tall-grass plantings were common (Robel et al., 1998; Hickman et al., 2009), though not planted exclusively. No previous study has evaluated differences among playa plant communities in native and introduced CRP grasslands.

Further, in croplands, land management practices also may influence wetland plant communities. Land management practices in croplands include those provided for by USDA wetland conservation provisions (Smith et al., 2011). Such provisions are the Highly Erodible Land Conservation and Wetland Conservation Compliance provisions (Swampbuster). Swampbuster conservation provisions for croplands were first introduced in the 1985 Farm Bill. Swampbuster provisions withhold USDA benefits from 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 frequent tilling of playas. Further, many wetlands are dry at some stage of their hydrologic cycle (Mitsch and Gosselink, 2007). Thus Swampbuster may generally fail to prevent tilling depressional wetlands in the US. Finally, Swampbuster always allows catchment tillage even when it prevents wetland tillage. We have little evidence that plowing catchments while leaving wetland basins unplowed protects wetlands. Moreover, studies should critically evaluate the effect 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 US 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.

2. Materials and methods

2.1. 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 six states, and can be considered to contain three sub-regions: the northern, central and southern High Plains (Fig. 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 30 cm in the west to 83 cm in the east (USGS, 2010).

We sampled 261 playas: 87 each embedded in native grassland (never previously plowed), USDA CRP (previously plowed and planted with 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 reduced matrix color (Luo et al., 1997), and distinct in appearance from non-Vertisol upland soils.

2.2. 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.

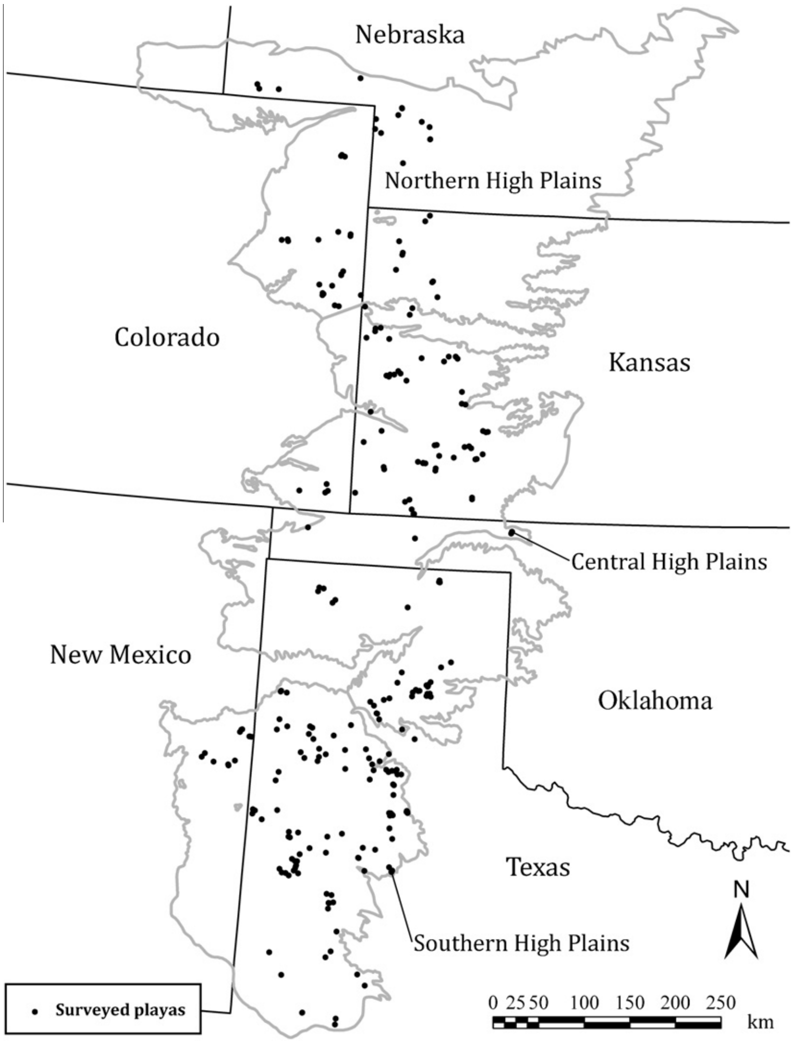

Fig. 1. Locations of playas surveyed ($n = 261$) within the non-glaciated High Plains of the United States. The High Plains Aquifer delineates the border of the short-grass in eco-region. Aquifer outline provided by USGS and modified by M. McLachlan, PL JV.

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 to 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 triplets. We collected all biomass (clipped to the soil surface) from 50 × 50-cm quadrats. We selected wetland triplets for clip-plots evenly across sub-regions, proportionate to playa density. We clipped one quadrat/playa 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.

2.2.1. 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).

2.2.2. Plant composition differences

We investigated differences in relationships between species richness, land-use and playa area with analysis of covariance (ANCOVA). 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 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 in Fig. 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 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.

2.2.3. 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 vs. dry by land-use.

2.3. 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.

3. Results

3.1. 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 ($F_{2,251} = 6.64$, $P = 0.002$, Fig. 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.

3.2. 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 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

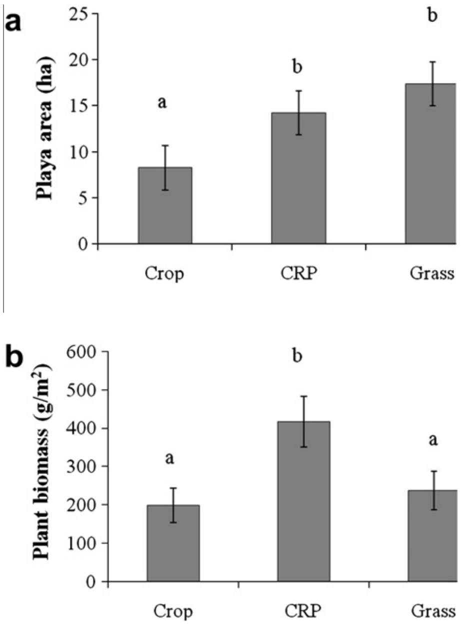

Fig. 2. Mean (±SE) among playas of different land-use and region of (a) playa area; (b) aboveground biomass. Lower-case letters designate differences among land-use ($P < 0.05$).

Table 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	0.12A	0.06–0.18	2.67A	2.52–2.83
CRP	0.15A	0.09–0.21	2.55A	2.41–2.69
Cropland	0.48B	0.39–0.57	1.22B	1.03–1.42
Playa plowed	0.40a	0.25–0.55	1.16a	0.91–1.41
Playa unplowed	0.31a	0.21–0.42	1.89b	1.61–2.17

by land-use; CRP biomass was twice that of other land-uses ($F_{2,52} = 4.4$, $P = 0.017$, Fig. 2b). Wetland plants generally had reduced cover in cropland playas vs. other land-uses, except in the northern sub-region, where they were equally low in CRP playas ($F_{4,421} = 2.92$, $P = 0.02$, Fig. 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: $F_{2,421} = 3.58$, $P = 0.029$, Fig. 3b).

All other models had 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% to 19% ($F_{4,421} = 4.06$, $P = 0.003$, Fig. 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 ($F_{4,421} = 8.36$, $P < 0.001$, Fig. 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, except in the southern region where native cover was similar between grasslands and CRP ($F_{4,421} = 5.7$, $P < 0.001$, Fig. 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 ($F_{4,421} = 3.43$, $P = 0.009$, Fig. 3f).

3.3. 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.

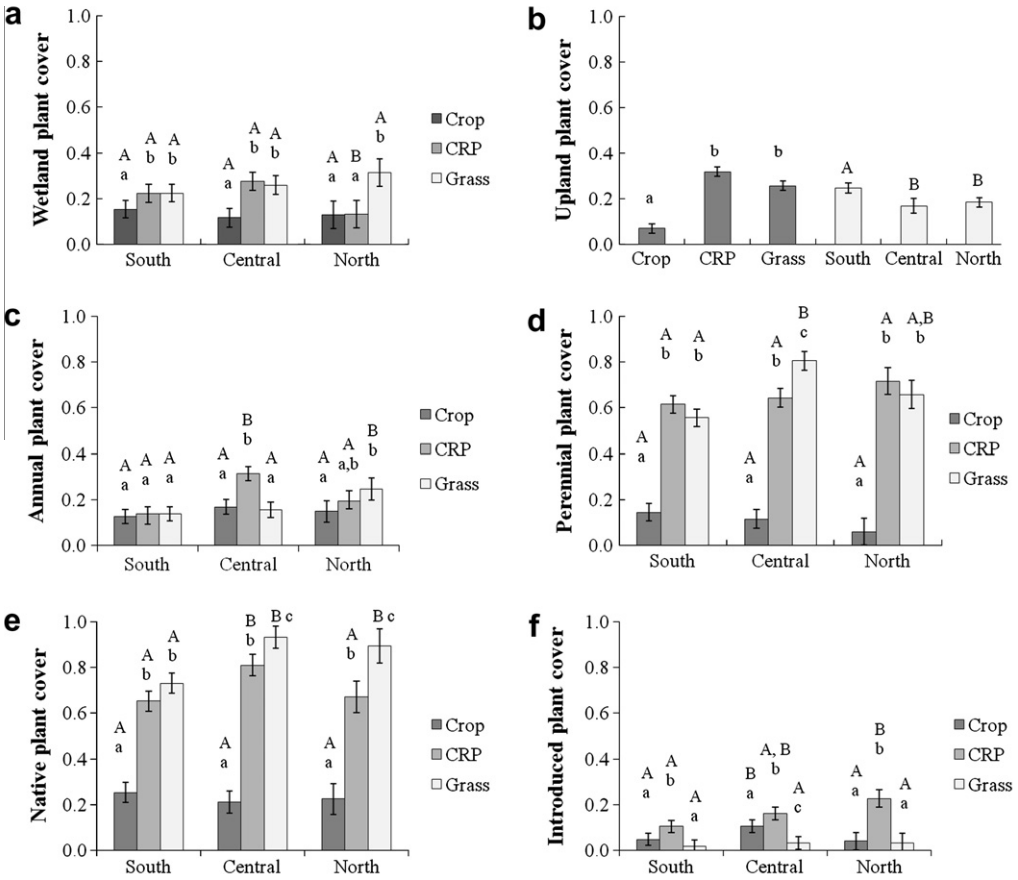

Fig. 3. Significant models for land-use, region, or land-use*region interactions for proportion of cover for (a) wetland plants; (b) upland plants; (c) annual plants; (d) perennial plants; (e) native plants; (f) introduced plants. Upper-case letters designate differences of the same land-use across regions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

Table 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
Invasive	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

3.4. 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 1). Cultivated playa basins also had reduced cover of all plants except annuals, which were 3% greater than in unplowed basins (Table 2). We detected no difference in plant biomass between cultivated and uncultivated crop playas ($F_{1,28} = 0.13$, $P = 0.72$, $\overline{X}_{unplowed} = 260.5 \pm 51$ g/m^2, $n = 12$; $\overline{X}_{plowed} = 330.1 \pm 117$ g/m^2, $n = 18$).

4. Discussion

4.1. Area of wetland habitat and species richness

Cropland playas were half the area of native grassland playas. There are two potential explanations for this. First, small playas may be easier to plow because 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 thus 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). Substantial upland sedimentation from croplands into playas 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.

4.2. 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 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., 2011). Introduced species other than planted grasses also were present and must have germinated from seed banks 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.

4.3. 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 in CRP 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).

4.4. 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 suggests that this practice does not reduce introduced species or 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. These native 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, CRP playas in Kansas did not have reduced cover of introduced plants relative to those in 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. Cover of native species in Kansas also was similar to other states after Holm–Bonferroni correction. Further, native species 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 have documented that introduced species may establish without decreasing native species (Tilman, 1997; Gurevitch and Padilla, 2004). In total, our data imply that planting native grass 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 (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.

4.5. 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 showed that 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. Plant cover in unplowed playas perhaps was reduced because of sediment accumulation in wetland basins. Also, unplowed playas likely were 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 plowing through any depressional wetland may generally be a destructive practice.

4.6. Suggestions for remediation

Native short-grass prairies were often converted to cropland and CRP in the High Plains, profoundly impacting depressional wetlands. Additionally, cultivated watershed erosion 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 catchment 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 other 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 prairie. 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., 2011). 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., 2011). 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., 2011).

The High Plains, is a highly altered landscape, and 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.

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