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Assessing wetland mitigation efforts using standing vegetation and seed bank community structure in neighboring natural and compensatory wetlands in north-central Texas

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Abstract It is often presumed plant recruitment from the soil seed bank and nearby wetlands will be sufficient to establish a wetland plant community following the restoration or creation of wetland hydrology. This approach to wetland restoration was examined in four compensatory wetlands and a natural oxbow wetland (Oxbow) in a floodplain of the West Fork Trinity River in north-central Texas. We assessed: (1) similarities in vegetation and seed bank composition among natural and compensatory wetlands, (2) within site similarity of vegetation relative to its seed bank community, and (3) the effects of hydrology (Wet vs. Drained soil) on the germination of seeds from the seed bank. Species richness of the standing vegetation was variable across sites and years, however when pooled across years (2008–2009) vegetation and seed banks showed similar species richness (66 vs. 70 species). Fewer wetland species (i.e., species occurring in wetlands $>50 \%$ of the time) were observed in the vegetation relative to the seed bank (25 vs. 41 species), and seed banks of compensatory wetlands were more similar to the natural

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wetland than was the standing vegetation. In the seed bank study, location (i.e., site) significantly affected total species richness, wetland species richness, diversity, and germinated seeds m^{-2} , however no significant effect of hydrology was detected. These results suggest hydrology alone is not sufficient to establish a desired wetland plant community in a created wetland and the inclusion of seed bank surveys with field vegetation surveys provides a more complete assessment of wetland creation and restoration.

Keywords Wetlands · Seed bank · Hydrology · Mitigation · Texas

Introduction

Wetlands provide numerous ecological and economic functions, including water quality improvement, soil retention, and the provision of rich wildlife habitat (Mitsch and Gosselink [2000\)](#page-16-0). However, in the United States, over 50 % of wetlands that existed prior to European settlement have been lost as a result of human activity (Dahl [1990\)](#page-16-0). Recognizing the importance of wetlands, the United States government under Section 404 of the Clean Water Act (33 U.S.C. 1344) has adopted a wetland policy of ''no net loss'' requiring compensatory mitigation—the creation of new wetlands, or the enhancement and/or restoration of existing wetlands—to replace wetlands unavoidably lost or adversely affected by United States Army

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Corps of Engineers-authorized activities (USACE [2002\)](#page-16-0). Comprehensive assessment of the plant community of compensatory wetlands (i.e., created or restored wetlands) is crucial to ensuring that mitigation projects construct viable wetland habitats equivalent to that of natural wetlands (Brinson and Rheinhardt [1996](#page-16-0); Mitsch et al. [1998\)](#page-16-0).

The restoration of wetland habitat, and the design of compensatory wetlands, has classically been perceived as an environmental restoration to reinstate or create a desired wetland plant community by establishing hydric soils (Madsen [1986](#page-16-0); Zedler [2000;](#page-17-0) van der Valk [2013](#page-16-0)). Inherent in this approach is the assumption that sufficient seeds and/or propagules exist in, or will enter a given area and a wetland ecosystem will establish by self-design once wetland hydrology has been restored (Galatowitsch and van der Valk [1996](#page-16-0); Mitsch et al. [1998](#page-16-0)). Under the hypothesis of community self-assembly, active means of community assembly (e.g., supplementary planting, seeding, soil transplantation) are, therefore, not necessary to construct or restore wetland habitat (La Grange and Dinsmore [1989\)](#page-16-0). This concept, referred to as the ''efficient community hypothesis'' (ECH) (sensu Galatowitsch and van der Valk [1996](#page-16-0)), is widely employed. However, long-term data supporting the ECH approach in wetlands is lacking (Zedler [2000](#page-17-0); Aronson and Galatowitsch [2008](#page-15-0)). Alone, passive means of community assembly may be insufficient to create a wetland community of comparable diversity to that of natural wetlands (i.e., for mitigation), or to restore a wetland plant community to a prior state of diversity (i.e., habitat restoration) (Galatowitsch and van der Valk [1996\)](#page-16-0).

Assessments of the ECH approach have shown limitations in its success and indicate steps for active community assembly may be necessary in some cases. In historic wetland sites, the soil seed bank may become depauperate of wetland species due to time dependent mortality of buried seeds, reduced influx of propagules, and shifts in vegetation and seed bank composition as a result of long-term disturbances from recent events associated with a location's present usage and/or more recent history (Galatowitsch and van der Valk [1996;](#page-16-0) Brown and Bedford [1997](#page-16-0); Ficken and Menges [2013\)](#page-16-0). Furthermore, in newly restored wetlands, soil disturbance during restoration may reduce wetland diversity by facilitating the establishment of invasive opportunistic species (Brown [1995](#page-16-0);

Ficken and Menges [2013](#page-16-0)). For instance, three years after reflooding, restored wetlands in the prairie pothole region of North America possessed fewer species compared to reference sites (Galatowitsch and van der Valk [1996](#page-16-0)). In a marsh of the Florida Everglades, a laboratory experiment concluded soil seed bank propagules were insufficient to restore desired community composition upon reestablishment of historic hydrology, and furthermore, soil rehydration encouraged the germination of undesirable species (Smith et al. [2002](#page-16-0)). Therefore, it is important to evaluate both the present and historical potential of an area to function as a wetland system prior to implimenting construction or restoration (van der Valk and Penderson [1989](#page-16-0)).

Plant community structure is a key indicator of wetland status, and the presence of wetland plants is a major criterion for wetland delineation and the functional assessment of wetlands (USACE [1987](#page-16-0)). Consequently, vegetation surveys are a key indicator of the success of wetland mitigation efforts. However, standing vegetation surveys may underestimate species richness, diversity and the success of wetland mitigation efforts (Thompson and Grime [1979](#page-16-0)), especially in cases where surveys are not performed over multiple seasons or years (Mitsch et al. [1998](#page-16-0); Zedler [2000](#page-17-0)). In areas prone to periods of extreme weather or hydrological variation, considerable variability may be apparent in both the composition and biomass of standing crop at a single location within seasons and across years (Hobbs and Mooney [1995](#page-16-0); Baldwin et al. [2001;](#page-16-0) Whigham et al. [2002\)](#page-17-0). Conditions favoring the germination and establishment of key indicator species may not have occurred prior to the period in which sampling occurs, therefore, these species would be deemed absent despite persisting as long-lived propagules within the soil seed bank (van der Valk [1981](#page-16-0)). For instance, during times of flooding, increased water depth can reduce vegetation growth and inhibit seed germination (Baldwin and DeRico [1999;](#page-16-0) Baldwin et al. [2001](#page-16-0)), as well as, reduce seedling survivorship (Fraser and Karnezis [2005\)](#page-16-0) and favor germination of undesirable species (Smith et al. [2002](#page-16-0); Collins et al. [2013](#page-16-0)). Conversely, moist and drawdown conditions can stimulate seed germination (Smith and Kadlec [1983;](#page-16-0) Collins et al. [2013\)](#page-16-0) and lead to an overall increase in species richness (Baldwin et al. [2001\)](#page-16-0). The inclusion of soil seed bank assessments with vegetation surveys may more accurately reflect the potential plant community composition (van der Valk and Penderson [1989\)](#page-16-0) and allow for assessments when prevailing conditions do not favor germination of key indicator species. Knowledge of a site's combined vegetation and soil seed bank communities, and the role of hydrology in shaping these communities, is essential for project managers to effectively meet wetland restoration or mitigation project goals (Ficken and Menges [2013\)](#page-16-0).

In this study, we evaluate the effectiveness of the ECH approach to wetland creation in several constructed wetlands at a mitigation site in north-central Texas. The community structure in restored and natural wetlands was compared using a combination of standing vegetation and wetland seed bank studies. To test the effects of hydrology on plant community composition, seed bank studies were experimentally conducted under two levels of water availability: saturated and non-saturated soil conditions. We asked: (1) is standing vegetation and seed bank composition comparable between natural and constructed wetland sites; (2) does existing vegetation reflect the seed bank community structure; (3) do changes in hydrology affect seed bank seedling emergence within and among sites? If the ECH is effectual, we hypothesized that the community structure at each constructed wetland would be comparable to that of an adjacent natural reference wetland. Furthermore, given the recognized importance of hydrology in structuring plant community composition (van der Valk [1981](#page-16-0)), we predicted that water availability will affect seedling emergence from the soil seed bank and affect plant community composition among sites.

Methods

Study site description

The study site was located in Dallas County on a floodplain of the West Fork Trinity River (hereafter, West Fork) in the City of Grand Prairie, Texas, USA (lat $32^{\circ}46'24''N$, long $96^{\circ}56'32''W$) at the City of Grand Prairie's Municipal Landfill. Along the periphery of the landfill are four constructed wetland sites and a natural oxbow wetland. In 1984, a levee was constructed by the USACE along the West Fork to prevent encroachment of the West Fork onto the landfill property by an ephemeral oxbow channel. Isolation of the oxbow led to the creation of a natural oxbow wetland (3.50 ha) (hereafter, Oxbow), which remains hydraulically linked to the West Fork through a 122 cm diameter culvert (West Fork culvert) located at 120.1 m above sea level (Enwright et al. [2011](#page-16-0)). In 2001, expansion of the landfill and regulation of hydrology within the Oxbow required compensatory measures to account for habitat modification. As a result, \sim 32 ha of flood plain and surrounding bottomland hardwood forest were deed restricted in order to maintain the health of the Oxbow and surrounding watersheds. Four compensatory wetland sites were constructed (Fig. [1\)](#page-3-0): the Far western (0.65 ha), Near western (1.90 ha), Northern (0.32 ha), and Southern (0.20 ha) wetlands. At the time of our sampling, however the Far western site had been reduced to a ~ 0.30 ha parcel. Water sources for these constructed wetlands include: (1) direct precipitation or runoff, (2) inflow from the West Fork at high river stages, and (3) offsite wetland inflow into the Oxbow during intense rainfall events. These offsite wetlands are connected to the Oxbow through a channel along with several culverts and hold water under normal conditions (Enwright et al. [2011\)](#page-16-0). The Near Western and Far Western sites are hydraulically linked to the Oxbow by a culvert at 127.1 m and receive water from the West Fork and offsite wetlands at river stages of 127.4 m. The Northern and Southern sites are topographically linked to the Oxbow channel and waters from the West Fork and offsite wetlands will enter the Southern wetland at river stages >125.3 m through the West Fork culvert; West Fork river input into the Northern site only occurs in extreme river stages >129.0 m (Enwright et al. [2011](#page-16-0)). In summary, during high river stages, West Fork water input first enters the Oxbow wetland; water flows into Southern site and then to the Western sites (i.e., Near and Far Western sites) and will enter the Northern sites during extreme river stages. Based on model-generated plots and field observations, the Oxbow wetland retains water throughout the growing season; the Near western wetland is frequently flooded, and the Southern and Far western wetlands are briefly inundated during the growing season; the Northern wetland experiences few ponded days and receives negligible water input from the West Fork (Enwright et al. [2011](#page-16-0)).

The compensatory wetlands are located on a floodplain that had historically been horse-grazing

Fig. 1 Study site in Grand Prairie, Texas, USA, at the City of Grand Prairie Municipal Landfill along the West Fork of the Trinity River, showing sampling locations of the reference wetland (Oxbow wetland) and four contemporary wetland sites

lands. At the time of this study, some expansion of the Near western wetland was taking place, however study sites chosen for sampling had been in their present state since the construction of culverts in 2001; wetlands had not been recently disturbed and had not been planted or seeded with propagules. The goal of the City of Grand Prairie is to characterize the hydrology (see Enwright et al. [2011\)](#page-16-0), standing vegetation, and seed bank communities in the natural and compensatory wetlands in order to construct, and assess the development of, ecologically functional wetlands proximate to the Oxbow. Given its proximity, hydrological connection, and anticipated influence on the compensatory wetlands, the Oxbow was identified as the most appropriate reference site for this study. Although offsite wetlands are present, their histories were unknown and therefore were not considered suitable reference sites. To date there has not been an in depth examination of standing vegetation or the seed bank of the natural or compensatory sites.

Vegetation sampling

Vegetation sampling occurred in September–October 2008 and July 2009. The growing season in northcentral Texas typically begins in March, therefore field surveys later in the year (i.e., late summer/early autumn) likely encompass all species surviving to maturity within a growing season. To compare plant community composition among sites, a total of 20 transects, each with 3 quadrats $(1 \text{ m}^2 \text{ sampling area})$ were assessed. Three transects were established in the Northern, Southern, and Near western mitigation areas; two transects were established in the Far western site and nine transects established in the Oxbow wetland (Fig. 1). Transects were chosen haphazardly and extended across the long axis of each wetland, and quadrats were placed at both ends and the middle of the transect line. The number of transects assessed per site were chosen to ensure the relative area per site sampled, and sampling effort per unit area, was comparable across sites. Consequently, fewer transects were sampled in the smaller sites compared to the larger sites, however dependent variables were normalized to quadrat area to reduce potential sampling effort effects. For repeated sampling of transects across sampling periods, transect and quadrat coordinates were recorded with a Trimble Geo-XT (Environmental Systems Research Institute, Redlands, CA) and spatially mapped in ArcGIS 9.3 (ESRI).

All plant species were recorded as present or absent in the 1 $m²$ quadrat and identified following *Shinners* and Mahler's Illustrated Flora of North Central Texas (Diggs et al. [1999](#page-16-0)). The wetland indicator status (WIS) for species was obtained through the USDA National Plant Database (Region 6; USDA [2010\)](#page-16-0). The wetland indicator status is a tool for characterizing the plant community and classifies species based on their propensity for inhabiting wetland areas. Obligate wetland species (OBL) occur in wetlands \geq 99 % of the time; facultative wetland species (FACW) occur in wetlands 67–99 % of the time; facultative species (FAC) are equally likely to occur in non-wetlands and wetlands, (i.e., occurring in wetlands 34–66 % of the time); and facultative upland (FACU) and upland species (UPL) occurring in uplands 67–99 % and \geq 99 % of the time, respectively. Categories that may be subdivided by $(+)$ and $(-)$ modifiers, representing wetter and dryer ends of the habitat occurrence scale, respectively. If no information is available, or no agreement has been made by the regional USDA panel, not applicable or N/A is the applied status. Species that have a wetland indicator status of OBL, FACW, FAC+ and FAC are considered to be typically adapted for life in anaerobic soil conditions (i.e., Wetland+ species); species having a FAC-, FACU and UPL wetland indicator status are not considered adapted for life in anaerobic soil (i.e., Wetland-species) (USACE [1987\)](#page-16-0).

Seed bank sampling

Soil cores were taken from the five wetland sites (Oxbow $n = 24$; Northern, Southern, and Near Western $n = 9$ site⁻¹; Far western $n = 6$) (Fig. [1\)](#page-3-0) between 7 March and 10 March 2009 using a $5 \text{ cm} \times 30 \text{ cm}$ Signature split-core soil sampler with an auger tip (AMS, American Falls, ID). Soil sampling was performed in early spring to account for the most recent contribution of propagules to the soil seed bank prior to the start of the growing season. Due to a processing error, three cores from the Far western site were excluded from the analysis, therefore a total of 57 soil cores were obtained across all sites. Soil cores were obtained from the center of each quadrat delineated during survey of the standing vegetation. Cores were brought to the University of North Texas, weighed and divided in half lengthwise; each halved soil core (hereafter, half-core) was hydrated in

deionized water for 24 h and hand homogenized to disperse soil clumps. All non-soil debris (e.g., plant fragments, rocks) was removed.

To test for effects of hydrology on seedling germination, two levels of water availability were established: a non-saturated soil condition (i.e., Drained) and a saturated soil condition (i.e., Wet). Each half-core was randomly assigned to a hydrology treatment. The experiment was performed using 57 plastic seedling trays (52 cm \times 26 cm \times 6 cm) filled with Premier Pro-mix Mycorise Pro soil mixture (Premier Tech Horticulture, Quakertown, PA) each divided into two equal halves allowing each tray to house two soil half-cores from two separate locations; 3 additional trays treatment^{-1} were filled with potting soil alone and served as controls ($n = 60$ total trays t reatment⁻¹). Soil cores were evenly distributed across the surface of the soil; control trays filled with soil alone were monitored to ensure no contamination or spread of propagules during the study. Water treatments (Drained vs. Wet) were maintained using a drip irrigation assembly (DIG Corps, Vista, CA) that provided four daily waterings of ~ 10 mL reverse osmosis water to each treatment tray ($\sim 40-45$ mL H_2O tray⁻¹ day⁻¹). In the Drained treatment, this level of water availability is equivalent to the average precipitation (~ 1.40 L month⁻¹) for north-central Texas in the early months of the growing season (Feb– May), although precipitation can vary from 0.10 to 2.50 L month⁻¹ in dry versus wet years (NOAA [2013\)](#page-16-0). To regulate soil hydrology, a ~ 1 cm diameter drainage hole was placed 1 cm above the bottom of the Drained treatment trays. The water level was maintained at the soil surface in the Wet treatment trays. Trays were maintained under greenhouse conditions (16:8 light:dark cycle, \sim 24–30 °C) for 6 months, a period that reflected the growing season in northcentral Texas and allowed enumeration of species with differing phenologies.

Assessments of seedlings were performed by the seedling emergence assay (van der Valk and Rosburg [1997;](#page-17-0) Smith et al. [2002\)](#page-16-0), beginning the 10th and 21st day following the initiation of the experiment (25 March 2009) and every 3 weeks thereafter until the end (5 October 2009). The total number of plants per tray was recorded at each assessment and seedlings identified to the lowest possible taxon. When identification was not possible based on morphology, seedlings were potted and maintained under

greenhouse conditions until developed sufficiently for identification. To minimize crowding, seedlings were removed from trays once they had been identified. Species were identified using Shinners and Mahler's Illustrated Flora of North Central Texas (Diggs et al. [1999\)](#page-16-0) and their wetland indicator status obtained from the USDA plant database (USDA [2010\)](#page-16-0).

Statistical analysis

To assess community composition of standing vegetation among wetlands and sampling periods (e.g., 2008 and 2009), total species richness m^{-2} , Wetland+ species richness m^{-2} , and the proportion of Wetland + species were analyzed using a two-way ANOVA with location and year as main effects. The proportion of wetland species was calculated as the number of Wetland+ species relative to total species with known WIS; species with no known WIS status (i.e., N/A) were excluded. To measure community similarity between wetland sites, Sørensen's quotient of similarity (SQ) (Sørensen [1948](#page-16-0)) was calculated for all pairs of sites pooled across years.

The greenhouse soil seed bank experiment was analyzed using a two-way ANOVA to test for effects of water availability and location on species richness, diversity (Shannon-Weiner diversity index), and seedling density (seedlings m^{-2}) using treatment half-cores. Seedling density was calculated as the total number of germinated seeds in each treatment half-core through the duration of the study standardized to the surface area of the top of the soil core and expressed as seedlings m^{-2} . We assessed total seedling density, density by WIS, and seedling density of families present in \geq 5 treatment half-cores. To facilitate qualitative comparisons between the soil seed bank study and the field assessment of plant community, SQ was used to measure community similarity among wetland seed banks, and the total species richness, Wetland+ species richness, and the proportion of Wetland+ species were analyzed in a one-way ANOVA using species data pooled across reciprocal half-cores.

Shapiro–Wilk's test for normality and visual inspection of graphs of the residuals were used to validate assumptions of normality and homoscedasticity for ANOVA. Due to high variance, analysis of seedling density was conducted using ranked data. Post hoc multiple comparisons were performed by examining differences of least squares means. All data analyses were performed using SAS 9.1 (SAS Institute, Cary, NC).

Results

Assessment of standing vegetation

Thirty-seven species representing 19 taxonomic families were found in field sites during vegetation sampling in 2008, and 47 species (including eight unknown dicots) from 19 families were found in vegetation sampling in 2009 (Table [1\)](#page-6-0). Of the 66 total species, 19 and 29 species were found exclusively in 2008 and 2009, respectively; 18 species were observed to occur in both years. Unidentifiable species were identified to nearest taxa, however in these cases a WIS was unassigned. Species richness m^{-2} was affected by location ($F_{4,107} = 4.05$, $P = 0.004$), year $(F_{1,107} = 4.53, P = 0.036)$ and their interaction $(F_{4,107} = 3.49, P = 0.010)$. In 2008, species richness m^{-2} ranged from (mean \pm SE) 4.18 \pm 0.32 to 2.56 ± 0.38 in the Oxbow and Northern wetlands, respectively and was significantly greater in the Oxbow compared to the Northern and Near Western sites (Fig. [2a](#page-9-0)). A different trend was found in 2009 with richness m^{-2} being greatest in the Northern site and lowest in the Near western site $(3.78 \pm 0.72 \text{ vs.})$ 0.44 ± 0.24 0.44 ± 0.24 0.44 ± 0.24 species m⁻² (Fig. 2a). Richness m⁻² was significantly lower in the Near Western site compared to all other sites, while richness m^{-2} in the Northern site was significantly greater than the Oxbow. Relative to 2008, species richness m^{-2} in 2009 was significantly lower in the Oxbow and the Near western sites (Fig. [2](#page-9-0)a).

Wetland+ species richness m^{-2} was affected by location ($F_{4,107} = 16.96$, $P \lt 0.001$), year ($F_{1,107} =$ 14.77, $P < 0.001$) and their interaction ($F_{4,107} =$ 2.72, $P = 0.034$. In 2008 and 2009, Wetland+ richness m⁻² was greatest in the Oxbow (3.37 \pm 0.29 and 1.93 \pm 0.27 species m⁻²) and lowest in the Northern site (1.33 \pm 0.29 and 0.44 \pm 0.24 species m^{-2}). Whereas in 2008 Wetland+ richness m^{-2} was significantly greater in the Oxbow and Southern sites compared to the Northern, Near western and Far Western sites, in 2009 Wetland+ richness m^{-2} in

Table 1 Total species list from vegetation sampling and seed bank assessment for years 2008 and 2009

Dark circles indicate presence of a species in a respective survey

WIS wetland indicator status, OBL obligate wetland species, occurs in wetlands \geq 99 %, FACW facultative wetland, occurs in wetlands 67–99 %, FAC facultative wetland species, occur in wetlands 34–66 %, FACU facultative upland species, occurs in nonwetlands 67–99 %, UPL obligate upland species, occurs in non-wetlands \geq 99 %, N/A no agreement or no information, + more frequently found in wetlands, - less frequently found in wetlands (Diggs et al. [1999](#page-16-0); USDA 2010)

2009 was significantly greater in the Oxbow compared to all other sites (Fig. [2](#page-9-0)b). Relative to 2008, Wetland+ richness m^{-2} was significantly lower in the Oxbow and the Southern site in 2009.

The relative proportion of Wetland+ species differed among locations ($F_{4,90} = 37.83, P < 0.001$) but was not significantly affected by year ($F_{4,90} = 2.08$, $P = 0.388$) or the location x year interaction

Fig. 2 Vegetation species richness m^{-2} (upper panel) and Wetland + species richness m^{-2} (lower panel) for wetland sites in 2008 (black bars) and 2009 (gray bars). Lowercase letters (2008) and uppercase letters (2009) represent significant differences ($P < 0.05$) determined from post hoc multiple comparisons within a sampling year; asterisks indicate significant differences among sampling years within a wetland site; Oxbow $n = 27$; Northern, Southern, and Near western $n = 9$; Far western $n = 3-6$; values are mean \pm SE

 $(F_{4,90} = 2.08, P = 0.090)$. Pooled across years, the proportion of Wetland $+$ species was not statistically different between the Oxbow (96 \pm 2 %) and Near western site $(80 \pm 10 \%)$; the Southern site $(87 \pm 7 \%)$ was not different from the Near western site but was significantly different from the Oxbow. The Far Western site $(62 \pm 13 \%)$ and the Northern site (20 \pm 6 %) were each different from all other sites. SQ for the combined 2008 and 2009 sampling period suggests that the standing vegetation of the plant community in the Near western and Southern

Table 2 Sorensen's quotient of similarity of plant communities between wetland sites

Wetland site	Wetland site						
	Oxbow	Northern	Southern	Near western	Far western		
Oxbow	1.00	0.18	0.29	0.32	0.08		
Northern		1.00	0.35	0.14	0.33		
Southern			1.00	0.29	0.33		
Near western				1.00	0.17		
Far western					1.00		

wetland sites is most similar to the Oxbow community, however, there is less than 50 % congruency (SQ of 0.32 and 0.29, respectively) (Table 2). The Oxbow shared limited plant community similarities with the Northern (0.18) and Far western mitigation site (0.08) (Table 2). The Northern site's plant community composition was most similar to the Far Western and Southern wetland sites but this also showed $a \lt 50 \%$ congruency (SQ of 0.35 and 0.29, respectively).

Seed bank assessment

Over the course of the seed bank study 3,269 seedlings representing 70 species and 23 taxonomic families germinated from soil core samples (Table [1](#page-6-0)). Control trays filled with soil alone were monitored for 6 months and found to be absent of propagules. Of the 70 species occurring in soil cores, only 24 species (34 %) were also found to occur in the combined 2008–2009 vegetation assessment. Comparison of complete cores revealed a significant effect of wetland site on species richness $(F_{4,52} = 13.33)$, $P < 0.001$), Wetland+ species richness ($F_{4,52} =$ 16.72, $P < 0.001$), and the proportion of Wetland+ species ($F_{4,52} = 3.65$, $P = 0.011$) (Fig. [3a](#page-10-0), b). Total richness core⁻¹ and Wetland+ species richness core⁻¹ displayed the same overall trend: richness was greatest in the Oxbow, lowest in the Northern site and did not differ significantly among the Southern, Near western and Far western sites (Fig. [3](#page-10-0)a). However, the proportion of Wetland+ species was high across all sites (71–98 %) although greatest in the Oxbow and lowest

Fig. 3 a Total species richness, Wetland+ species richness, and **b** the proportion of Wetland + species in complete soil cores. The proportion of Wetland+ species does not include species with unknown wetland status. *Lowercase letters* (total species core^{-1}) and *uppercase letters* (Wetland+ species $core^{-1}$) represent significant differences ($P < 0.05$) determined from post hoc multiple comparisons; Oxbow $n = 24$; Northern, Southern and Near western $n = 9$; Far western $n = 6$; values are mean \pm SE

in the Northern sites (Fig. 3b). SQ suggests the seed bank of the Oxbow site to be most similar to the Southern (0.53) and Near western (0.51) sites and least similar to the Northern mitigation site (0.34) (Table 3). All four constructed wetland sites displayed relatively high similarities with SQ values ranging from 0.51 (Southern and Far western sites) to 0.63 (Northern and Far western sites) (Table 3).

There were no detectable effects of hydrology or the interaction hydrology x location on plant diversity or species richness half-core^{-1}, however, diversity and richness half-core⁻¹ differed significantly among locations $(P < 0.001)$ (Table [4\)](#page-11-0). Diversity was

Table 3 Sorensen's quotient of similarity for the soil seed bank community between wetland sites calculated from whole soil cores

Wetland site	Wetland site						
	Oxbow	Northern	Southern	Near western	Far western		
Oxbow	1.00	0.34	0.53	0.51	0.38		
Northern		1.00	0.57	0.59	0.63		
Southern			1.00	0.59	0.51		
Near western				1.00	0.52		
Far western					1.00		

significantly higher in the Oxbow, Southern and Far western site compared to the Northern site and Near Western site (Fig. [4](#page-12-0)). Richness half-core⁻¹ displayed a similar trend and tended to be greatest in the Oxbow and lowest in the Northern site. Total seedlings m^{-2} $(P<0.001)$ and WIS seedlings m⁻² differed among locations ($P < 0.024$ $P < 0.024$) (Table 4, Table [5](#page-13-0)). The Oxbow had the greatest seedlings m^{-2} (49,404 seedlings m^{-2}) while the Northern site had the least seedlings m^{-2} $(2,354$ seedlings m⁻²). The greatest seedling density for OBL and FACW species occurred in samples from the Oxbow, however, FACW density in the Oxbow was not significantly different from the Southern Near western or Far western sites. The Near western site had the greatest seedling density in the FAC, FACU and UPL categories (Table [5](#page-13-0)), and more seedlings established in the dry treatment compared to the wet treatment for the FAC class $(P = 0.020)$. Neither hydrology nor the interaction of location x hydrology had a detectable effect on seedling establishment for OBL, FACW, FACU, or UPL classes.

Due to few occurrences in the seed bank, the effects of location and hydrology on seedling density were not assessed for the following families: Apiaceae, Juncaceae, Molluginaceae, Onagraceae, Portulacaceae, Primulaceae, Salicaceae, Ulmaceae, Verbenaceae. Location alone affected seedling density of the Alismataceae, Asteraceae, Cyperaceae, Euphorbiaceae, Lythraceae, Poaceae, Scrophulariaceae, and Solanaceae. Location and hydrology but not the interaction of the two affected the seedling density of the Amaranthaceae and Brassicaeae, (Table [4](#page-11-0)). Compared to all other sites, the Oxbow had greatest density of Alismataceae, Cyperaceae and Lythraceae

exceeding the density in all other sites by at least one order of magnitude (Table [5\)](#page-13-0). The Oxbow also had the greatest seedling density in the Brassicaceae compared to all sites except for the Far western, and the greatest density of Asteracea compared to all other sites except the Southern site (Table [5\)](#page-13-0). The Near western site had the greatest density of Euphorbiaceae and Amaranthaceae seedlings compared to all other sites; Euphorbiaceae density was equally low in all other sites and the fewest Amaranthaceae were found in the Northern and Far western sites (Table [5](#page-13-0)). The Southern and Far western sites had a greater density of Scrophulariaceae seedlings compared to all other sites. Although found in relatively low densities or absent throughout the study area, the density of Solanaceae seedlings was significantly greater in the Near western compared to the Oxbow and Northern sites (Table [5](#page-13-0)). Seedling density of the Amaranthaceae and Brassicaceae was significantly affected by hydrology as well as location (Table 4), being greatest in the Drained compared to the Wet treatments (Table [5\)](#page-13-0). Seedling density in the Fabaceae, Polygonaceae, Ranunculaceae, and Typhaceae were not affected by location, water availability or the interaction of the two (Table 4).

Discussion

In assessing wetland community structure and the potential for successful restoration or mitigation, the inclusion of seed bank community assessments and the role of hydrology in affecting germination and seedling establishment, can offer greater insight into wetland community structure than vegetation surveys alone (van der Valk and Davis [1978\)](#page-16-0). However, quantifying success of wetland creation/restoration is difficult due to dynamics in the community structure

Fig. 4 Shannon-Weiner diversity averaged across reciprocal Wet and Drained treatment half-cores. Lowercase letters represent differences ($P < 0.05$) determined from post hoc multiple comparisons; Oxbow $n = 48$; Northern, Southern and Near western $n = 18$; Far western $n = 12$; values are $mean + SE$

of standing vegetation and the soil seed bank (Brown [1998;](#page-16-0) Mitsch et al. [1998;](#page-16-0) Whigham et al. [2002\)](#page-17-0). On one hand, vegetation surveys may underestimate species richness and the potential for desirable plants (i.e., Wetland? species) to contribute towards habitat restoration (Galatowitsch and van der Valk [1996](#page-16-0); Leck and Leck 2005 ; this study) and may be an insufficient method in evaluating the legal (i.e., sanctioned mitigation) or ecological (i.e., ecosystem function) success of wetland creation/restoration, particularly when few surveys are performed. Similarly, characterization of the seed bank community alone may be a poor indicator of standing vegetation composition (Brown [1998](#page-16-0); Ficken and Menges [2013\)](#page-16-0) and may overestimate richness due to rare or exotic species (Greet et al. [2013](#page-16-0)). Nevertheless, vegetation surveys and seed bank studies are useful in assessing patterns of vegetation structure and community dynamics (Thompson and Grime [1979](#page-16-0); Baldwin and DeRico [1999](#page-16-0)) and in modeling pathways for restoration (Leck and Simpson [1987;](#page-16-0) van der Valk and Penderson [1989;](#page-16-0) Smith et al. [2002](#page-16-0)), especially when accounting for effects of hydrology on plant growth and seedling emergence (Smith et al. [2002](#page-16-0); Whigham et al. [2002](#page-17-0); Peterson and Baldwin [2004](#page-16-0); Collins et al. [2013;](#page-16-0) Ficken and Menges [2013](#page-16-0)). Therefore, the combination of vegetation and seed bank studies, accounting for soil hydrology effects (Smith et al. [2002;](#page-16-0) Ficken and Menges [2013;](#page-16-0) Collins et al. [2013\)](#page-16-0) may be a more comprehensive and informative approach to the planning and assessment of wetland mitigation. Additionally, this combined approach is effective at evaluating current and potential species richness and biodiversity in wetlands, as well as, identifying potential impacts of habitat modification (i.e., changes in hydrology) on plant community composition (Baldwin et al. [2001](#page-16-0); Collins et al. [2013;](#page-16-0) Ficken and Menges [2013](#page-16-0)). Finally, in the comparison of natural and constructed wetland communities, this approach may also provide insights into factors leading to similarities or disparities between communities while informing resource managers of viable options to guide future restoration efforts (Galatowitsch [2006\)](#page-16-0).

In the present study, the standing vegetation of both natural and compensatory sites had fewer total species and Wetland+ species relative to the soil seed bank. However, all sites (with the exception of the Northern site) had a relatively high proportion of Wetland+ species in the standing crop across surveys, despite variability in total species richness and Wetland+ species richness across years. Changes in species richness across years are to be expected and may have been affected by annual variation in rainfall and soil hydrology (Whigham et al. [2002\)](#page-17-0), with changes in annual precipitation and ponding across surveys (C. B. Wall, unpublished data) affecting germination and the survival of adult plants. Field surveys need to be tailored to capture heterogeneity in a plant community resulting from annual and seasonal variation in environmental factors, as well as seed germination and dormancy. In the present study, the change in standing vegetation among years emphasizes the importance of multiple surveys to accurately characterize habitat prior to, and during, the construction of a compensatory wetland (Mitsch et al. [1998](#page-16-0); Zedler [2000\)](#page-17-0).

In years of low rainfall and drought conditions, low river stages may limit hydrologic inputs to the compensatory wetlands, as well as, decrease propagule influx of hydrochorous species. Conversely, high river stages, episodic flooding events, and high annual rainfall will likely increase hydrochory from the Oxbow and the West Fork. Low rainfall in 2008 (~ 20 cm below annual mean; NOAA [2013\)](#page-16-0) and high rainfall in 2009 (~ 15 cm above annual mean; NOAA

OBL obligate wetland species, FACW facultative wetland species, FAC facultative wetland species, FACU facultative upland species, UPL obligate upland species, all values

mean \pm SE

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[2013\)](#page-16-0) may have increased seed input to all locations in 2009 relative to 2008. Alternatively, high rainfall in 2009 may have washed away recently deposited seeds prior to burial in the soil seed bank. In drought prone areas, such as north-central Texas, passive means of re-vegetation (e.g., seed bank recruitment, seedling dispersal) may be insufficient in wetland restoration due to the reestablishment of non-wetland species in dry years (De Steven et al. [2006\)](#page-16-0), and the introduction of desirable species may be necessary (Zedler [2000\)](#page-17-0) either by planting, seeding, or soil transplantation (Brown and Bedford [1997\)](#page-16-0). Similarly, Smith et al. [\(2002](#page-16-0)) reported desirable wetland species were absent from soil seed banks in a restored marsh in the Everglades and a lack of external propagule input was inhibiting the establishment of target species. In Grand Prairie, OBL and FACW+ seedlings for example, Cyperus spp. (OBL: Cyperaceae) and Ammania spp. (OBL: Lythraceae) were abundant throughout Oxbow soil cores, and soil transplantation from the Oxbow or other natural wetlands may be a useful mean of propagating desirable wetland species in compensatory wetlands. However, soil transplantation is not without risk, and may contribute to the spread of invasive species present in seed banks but not observed in this study, therefore a preliminary assessment of transplantation effects at this location would be required (see Brown and Bedford [1997\)](#page-16-0).

Seedling densities in natural and compensatory wetland seed banks were comparable to those reported for freshwater wetlands (Leck and Simpson [1987\)](#page-16-0), the Florida Everglades (van der Valk and Rosburg [1997](#page-17-0)), and tidal marshes (Baldwin and DeRico [1999](#page-16-0)). However, seedling density, species richness, and Wetland+ species richness were reduced in seed bank samples from compensatory sites, particularly at the Northern site, relative to the Oxbow wetland. Increased species richness in the seed bank of the Oxbow relative to compensatory wetlands may in part be an effect of greater hydrological input from the West Fork via the West Fork culvert increasing hydrochory and the diversity of soil hydrology (i.e., flooded, saturated, dry conditions). As a result, habitat patchiness from non-uniform soil conditions may favor the establishment of Wetland+ and Wetlandspecies in wet and dry seasons, respectively (Collins et al. [2013](#page-16-0)). Patterns in both the standing vegetation and the soil seed bank suggest sites most proximate to the Oxbow (i.e., Southern, Near western) share the greatest community similarities (Table [2](#page-9-0) and Table [3\)](#page-10-0) and generally have increased Wetland $+$ species. Additionally, the greatest OBL seedlings m^{-2} (Table [5](#page-13-0)), and taxonomic families abundant in the Oxbow seed bank were also abundant in the Southern and Near western sites (Amaranthaceae, Asteracea, Lythraceae, Ranunculaceae), potentially indicating increased connectivity among adjacent wetlands.

The greater similarities in the seed bank community of the Southern and Near western sites to the Oxbow (0.53 and 0.51 similarity, respectively [Table [3\]](#page-10-0)) may in part reflect the hydrologic linkage between these sites. During high river stages, water flow into the Southern site and subsequently into the western mitigation area (i.e., the Near and Far western sites) through a series of culverts. The Southern site receives more hydrologic input from the West Fork, however sandy/silty loam soils in the Southern site contribute to high soil drainage rates $(0.012 \text{ m day}^{-1})$, whereas less hydrologic input from the West Fork at the Near Western is compensated for by clay soils contributing to slow drainage rates $(0.198 \text{ m day}^{-1})$ and increased ponding (see Enwright et al. [2011\)](#page-16-0). Poor community similarity of the standing crop at these sites (Table [2\)](#page-9-0) may be due to high drainage rates at the Southern site not facilitating the germination and colonization of species adapted to hydric soils, and slow drainage at the Near western site contributing to adult mortality and inhibiting seedling germination (i.e., 2009 field sampling [Fig. [2\]](#page-9-0)) (Peterson and Baldwin [2004\)](#page-16-0). At the Northern site, despite similar soil to the Southern site and topographical linkage to the Oxbow, the standing vegetation and seed bank are depauperate in Wetland + species and may not function as a wetland ecosystem due to the presence of non-hydric soils (Enwright et al. [2011\)](#page-16-0) and the absence of a relict wetland seed bank. Considering hydrologic inputs from the West Fork only enter the Northern site during extreme river stages $(>129.0 \text{ m},$ Enwright et al. [2011](#page-16-0)), limited similarities between the Northern site and adjacent wetlands may be expected, and passive means of wetland plant community assembly are likely to be particularly unsuccessful at this location.

As a result of the numerous abiotic and biotic factors, seed bank community structure is often dissimilar to that of standing vegetation (Baldwin and DeRico [1999;](#page-16-0) Smith et al. [2002;](#page-16-0) Greet et al. [2013](#page-16-0)). The seed bank may be more diverse or species rich relative to the standing vegetation, however the density of desirable species in the soil seed bank may be too low to restore or create a wetland habitat. In Grand Prairie, an increase in soil saturation did not alter the emergence of seedlings from the soil seed bank. The soil seed bank was, however, more species rich and had a higher Wetland+ species richness relative to the standing vegetation, and seed bank community structure was more similar across sites than was the standing vegetation. Considering the presence of Wetland+ propagules in compensatory wetlands (although in lower density relative to the Oxbow), managers in Grand Prairie may benefit from active means of increasing the germination of desirable species from the soil seed bank (Baldwin et al. [2001\)](#page-16-0) and subsequent seed production (Haukos and Smith [1993](#page-16-0)), including early season flooding and subsequent drawdown (Fredrickson and Taylor [1982](#page-16-0)). While flooding can drastically decrease seedling survivorship (Peterson and Baldwin [2004](#page-16-0); Fraser and Karnezis [2005](#page-16-0)), inhibit germination (Smith et al. [2002\)](#page-16-0), and decrease species richness and seed bank recruitment (Baldwin and DeRico [1999](#page-16-0)), drawdown conditions can increase seedling emergence (Smith and Kadlec [1983](#page-16-0); Baldwin et al. [2001](#page-16-0); Collins et al. [2013\)](#page-16-0) and promote the germination, establishment, and seed production of desirable plant species (Fredrickson and Taylor [1982](#page-16-0); Haukos and Smith [1993](#page-16-0)). For example, early season flooding and drawdown in east-central Texas wetlands increased seed germination and the presence of desirable wetland plant species (Collins et al. [2013\)](#page-16-0) and may provide favorable conditions for wetland plants to exploit, thereby contributing to shifts in plant community composition (Smith and Kadlec [1983\)](#page-16-0). In the soil seed bank of disturbed and undisturbed seasonal wetlands of Florida, drawdown and flooding hydrology conditions increased seed germination relative to dry soil conditions, and increased soil saturation reduced differences in seedling abundance between disturbed and undisturbed wetlands (Ficken and Menges [2013](#page-16-0)). However, in the present study, seed germination did not differ between drained and saturated soils for the majority of species assessed. Therefore, early season flooding and drawdown may only be effective in increasing the germination of Wetland+ species–and ultimately the abundance of Wetland+ species in the standing crop—when applied along with other active means of community assembly (e.g., seeding, soil transplantation, non-desirable plant removal).

Conclusions

In the present study, the current wetland design relies upon community self-assembly, as opposed to formal planting or seeding. We report marked differences between the composition of standing vegetation and seed bank within each wetland site, and among compensatory wetlands relative to the reference Oxbow wetland. Contrasting water availability treatments revealed that a drained or un-drained hydrologic regime would not increase species richness, diversity, or assist in the establishment of Wetland+ plants in the compensatory wetlands. In the short-term, an approach solely reliant on the self assembly of a wetland community by increasing soil hydrology (i.e., ECH) is unlikely to be successful in producing compensatory wetlands similar to neighboring natural wetlands. However, hydrology treatments used here (i.e., soil saturation) were not equivalent to submerged conditions and were not designed to simulate in situ patterns of hydrology where seasonal patterns of flooding and drawdown may depress or favor the establishment of seedlings (Baldwin et al. [2001;](#page-16-0) Collins et al. [2013\)](#page-16-0). Therefore, it is critical to consider the implications of hydrology in the design and monitoring of wetland restoration projects and to determine a proper hydrological regime to maximize recruitment and seed production for desirable wetland species (Collins et al. [2013](#page-16-0); Ficken and Menges [2013](#page-16-0)). In the context of wetland restoration in the north-central Texas, this study demonstrates that sampling of the standing crop, along with the soil seed bank and water-availability experiments, are useful in determining successful approaches to wetland mitigation, and may be of particular importance in selecting the method of mitigation (e.g., planting, seeding, hydrological modification).

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