

Land use and wetland drainage affect water levels and dynamics of remaining wetlands

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Abstract. Depressional wetlands are productive and unique ecosystems found around the world. Their value is due, in part, to their dynamic nature, in which water levels fluctuate in response to climate, occasionally drying out. However, many wetlands have been altered by consolidation drainage, where multiple, smaller wetlands are drained into fewer, larger, wetlands causing higher water levels. We evaluated whether current (2003–2010) water surface areas were greater than historical (1937–1969) water surface areas of 141 randomly selected semipermanent and permanent wetlands across the Prairie Pothole Region of North Dakota, USA. We also evaluated whether differences between historical and current hydrology of these wetlands were attributable to consolidation drainage. For each of these wetlands, we digitized water surface areas from aerial photography during historical and current eras. Our results indicated that water surface areas are currently 86% greater in sample wetlands than they were historically and that differences can be attributed to consolidation drainage. Water surface areas of consolidated wetlands in extensively drained landscapes were 197% greater than those with no drainage and now require more extreme drought conditions to dry out. Wetlands in extensively drained catchments were larger, dry out less frequently, and have more surface-water connections to other wetlands via ditches. These factors make conditions more favorable for the presence of fish that decrease abundances of aquatic invertebrates and reduce the productivity and quality of these wetlands for many species. Our results support the idea that intact wetlands serve an important role in water storage and groundwater recharge and reduce down-stream runoff.

Key words: consolidation drainage; isolated wetlands; migratory waterfowl; North Dakota; Prairie Pothole Region; wetland water levels.

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INTRODUCTION

Depressional wetlands are productive ecosystems found around the world and are unique when compared to more permanent freshwater systems. The biological uniqueness of these

ecosystems is due, in part, to their typically weak surface water connections to more-permanent waters (Whigham and Jordan 2003, Winter and LaBaugh 2003) and their dynamic nature, in which surface water levels fluctuate in response to wet and dry periods in a given region (Euliss

et al. 1999, Johnson et al. 2004). Dry climate periods can dry out wetland benthic zones, exposing sediment that facilitates nutrient cycling through oxidation, and leads to a subsequent pulse of productivity when wet conditions return (Murkin 1989, Euliss et al. 1999). Additionally, depressional wetlands that dry out and have fewer surface-water connections often lack fish, leading to higher abundances of invertebrates and more productive habitat for amphibians and breeding waterfowl (Semlitsch and Bodie 1998, van der Valk and Pederson 2003, Zedler 2003). The water levels of depressional wetlands may vary intra-annually, with smaller wetlands filling up in the spring and drying out by mid-summer (Brooks 2004, Machtinger 2007) or inter-annually, with larger wetlands responding to multi-year wet-dry periods (Euliss et al. 2004, Johnson et al. 2004).

In agricultural regions around the world, wetlands are often drained to make way for increased or more efficient agricultural production. This drainage is sometimes focused on smaller, seasonally and temporarily flooded wetlands that result in the consolidation of surface water into fewer, more-permanent basins that likely become larger and deeper with more drainage. Interestingly, this consolidation drainage has received little attention in the literature. Consolidation drainage can increase connectivity among remaining wetlands through drainage ditches that can increase water levels in consolidated wetlands (Merkey 2006). Higher water levels in consolidated wetlands could mean that those wetlands will need a much more extreme drought to dry out completely, simply because they are larger and deeper. This process changes the wetland from one with fluctuating hydrology to one that is essentially permanently flooded, fundamentally changing the community composition of the wetland and its function in the landscape (van der Valk et al. 1994, Wellborn et al. 1996, Snodgrass et al. 2001).

In this paper, we examine the hydrologic and ecological implications of consolidation drainage on remaining wetlands located in the Prairie Pothole Region (PPR) of North America, a region where surface-water levels of wetlands respond to wet and dry climate periods (Kantrud et al. 1989, van der Valk 2005). Wetlands in the PPR are ecologically and economically important on a

continental scale because they are major waterfowl breeding habitat for 50–80% of North American duck production (Batt et al. 1989, Skagen et al. 1999, Brown et al. 2001). Additionally, these wetlands maintain regional biodiversity, provide flood storage, and recharge groundwater (Hubbard et al. 1988, Gleason et al. 2008, 2011). However, within the past two centuries a large number of wetlands within the PPR have been drained for agriculture (Dahl 1990, Bethke and Nudds 1995, Krapu et al. 1997) and much of this drainage was consolidation drainage.

We evaluated the expectation that, before extensive consolidation drainage occurred, water surface areas in many PPR wetlands were smaller than they are currently, frequently going dry or nearly dry, but consolidation drainage has led to wetlands with greater water surface areas that rarely dry out. Specifically, our objectives were to (1) evaluate whether current water surface areas in semipermanent and permanent wetlands are greater than historical water surface areas and (2) evaluate whether differences between historical and current water surface areas in semipermanent and permanent wetlands are attributable to changes in land use or consolidation drainage.

MATERIAL AND METHODS

Study area and sample wetland selection

Our study focused on wetlands in the PPR of North Dakota, USA (Fig. 1) because drainage and land use changes occurred recently enough in this area to have been captured in the aerial photographic record. Semipermanent and permanent wetlands were selected because they were more likely to receive drainage water if consolidation drainage has occurred. These wetlands were classified as semipermanent and permanent according to the National Wetlands Inventory classification system (Cowardin et al. 1979) but may still dry down substantially during significant droughts. We selected wetlands by allocating sampling clusters of randomly selected wetlands within randomly selected townships following procedures in Anteau and Afton (2008b) and Appendix A. In total, our sample included 141 wetlands (Fig. 1) that ranged in size from 0.5 to 705 ha (National

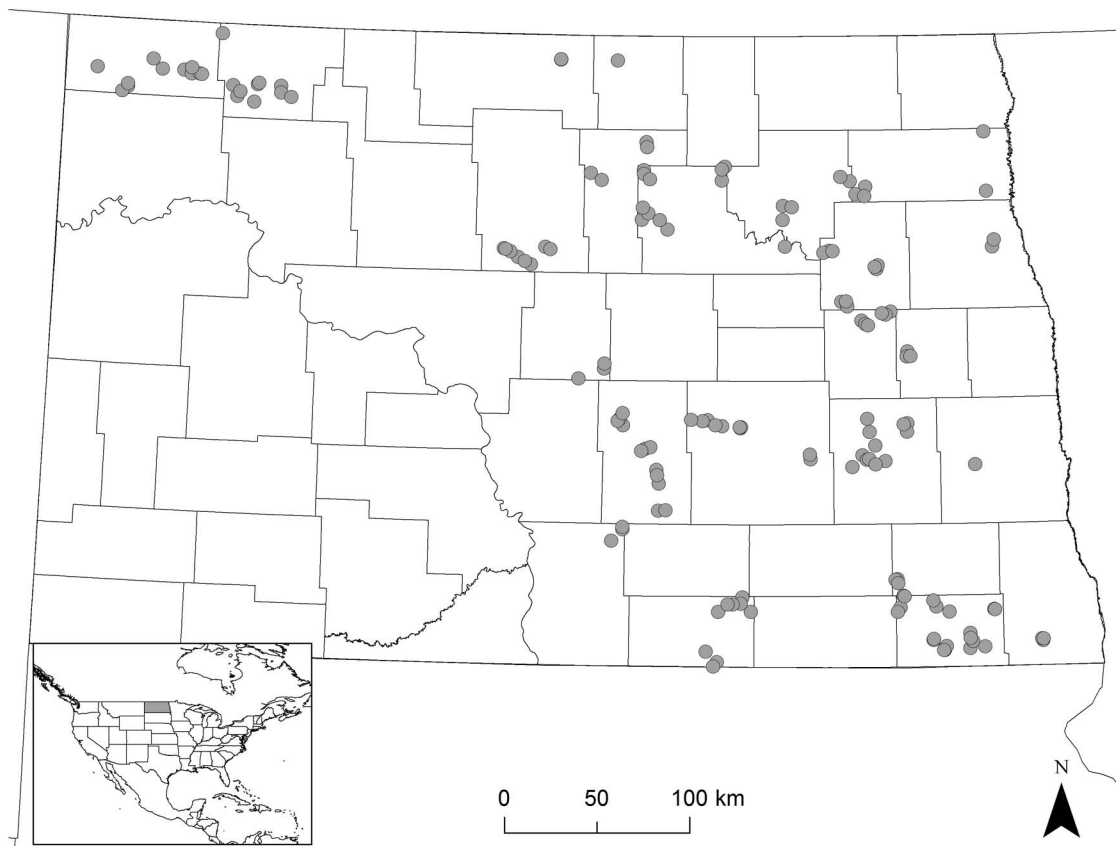


Fig. 1. Sample wetland locations within the Prairie Pothole Region of North Dakota.

Wetlands Inventory, NWI, U.S. Fish and Wildlife Service 2003).

Wetland catchment delineation

For this study, we defined a wetland catchment as the portion of the landscape in which surface water flows into a subject wetland; the catchment often includes other wetlands if it were likely they would fill and spill into the subject wetland (McCauley and Anteau 2014). Thus, our definition of a wetland catchment is a watershed-derived wetland complex that may include other wetlands and their catchments. Wetland size is a function of the catchment area (McCauley and Anteau 2014), and conversely the area that influences a wetland is different for wetlands of different sizes and also varies with topography. We delineated catchments for each of our 141 sample wetlands to allow us to identify land-use changes in the portion of the landscape that directly affected each wetland. We delineated

boundaries of wetland catchments using ArchHydro (ArcGIS v.10; ESRI 2010) and two types of digital elevation models (DEMs) with varying resolutions (see Appendix A). We followed catchment generation methods in McCauley and Anteau (2014) and Appendix A to generate catchments. We will hereafter refer to sample wetlands as the terminal wetland because it is the wetland at the bottom of its catchment to where all surface water in the catchment flows. However, if a terminal wetland has enough water to reach its spill point, it can spill surface water into adjacent catchments. The term terminal wetland also distinguishes them from smaller, temporary or seasonal wetlands in the upper portion of the catchments that are often drained.

Some catchments were prohibitively large to digitize subsequent data (see Drained wetlands index, Pre-drainage wetlands index, Crops, and Roads sections below) within the entire catchment. We truncated each catchment at 2.5 km

from the edge of the wetland and subsequent data was digitized only in the truncated catchments and extrapolated to the entire catchment. The 2.5-km truncation encompassed >90% of the catchment area for 75% of catchments. We assumed that the land uses within the catchment were uniform and that the area that was nearest the wetland was the most influential on the wetland.

Estimating water surface area

We collected more than 2,500 historical aerial photographs from USGS Earth Explorer, US Fish and Wildlife Service (USFWS) offices, and Natural Resource Conservation Service (NRCS)/Farm Service Agency (FSA) county offices. We collected all available aerial imagery of each terminal wetland that was photographed prior to 1970 (see Appendix B). We defined the historical era as the years (1937–1969) prior to 1970 because we expected that most of the drainage occurred after that time period but our drainage estimates (see *Drained wetlands index* below) were year-specific and thus, accounted for the small percentage of drainage that occurred prior to 1970. We georeferenced all photos in ArcGIS 10.0 (ESRI 2010) to datum NAD 1983, UTM Zones 13 and 14. The number of years that photos were available for the terminal wetlands ranged from 7 to 14 years with a total of 500 observations in the historic era (Appendix B: Table B1).

We defined the current era as the years that ranged from 2003 through 2010 because we expected that most of the drainage occurred prior to 2003 and aerial photographs were available. We obtained current photographs from the National Agriculture Imagery Program (NAIP) for the available years of 2003–2006 and 2009–2010, with 987 observations in the current era (Appendix B: Table B2). These images were true-color, but we viewed them as panchromatic (grayscale) when digitizing subsequent data to facilitate fair comparisons with historical aerial photographs.

We digitized the water surface areas in ArcGIS v.10.0 (ESRI 2010) of each terminal wetland and from all available photographs. All digitization was done at the scale of 1:2,500. Water surface area was directly digitized from the photographs when the water boundary was readily visible or could easily be estimated on the photograph.

When the water boundary was hidden by emergent vegetation, we calculated the water surface area as: area of visible water + (area of emergent vegetation/2). This method interpolated the water surface boundary as the halfway point between the visible water boundary and the outer edge of the emergent vegetation. In some terminal wetlands, especially in more contemporary images, water surface areas greatly increased and became connected on the surface to other wetlands and crossed roads. Because there was a lack of certainty about the wetland boundary when it crossed a road and NWI considers wetlands on each side of a road as discrete, we digitized the boundary of the wetland at the road. This created conservative estimates of wetland size. In cases where multiple smaller wetlands in historical photos became one large wetland in current photos, the areas of the smaller wetlands from the historical photos were summed together.

We expected 2007 and 2008 to be among the driest in the current era, but aerial photographs were not available for those years. However, high resolution elevation data for the area was collected in 2007 and 2008, and since that data derived from LiDAR does not penetrate water and records water levels as ground levels, we interpreted the water surface areas from the high-resolution elevation data products for those years.

Developing drought indices

We created a fine-scale drought index to estimate the effect of climate on water surface areas in the historical era. We used monthly precipitation values from the Parameter-elevation Regressions on Independent Slopes Model (PRISM Climate Group, Oregon State University 2014) and calculated Standardized Precipitation-Evapotranspiration Index (SPEI) values in R (R Development Core Team 2011) using SPEI package (Vicente-Serrano et al. 2010, Beguería and Vicente-Serrano 2012). SPEI is a drought index that relies on climate data and can be applied at different spatial and temporal scales. This index does not suffer from the same limitations of the Palmer Drought Severity Index (PDSI, e.g., fixed time interval and sensitivity to location of initial calibration), but like PDSI it does account for evaporative demand caused by

temperature. Like the Standardized Precipitation Index (SPI), SPEI can also be computed across various climates and time scales (Vicente-Serrano et al. 2010). Because of this flexibility, SPEI has also been shown to perform better than SPI or PDSI when comparing impacts of drought over multiple spatial scales (Vicente-Serrano et al. 2012). We tested multiple time scales from 1 year to 50 years and the SPEI time-scale that best explained water surface areas in the historical era was a weighted average of the previous 10 years (from the photo date) of monthly precipitation data at that wetland (M. Post van der Burg, M. J. Anteau, L. A. McCauley, and M. T. Wiltermuth, *unpublished manuscript*). Drought index values on the 10-year time scale were calculated for all terminal wetlands in all years and ranged from -2.2 to 2.6 (historic years range = -2.2–2.6; current years range = -1.5–1.8), with negative values indicating drier conditions and positive values indicating wetter conditions.

Drained wetlands index

To index drainage, we digitized all wetlands within the catchment of each terminal wetland where drainage was visible. To determine whether a wetland was partially or completely drained, we identified ditches from high-resolution elevation models, ArcHydro-generated water-flow accumulation lines, and aerial photographs. We digitized all wetlands that were visible on historical photographs taken during wet years, visible on current aerial photographs and/or in NWI data, or were a depression with hydric soils indicative of a wetland (McCauley and Jenkins 2005). We classified wetlands as drained if ditches were present and flow-accumulation lines showed water being drained out of the wetland. Thus, drained wetlands could include both wetlands that no longer exist because of drainage or wetlands that still exist, but a ditch was present that had potential to drain all or part of it. We digitized all drained wetlands within each catchment (or truncated catchment) and calculated the proportion of catchment area that was drained wetland for each available year (hereafter drained wetlands index).

Pre-drainage wetlands index

To index the total area of wetlands that was present before drainage, we combined all current

wetlands (NWI) within the catchment of each terminal wetland with the drained wetlands in each catchment. We selected all wetlands from NWI that did not include our terminal wetlands or our previously identified drained wetlands and combined them with our drained wetlands to quantify the total amount of pre-drainage wetlands in the catchment. We calculated the proportion of catchment area that we defined as a pre-drainage wetland (hereafter pre-drainage wetlands index).

Crops

Land use has changed markedly in North Dakota from the historical to the current era, and land use changes have accelerated with the recent (ca. 2007) increases in agricultural commodity prices (Gleason et al. 2008, 2011). We expected that crops or soil tillage would affect wetland hydrology (Euliss and Mushet 1996, van der Kamp et al. 2003, Voldseth et al. 2007). Accordingly, we estimated agricultural land use during the historical era (1937–1969; using the earliest year in which ~1-m cell size photos for the entire catchment were available) and multiple times during the current era (2003/2004, 2009, and 2010).

For each catchment, we calculated the proportion of upland that was cropped (any row crop or small grain; hereafter crops) using aerial photographs. Specifically, we classified each quarter-quarter section (~16 ha) in the catchment as cropped if $\geq 50\%$ of the upland portion of the quarter-quarter was cropped, or non-cropped if $< 50\%$ of the upland area was cropped (mostly grasses including native prairie, hay, alfalfa, CRP, and rangeland).

Roads

We suspected that the amount of roads within a catchment could affect wetland hydrological responses because they can form barriers to flow or can facilitate flow in ditches. Assuming that road length in each catchment was unchanged within eras, we digitized roads once from aerial photographs in the current era (2010 photos) and once from photographs in the historical era (oldest available photo for each catchment). For each era, we summed road lengths (m) within each catchment and divided that by the area of the catchment (ha).

Table 1. Results of variable selection based on AIC mixed-effects regressions examining if water surface area dynamics differed from historical to current times.

Predictor variable	Coefficient	SE	t	ΔAIC_c
Random effects				
Wetland (Intercept)	0.8700	0.9327		1724.0
Season (Intercept)	0.0120	0.1095		22.1
Township				-2.0
Fixed effects				
Intercept	-0.1337	0.2870	-0.466	
Era (Historic)	-0.5563	0.0257	-21.614	+389.2
Catchment size	0.5014	0.0452	11.085	+86.3
Era:Drought Index	0.1149	0.0328	3.508	+7.7
Catchment:Drought Index	0.0283	0.0040	7.162	+10.9
Drought Index	0.0004	0.0560	0.007	-2.0
Bank slope	-1.9
Bank slope:Drought Index	-1.3

Notes: A colon indicates an interaction term without the main effects. Coefficient, SE, and t-statistic are results from the final model. The predictor variables in the final model appear in boldface. ΔAIC_c is the change in AIC after removal of that variable from the full model (which included all listed predictor variables).

Bank slope grade

We calculated the bank slope grade of each terminal wetland because we expected wetlands with steeper sides would have a smaller change in water surface area with added volume than

wetlands with flatter sides. Using DEMs, we recorded the average elevation of the water surface for all terminal wetlands in 2007/08 (the driest years) and in 2010 (the wettest year). We calculated the average radius of each wetland polygon in 2007/2008 and 2010 using water surface area calculations of each wetland ($\text{radius} = \sqrt{\text{area}/\pi}$). Bank slope grade was calculated as Δdepth from 2010 to 2007/2008 $\div \Delta \text{radius}$ from 2010 to 2007/2008. Mostly, 2010 was a wetter year and water surface areas were greater than in 2007/2008, but in those rare cases (~5%) in which 2010 water surface areas were actually smaller than in 2007/2008, another wetter year was substituted.

Statistical analyses

All analyses were conducted using linear mixed-effects regression models (lme4 package in R v. 2.13.2; Bates et al. 2011, R Development Core Team 2011). First, we evaluated if there were changes in water surface areas of terminal wetlands from historical to current eras. We evaluated a set of a priori selected predictor variables and interactions (full model; see Tables 1 and 2 for list of all variables) using AIC_c to determine if each variable contributed to model fit. Specifically, we started with one a priori full model and iteratively removed and replaced each

Table 2. Results of variable selection based on AIC mixed-effects regressions examining the land use variables that influence water surface areas.

Predictor variable	Coefficient	SE	t	ΔAIC_c
Random effects				
Wetland (Intercept)	0.8130	0.9017		1531.3
Season (Intercept)	0.0223	0.1495		35.6
Township				-2.0
Fixed effects				
Intercept	-0.0595	0.2917	-0.204	
Drained Wetlands Index	0.4051	0.0273	14.843	+199.4
Catchment size	0.5738	0.0470	12.199	+93.4
Historic Wetlands	-1.4517	0.2933	-4.950	+21.8
Crops	-0.5427	0.1289	-4.212	+17.0
Drought Index	0.1311	0.0344	3.813	+16.7
Crops:Drought Index	0.2844	0.0833	3.415	+9.7
Historic Wetlands: Drought Index	-2.0
Roads	-1.9
Bank slope	-1.8
Region	-1.6
Bank slope:Drought Index	+1.4
Coulee	+1.0
Roads:Drought Index	-0.3
Drained Wetlands:Drought Index	+0.1

Notes: A colon indicates an interaction term without the main effects. Coefficient, SE, and t-statistic are results from the final model. The predictor variables in the final model appear in boldface. ΔAIC_c is the change in AIC after removal of that variable from the full model (which included all listed predictor variables).

variable or interaction and compared the AIC_C value of the reduced model to that of the full model. If removal of a variable increased the AIC_C by >2 , it was considered a useful variable and retained for the final model. If removal of a variable changed AIC_C value by ≤ 2 , it was considered uninformative and was excluded from the final model (Burnham and Anderson 2002, Arnold 2010, Lachish et al. 2012). Interactions were removed separately from the main effects in the variable selection procedure to determine if the interaction was informative separate from its main effects. However, if an interaction was found to be informative, we included the main effects of that interaction in the final model. We included wetland and season as random effects. Season was recorded by the month the photo was taken with March–May recorded as spring (5% of historic photos and 9% of current photos), June–August recorded as summer (67% of historic photos and 89% of current photos), and September–November recorded as fall (27% of historic photos and 2% of current photos). Since townships were used to allocate sampling clusters, township was initially included as a random variable but was found to be uninformative ($\Delta AIC \leq 2$) so removed from further analysis. Correlation among continuous variables included in our a priori full model was low (maximum correlation coefficient = 0.11).

Second, we evaluated whether land use or drainage in the catchment of terminal wetlands influenced water surface areas using the same random variables. We used the same variable selection procedure to obtain the most parsimonious group of variables representing our a priori model (Table 2). Water surface area, catchment size, drained wetlands index, pre-drainage wetlands, roads, and crops variables were log transformed because we expected the effects of these variables would be less strong at greater values; before log transformation one was added to any variable that had zero values. Correlation among continuous variables included in our a priori full model was low (maximum correlation coefficient = 0.31). Goodness-of-fit of the final land use model was estimated from marginal ($R^2_{GLMM(m)}$) and conditional ($R^2_{GLMM(c)}$) coefficients of determination (Nakagawa and Schielzeth 2013). The $R^2_{GLMM(m)}$ shows the variance in the fixed effects only, while the $R^2_{GLMM(c)}$ shows

the variance in both the fixed and random effects.

In a separate analysis, we also evaluated the hypothesis that the drained wetlands index in each catchment has increased since historical times ($\alpha = 0.15$; Arnold 2010) using the same random variables.

Model-predicted values and confidence intervals from the final models were calculated by varying the chosen independent variable within its range and holding all other parameters at their medians. To display continuous data interactions as 2-D plots, we classified the variable with values from the minimum, maximum, and mid-point of the distribution. All model predictions were back-transformed for display in graphs and 85% confidence intervals were used (Arnold 2010).

RESULTS

We had a total of 1,487 water surface area measurements on our 141 terminal wetlands during all years of the study (current era = 987; historical era = 500). Historical water surface areas of terminal wetlands ranged from 0 ha (dry) to 693 ha, with an average area of 28 ha ($SD = 74$). Current water surface areas ranged from 0.1 ha to 965 ha, with an average area of 51 ha ($SD = 112$).

Our final model for evaluating whether water surface areas were different in the historical and current eras included: era; catchment size; drought index; era-by-drought index interaction; and a catchment size-by-drought index interaction (Table 1). Drought index was not found to be informative but was included in the final model because it was a main effect of informative interactions. Bank slope grade (and its interaction with drought index) did not improve model fit and was not included in our final model. Based on model-predicted values, in a moderate climate (drought index = 0), water surface areas in the current era were 86% greater than they were historically and the dynamics in response to climate had decreased 41% (% difference in slopes; Fig. 2). In addition, confidence intervals for predicted water surface areas for a given drought index value are larger in the current era than they were for the historical era, despite a 97% greater sample size in current years. Drainage of wetlands has increased since historic

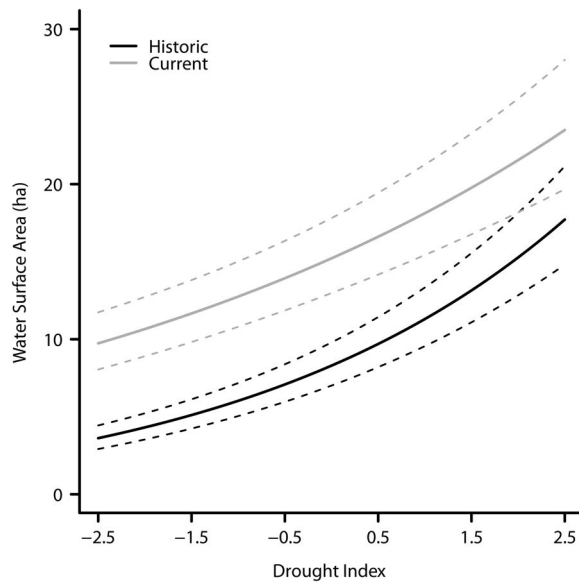


Fig. 2. The influence of climate on predicted water surface areas (ha) of terminal wetlands during historical (black; 1937–1969) and current (gray; 2003–2010) eras. Dashed lines represent 85% confidence limits.

times; the current era had a greater proportion of their catchment area covered by drained wetlands than that of the historical era ($\hat{\beta}_{\text{Intercept}} = 0.88$, $\text{SE} = 0.09$; $\hat{\beta}_{\text{Historical}} = -0.68$, $\text{SE} = 0.02$; Fig. 3).

Our final model, evaluating the effects of land-use on surface water areas included: drought index; drained wetlands index; catchment size; pre-drainage wetlands; crops; and a crops-by-drought index interaction (Table 2; $R^2_{\text{GLMM(m)}} = 0.49$; $R^2_{\text{GLMM(c)}} = 0.9$). The following variables did not improve model fit and were excluded from our final model: region; roads (and its interaction with drought index); pre-drainage wetlands-by-drought index interaction; and bank slope (and its interaction with drought index).

Based on model-predicted values, high-drainage catchments (drained wetlands index = 0.11) have 197% (nearly three times) greater water surface areas than low-drainage catchments in a moderate climate (Fig. 4). Catchments with greater proportions of pre-drainage wetlands have smaller water surface areas (Fig. 5) than those with fewer pre-drainage wetlands. In wetter periods, the proportion of crops within the catchment does not affect water surface areas. However, in moderate and drier periods

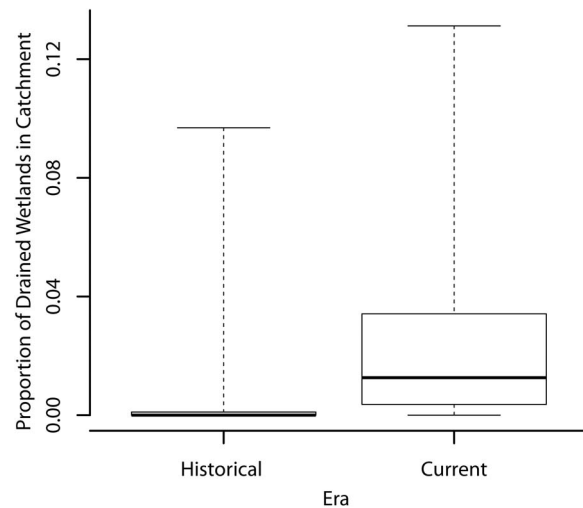


Fig. 3. Box plot showing the proportion of catchment area identified as drained wetlands for each era. Dark line represents the median, the top and bottom of the boxes represent the 75th and 25th quartiles, respectively, and whiskers represent the observed data range.

(drought index ≤ 0), catchments with more crops tend to have smaller water surface areas (Fig. 6).

DISCUSSION

We found that current water surface areas of semipermanent and permanent wetlands in the PPR are greater than they were historically while accounting for potential changes in climate and climate variability. Furthermore, wetland drainage within the catchment was by far the most important factor we considered for explaining changes in observed wetland hydrology. Terminal wetlands in extensively drained catchments are nearly three times larger than those in catchments with no drainage. Because terminal wetlands in drained landscapes are larger, it will take a more extreme drought for them to completely or nearly dry out (Fig. 4). Consolidation drainage appears to have transitioned semipermanently flooded wetlands into permanently flooded wetlands or lakes in the Prairie Pothole Region.

Wiltermuth (2014) found that water surface areas of terminal wetlands in extensively drained catchments increased more during wet periods and decreased less during dry periods than those in less-drained catchments. He suggested that

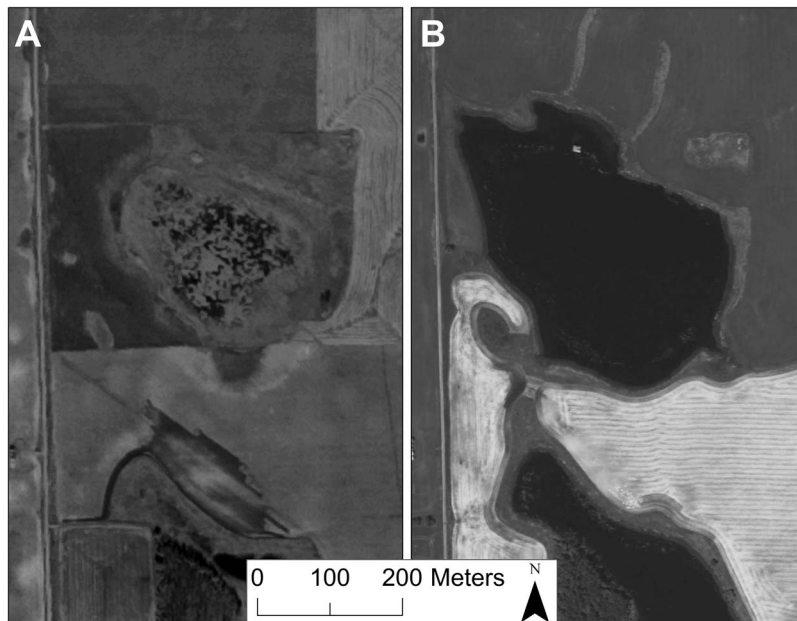


Fig. 4. Aerial photographs of an example wetland pre- and post-drainage in similar climates. (A) Wetland in 1965, before drainage, during a moderate climate with drought index value of 0.17. (B) Wetland in 2005, after 4.3% of its catchment had been drained, during a moderate climate with a drought index value of 0.11.

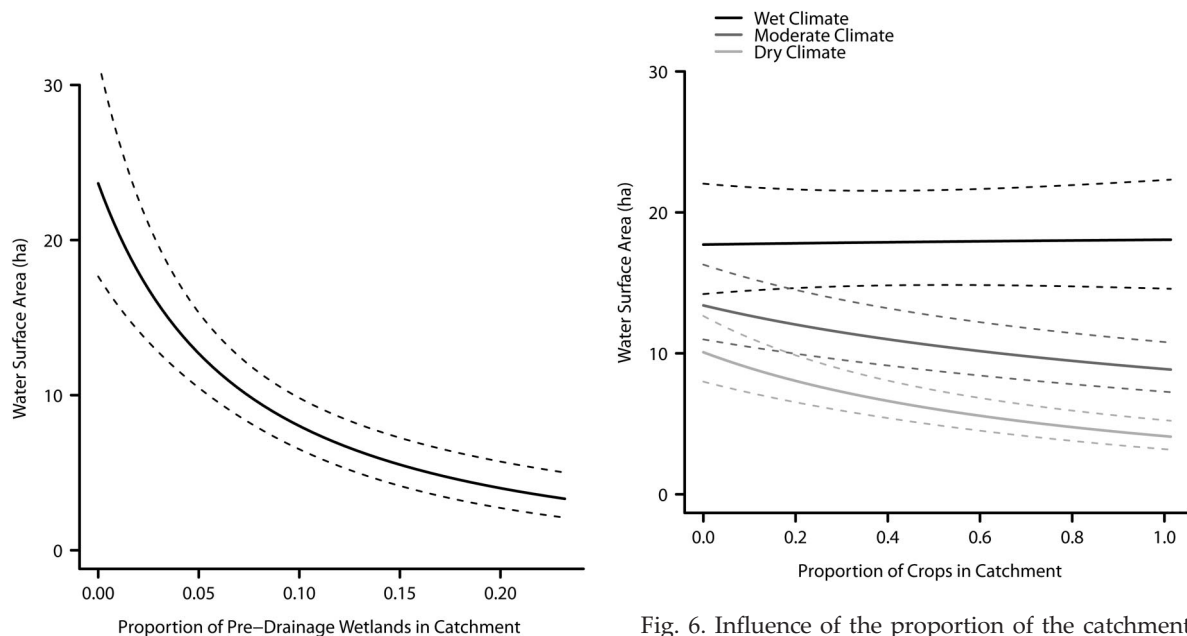


Fig. 5. The influence of the proportion of pre-drainage wetlands on predicted water surface area (ha) of terminal wetlands. Dashed lines represent 85% confidence limits.

Fig. 6. Influence of the proportion of the catchment area that is cropped on predicted water surface area (ha) during a wet climate (black; drought index = 2.5), a moderate climate (medium gray; drought index = 0), and a dry climate (light gray; drought index = -2.5). Dashed lines represent 85% confidence limits.

drainage has a progressive and chronic influence on wetland water surface area and that terminal wetlands in drained catchments will continue to get larger up to the elevation of their basin spill point with every shift between wetting and drying phases even without additional drainage. Coupling our results with those of Wiltermuth (2014) suggests that terminal wetlands in drained catchments will continue to get larger with each subsequent wetting phase but the dry down during drying phases will not match that of the wetting phase and will likely not reach the drying seen prior to drainage without more extreme and prolonged droughts. Our results also support the hypothesis that consolidation drainage is likely occurring in other parts of the PPR and that it may contribute to increased water surface areas as wetlands increase in size to their spill point.

Catchments that historically had more wetlands had smaller water surface areas in the terminal wetland. Catchments with more wetlands, even if some are drained, are likely to have more undulating topography that should allow for more upper-catchment water storage during large precipitation events (including snow melt), reducing water surface areas of consolidated wetlands (Hayashi et al. 2003, Winter 2003, Euliss et al. 2004). While catchments with more wetlands have more wetlands to potentially drain, we found only weak evidence that proportions of drained and pre-drainage wetlands were correlated (correlation coefficient = 0.106).

Where wetlands are drained, there could be detrimental effects on water storage and groundwater infiltration (van der Kamp and Hayashi 2009). Consolidation drainage eliminates wetlands in the upper portion of the catchment and ditches increase the speed of water flow into terminal wetlands, both of which have potential to decrease upper-catchment water storage and lower local groundwater (van der Kamp and Hayashi 1998). Wetlands in the PPR can have substantial connections to groundwater and due to the soil types of much of the PPR, groundwater movement in the PPR can be slow (Sloan 1972, LaBaugh et al. 1998). In fact, we found when calculating the drought index, that a 10-year time scale best explained water surface areas in the historic era, indicating a strong connection

with groundwater. However, when we evaluated different time scales in the current era, the time scale that best explained water surface areas was 6 years (M. Post van der Burg, M. J. Anteau, L. A. McCauley, and M. T. Wiltermuth, *unpublished manuscript*). We hypothesize that this indicates that more surface-water connections via ditches from consolidation drainage has reduced the connection of these wetlands to groundwater. Thus, even during wetter periods, groundwater levels in drained catchments could potentially be lower than they were historically and lower than those that were not drained. Our results support the idea that wetlands serve an important role in water storage and groundwater recharge and they reduce down-stream runoff. Furthermore, wetland protection and restoration should be an effective strategy for reducing flooding in down-stream areas and increasing groundwater levels.

Given the climate history of this region, the 10-year time scale used to create the drought index could include one full wet-dry cycle and could include a carry-over effect of an extreme climate event. The late 1990s was among the wettest in history for this region and could be expected to have contributed to the larger water surface areas in the current era instead of drainage. However, our results indicated that the historical era had similar wet periods (historic drought index interquartile range [IQR]: -0.76 to 0.45; current drought index IQR: -0.42 to 0.69) and within the current era we had both drained and undrained catchments allowing for a wide range of water surface area responses. Additionally, the drought index was included in our models, controlling for potential small differences in climates between catchments and years, and drainage still remained the most important factor in determining water surface areas.

It has been suggested that row-cropped landscapes have more runoff and this would tend to increase water surface areas in terminal wetlands of cropped landscapes during wet climates (Euliss and Mushet 1996, van der Kamp et al. 2003, Voldseth et al. 2007). However, our data do not agree with that because, in wet periods, the proportion of crops in a catchment did not appear to affect water surface areas; although it is possible that highly cropped catchments also had terminal wetlands that were already at their spill point, which would not allow them to get

larger. Conversely, in drier periods, climate conditions not examined in previous studies, a higher proportion of cropland in the catchment led to decreased water surface areas. These results could be confounded by topography and soil type driving land use practices (Biswas et al. 2012, Gala et al. 2012); however, our study did occur over a long time frame and we did observe land use changes during that period in individual catchments. Alternatively, row crops have greater evapotranspiration rates than grasses thus, they could be essentially pulling or intercepting groundwater from a wetland (see Hayashi et al. 1998). We suspect that, during drier periods, terminal wetlands in cropped landscapes had smaller water surface areas because crops were utilizing precipitation before it ran off into the wetlands or perhaps that the deep roots of crops (Mengel and Barber 1974, Mayaki et al. 1976) were utilizing groundwater and decreasing the water surface areas of the wetlands by changing flow direction. We believe this hypothesis deserves future study, especially in light of the marked changes in cropping practices (e.g., shift from small grains to corn and soybeans) that have occurred recently in this region. Our study also suggests that when evaluating wetland water surface area responses to land cover, the results can vary between wet and dry periods.

Ecological implications

As in other dynamic wetland ecosystems, our results indicate that water surface areas of semipermanent and permanent wetlands in the PPR historically had periodic decreases in response to drought that would lead to dry or nearly dry conditions. The dynamic nature of these wetlands, along with the rare surface water connections to other waters, led to many wetlands in the PPR being devoid of fish (Peterka 1989). The lack of fish in wetlands leads to increased abundance, biomass, and size of aquatic invertebrates (Scheffer et al. 1993, Wellborn 1994, Bouffard and Hanson 1997, Duffy 1998, Zimmer et al. 2001, Hanson et al. 2005, Anteau et al. 2011) providing better habitat for amphibians and breeding waterbirds (van der Valk and Pederson 2003, Zedler 2003, Brooks 2004, Machtinger 2007). However, our results indicate that wetlands that receive consolidation drainage no longer dry down as far as they did

prior to drainage and rarely dry out completely. Additionally, consolidation drainage increases the amount of ditches on the landscape, connecting previously isolated wetlands, and providing corridors for fish dispersal. The lack of drying and increased connectivity likely explain the increases in abundance and presence of fish observed in this system (Anteau and Afton 2008b, Wiltermuth 2014), decreases in invertebrates in these wetlands, and overall lower-quality habitat for many species (Anteau and Afton 2008a, 2008b, 2011, Wiltermuth 2014). Greater water surface areas also tend to be associated with deeper water that could lead to less sunlight availability at deeper depths, reducing the submerged aquatic vegetation used as invertebrate habitat. Indeed, landscape-level assessments of aquatic-invertebrate densities indicate that their numbers have declined throughout the PPR (Anteau and Afton 2008a, 2008b). It is conceivable that consolidation drainage could ultimately be the cause of these declines in invertebrate abundance through increased wetland connectivity, fish, and increased water levels.

In addition to lower densities of aquatic invertebrates, which are important food sources for waterbirds, consolidation drainage could be ultimately responsible for the previously observed diminished habitat quality for migrating waterfowl (Anteau and Afton 2009, 2011). The draining of seasonal and temporary wetlands alone can decrease the number of ducks found on the landscape (Kantrud and Stewart 1977, Cowardin et al. 1995, Reynolds et al. 2006) and the loss of short-hydroperiod wetlands may have a large impact on the biodiversity of the region (LaBaugh et al. 1998, Niemuth et al. 2010). Additionally, our fine-scale drought index provides data that support the hypothesis that climate can vary across a relatively small spatial scale; portions of the PPR could be in different parts of the wet-dry cycle at any given time (Niemuth and Solberg 2003, Niemuth et al. 2008). Before drainage, a migrating bird may not have to travel far to find suitable stopover habitat because a mosaic of habitat conditions would have been available (Anteau 2012). Furthermore, in cases of extreme widespread drought, when seasonal and temporary wetlands are dry, larger more-permanent wetlands become the only

remaining habitat for waterbirds and because they have smaller water surface areas, shorelines and mudflats are exposed that provide valuable foraging habitat. Additionally, with less water in the wetland, invertebrate prey are concentrated and more accessible. However, our data indicate that wetland water surface areas are now greater and current dry downs may not be enough to concentrate invertebrates or expose shoreline-foraging habitat. Thus, it requires more extreme climate events to cause a historical dry down response in wetlands and there may be less spatially variable wetland conditions with altogether poorer quality habitat for migratory birds. Historically, multiple species groups utilized the mosaic of wetland habitat conditions, but now greater water surface area in permanent wetlands and fewer seasonal wetlands likely have reduced available habitat for some species groups (Kant-rud and Stewart 1984, Niemuth et al. 2006).

Conservation implications

Our study demonstrates that the hydrology of isolated wetlands, including those already set aside for conservation, can be influenced by drainage of other wetlands in their catchments. These findings may become important factors influencing conservation policy. Drainage of wetlands continues worldwide and our models predict that increases in drainage will lead to consistently greater water surface areas in wetlands that receive that drainage water. Our analysis could also provide insight into the implications of drainage in other regions with similar topographic characteristics (e.g., Iowa, Minnesota, etc.), but where the drainage occurred prior to the aerial photographic record.

Conservation and restoration projects have the potential to restore water levels of terminal wetlands if they restore enough wetlands in their catchments. Restoration efforts of large, semipermanent wetlands often include plugging ditches that drain the basin, sediment removal, and removal of fish (Gleason and Euliss 1998, Anteau et al. 2011) but may not include restoration of drained wetlands within the catchment. Similarly, conservation of existing less-permanent wetlands usually involves land acquisition or easements that prevent individual wetland drainage or filling but often only occur as opportunities arise. Our results suggest that

restoration and conservation of seasonal and temporary wetlands within the catchment of a semipermanent or permanent wetland may be required to restore or maintain the natural hydrology of those larger basins. Moreover, if individual efforts to restore and protect more seasonal or temporary wetlands were focused within watershed-derived wetland complexes they have the potential to protect and restore the hydrology of larger wetlands lower in the complex. Anteau's (2012) case-study corroborates our findings, where a large proportion of wetlands in a catchment were restored and resulted in a decrease in water surface areas in the terminal wetland. Moreover, our model could provide insight into the amount of wetland area in a basin that would need to be restored or conserved to affect water-level dynamics and help identify wetlands that will have the greatest probability of restoration success. Quantifying restoration outcomes and the efforts required to restore natural water-level dynamics may also help to protect personal property or public infrastructure that may become threatened as water rises in large wetlands.

Finally, our results indicate that wetlands respond differently to climate based on land use and manipulations in their catchments. As future climate change is expected, so is future land use change. This study underscores the importance of considering land use in conjunction with climate change to predict outcomes on ecological systems. Models evaluating ecosystem response to projected climate change that do not include land use may perform poorly and would not be likely to provide good predictions of ecological outcomes.

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SUPPLEMENTAL MATERIAL

APPENDIX A

Additional Detailed Methods

We selected 128 wetlands at random following procedures in Anteau and Afton (2008b). However, preliminary analyses indicated that randomly selected wetlands slightly under-represented landscapes that were >90% tilled agriculture and minimally disturbed. So, we randomly selected 13 additional wetlands that were situated in those landscapes

Additional wetland selection

To select additional wetlands, we used land cover data (Habitat and Population Evaluation Team 1996) to estimate the proportion of cropland within 402 m of the initial wetlands and also of 1000 randomly selected supplemental candidate wetlands (>4 ha, within 50 km of initial wetlands; National Wetland Inventory data) throughout 3 ecoregions (same proportions as Anteau and Afton 2008b). We compared the distribution of surrounding land cover amounts of the initial wetlands to the supplemental candidate wetlands. It appeared that the initial wetland selection slightly underrepresented wetlands in extremely modified landscapes, those with >90% of the upland composed of cropland. To get a more representative sample, we randomly selected 5 wetlands with 90–99% cropland and 5 wetlands with 100% cropland from the candidate list to be included in our sample. Additionally, we added 3 wetlands to represent wetlands in an area with minimal landscape disturbance. Wetlands that

were engulfed by Devil’s Lake in current years or were created by a stream impoundment were not included as sample wetlands, as both would affect water surface areas.

Generating wetland catchments

We delineated boundaries of wetland catchments using ArcHydro (ArcGIS v.10; ESRI 2010) and two types of digital elevation models (DEMs), with varying resolutions. The higher-resolution, LiDAR (Light Detection and Ranging)-derived DEM (3 m) was available in the eastern and flatter portion of the study area. In the western, hillier portion of the study area we used a lower-resolution, IfSAR (Interferometric Synthetic Aperture Radar)-derived DEM (5 m). McCauley and Anteau (McCauley and Anteau 2014) found no difference in catchment sizes generated from those DEMs, where both data sources were available.

We modeled the direction of water flow across the landscape using hydrologically correct DEMs (see below). We then delineated catchments for each wetland using the flow direction model and the boundary of each sample wetland using ArcHydro. A few times ($n = 21$) a subject wetland’s catchment was nested within another subject wetland’s catchment. Due to the limitations of ArcHydro (ESRI 2010), which is unable to delineate multiple non-discrete catchments at one time, we delineated a catchment for each wetland individually and then merged them together, creating non-discrete, sometimes nested

catchments (McCauley and Anteau 2014).

Creating a hydrologically correct DEM

A hydrologically correct DEM was created from each initial DEM. A hydrologically correct DEM is one in which “errors” have been removed and proper modeling of hydrologic flow across the landscape is allowed. This includes properly identifying non-contributing areas, also known as real sinks, “filling” depressions that are errors (or not real sinks), and incorporating culverts into the DEM to allow modeled flow of water past roads. Non-contributing areas were identified as depressions that had a fill depth greater than 1 meter and that intersected with a flooded NWI wetland (National Wetlands Inventory wetland with a code identifying it as lacustrine or palustrine with permanently flooded, semipermanently flooded, intermittently exposed, or artificially flooded hydrological regime). Those sinks that were estimated to not be real, and thus contributed to the water flow of the area, were filled. The filling process involves increasing the elevation of the sink to match the surrounding elevations so modeled water is able to flow across the sink. In many areas, especially those in the LiDAR

portion of the study area, where the topography is much flatter, real closed-basin depressions were much less common and all the polygons in the sinks layer were filled.

High-resolution elevation data can present additional problems when modeling water flow because some elements, such as bridges and roads, are present in the data (Duke and Kienzie 2003, Wang and Liu 2006, Murphy et al. 2008, Poppenga et al. 2010). In reality, water flow is possible past these features by flowing underneath a bridge or through a culvert, but in a DEM the elevation of the road or bridge masks that and obstructs modeled flow of water. Thus, culverts and bridge locations need to be identified and incorporated into the DEM to allow proper hydrologic flow. To allow modeling of water flow past roads, culverts need to be “burned” into the DEM, which involves lowering the elevation at a culvert so that the hydrologic flow is allowed past the road. In areas where roads were preventing hydrological flow that affected the boundary of the catchment, we evaluated the area using the DEM, aerial photographs and digital streams layers to determine if a culvert was likely to exist. In those cases where it was found necessary, we burned culverts into the DEM.

APPENDIX B

Table B1. The years of photos available for each sample wetland from 1937 to 1959.

Wetland ID	County	37	38	40	41	44	46	48	51	52	53	54	55	57	58	59
CLSA01	Stutsman					X			X	X				X		
CLSA02	Stutsman					X			X	X				X		
CLSA03	Stutsman					X			X	X				X		
COT1201-1	McIntosh		X							X						
COT1201-2	McIntosh		X							X						
COT1201-3R	McIntosh		X							X						
COT1202-1R	McIntosh									X						
COT1202-2R	McIntosh		X							X						
COT1202-3	McIntosh									X						
COT1203-1	McIntosh		X							X						
COT1203-2R	McIntosh		X							X						
COT1203-3	McIntosh		X							X						
COT1301-1R	Emmons		X							X						
COT1301-2R	Emmons		X							X						
COT1301-3R	Emmons		X							X						
COT1302-2R	Kidder									X	X					
COT1302-3	Kidder									X	X					
COT1303-1R	Kidder								X	X	X			X		
COT1303-2R	Kidder								X	X	X			X		
COT1303-3R	Kidder								X	X	X			X		
COT2201-1	Kidder								X	X	X			X		
COT2201-2R	Kidder								X	X	X			X		
COT2201-3R	Kidder								X	X	X			X		
COT2202-1R	Kidder									X	X					
COT2202-2R	Kidder									X	X					

Table B1. Continued.

Wetland ID	County	37	38	40	41	44	46	48	51	52	53	54	55	57	58	59
COT2202-3	Kidder									X	X					
COT2203-1R	Sheridan									X						
COT2203-2R	Sheridan									X						
COT2301-1	Stutsman					X			X	X				X		
COT2301-2	Stutsman					X			X	X				X		
COT2301-3	Stutsman					X			X	X				X		
COT2302-2R	Stutsman					X			X	X				X		
COT2302-3R	Stutsman					X			X	X				X		
COT2303-2	Kidder									X	X					
COT2409-1R	Divide						X				X					
COT2410-2	Sheridan								X	X						
COT3201-2R	Burke		X								X					
COT3201-3R	Burke		X								X					
COT3202-1R	Burke		X								X					
COT3202-2	Burke		X								X					
COT3202-3R	Burke		X								X					
COT3203-1R	Burke		X								X					
COT3203-2R	Burke		X				X				X					
COT3203-3R	Burke		X				X									
COT3301-1	Divide						X				X					
COT3301-2	Divide						X				X					
COT3301-3	Divide						X				X					
COT3302-2R	Divide						X				X					
COT3302-3	Divide						X				X					
COT3303-1	Divide						X				X					
COT3303-2	Divide						X				X					
COT3303-3	Divide						X				X					
COT3409-2	Divide						X				X					
COT3410-1R	Divide										X					
NGP12A02-1R	Sargent				X				X	X						
NGP12A02-2R	Sargent				X				X	X						
NGP12A02-3R	Sargent				X					X						
NGP12A03-1R	Sargent				X											
NGP12A03-3R	Sargent				X					X						
NGP12B01-1R	Ransom/Sargent	X			X					X						
NGP12B01-2	Sargent	X								X						
NGP12B01-3R	Sargent/Dickey	X								X						
NGP12B02-1R	Sargent				X					X						
NGP12B02-2R	Sargent				X					X						
NGP12B02-3	Sargent				X					X						
NGP13A01-1	Sargent				X					X						
NGP13A01-3	Sargent				X				X	X						
NGP13A02-1R	Sargent				X					X						
NGP13A02-2	Sargent				X					X						
NGP13A02-3	Sargent				X					X						
NGP13A03-1R	Ransom				X											
NGP13A03-2	Ransom				X											
NGP13A03-3R	Ransom				X											
NGP13B01-1	Barnes				X					X						X
NGP13B01-2	Barnes				X					X						
NGP13B01-3R	Barnes				X					X						X
NGP13B02-1R	Barnes				X					X						X
NGP13B02-2	Barnes				X					X						X
NGP13B02-3	Barnes				X					X						X
NGP13B03-1	Stutsman					X		X	X	X				X		
NGP13B03-2	Stutsman					X		X	X	X				X		
NGP22A01-1R	Barnes				X					X					X	X
NGP22A02-1	Barnes				X					X						X
NGP22A02-2R	Barnes				X					X						X
NGP22A02-3	Barnes				X					X						X
NGP22A03-1	Steele				X					X						
NGP22A03-2	Steele				X					X						
NGP22A03-3	Steele				X					X						
NGP22B01-1	Griggs				X					X						X
NGP22B01-2R	Griggs				X					X						X
NGP22B01-3R	Griggs				X					X						X
NGP22B02-1	Griggs				X					X						X
NGP22B03-1	Nelson				X					X						X

Table B1. Continued.

Wetland ID	County	37	38	40	41	44	46	48	51	52	53	54	55	57	58	59
NGP22B03-2R	Nelson				X					X						X
NGP22B03-3R	Nelson				X					X						X
NGP23A01-3	Nelson				X					X						X
NGP23A02-1R	Nelson				X					X						X
NGP23A02-2	Nelson				X					X						X
NGP23B01-1	McHenry										X					
NGP23B01-3R	McHenry										X					
NGP23B02-1R	McHenry										X					
NGP23B02-3R	McHenry										X					
NGP23B03-1R	McHenry															
NGP23B03-2R	McHenry										X					
NGP23B03-3R	McHenry										X					
NGP2409-2	Ransom/Sargent	X			X					X						
NGP32A01-2R	Benson			X					X	X						X
NGP32A01-3	Benson									X						X
NGP32A03-1R	Benson			X						X						X
NGP32A03-2R	Benson			X						X						X
NGP32A03-3R	Benson									X						X
NGP32B02-1R	Rolette								X	X	X					
NGP32B03-1R	Bottineau		X						X		X	X	X			
NGP32B03-2R	Bottineau		X						X		X	X	X			
NGP33A01-1R	Ramsey					X			X	X						X
NGP33A01-2	Ramsey					X			X	X						X
NGP33A01-3	Ramsey					X			X	X						X
NGP33A02-1	Walsh									X		X				
NGP33A02-2	Walsh									X		X				
NGP33A02-3	Walsh									X		X				
NGP33A03-1R	Ramsey					X			X	X						X
NGP33A03-2	Ramsey					X			X	X						X
NGP33B01-1	Benson			X						X						X
NGP33B01-2	Benson			X						X						X
NGP33B01-3	Benson			X						X						X
NGP33B02-1	Benson			X					X	X						X
NGP33B02-2	Benson			X					X	X						X
NGP33B02-3	Benson			X						X						X
NGP33B03-1	Pierce					X			X	X						
NGP33B03-3R	Pierce					X			X	X						X
NGP3409-1R	Pierce															X
NGP3410-1	Pierce															X
NGP3410-2R	Burke		X								X					
NGP3410-3	Barnes				X					X					X	X
RRV1201-1R	Richland				X					X						
RRV1201-2R	Richland				X					X						
RRV1201-3	Richland				X					X						
RRV1202-1R	Sargent				X					X						
RRV1202-2	Sargent				X					X						
RRV1410-1	Cass				X					X		X				
RRV3301-2R	Grand Forks				X					X		X				

Notes: We did not include any photographs where the wetlands were frozen and most photos (~90%) were taken during spring and summer. We also collected photos of the entire wetland catchments for available wet months (according to the Palmer Drought Severity Index) during the same time period. Photos from Earth Explorer were downloaded at the highest available resolution and some photos were provided to us by the USFWS as scanned, georeferenced digital photos with resolutions of ≤ 1 -m cell size. We collected printed photos from NRCS/FSA county offices, scanned them in at 600 dpi and saved them in a .tif file format. Most photos had a resolution of ≤ 1 -m cell size but some photos ($< 5\%$; from USGS Earth Explorer) were only available with ~ 4 -m cell size.

Table B2. The years of photos available for each sample wetland from 1960 to 2010.

Wetland ID	County	60	61	62	64	65	67	68	69	03	04	05	06	07	09	10
CLSA01	Stutsman				X					X	X	X	X	X	X	X
CLSA02	Stutsman				X					X	X	X	X	X	X	X
CLSA03	Stutsman				X					X	X	X	X	X	X	X
COT1201-1	McIntosh	X						X		X	X	X	X	X	X	X
COT1201-2	McIntosh	X						X		X	X	X	X	X	X	X
COT1201-3R	McIntosh							X		X	X	X	X	X	X	X
COT1202-1R	McIntosh	X						X		X	X	X	X	X	X	X
COT1202-2R	McIntosh	X					X	X		X	X	X	X	X	X	X
COT1202-3	McIntosh	X						X		X	X	X	X	X	X	X
COT1203-1	McIntosh	X						X		X	X	X	X	X	X	X
COT1203-2R	McIntosh	X						X		X	X	X	X	X	X	X
COT1203-3	McIntosh	X						X		X	X	X	X	X	X	X
COT1301-1R	Emmons							X		X	X	X	X	X	X	X
COT1301-2R	Emmons									X	X	X	X	X	X	X
COT1301-3R	Emmons									X	X	X	X	X	X	X
COT1302-2R	Kidder							X		X	X	X	X	X	X	X
COT1302-3	Kidder							X		X	X	X	X	X	X	X
COT1303-1R	Kidder							X		X	X	X	X	X	X	X
COT1303-2R	Kidder							X		X	X	X	X	X	X	X
COT1303-3R	Kidder							X		X	X	X	X	X	X	X
COT2201-1	Kidder							X		X	X	X	X	X	X	X
COT2201-2R	Kidder							X		X	X	X	X	X	X	X
COT2201-3R	Kidder							X		X	X	X	X	X	X	X
COT2202-1R	Kidder							X		X	X	X	X	X	X	X
COT2202-2R	Kidder							X		X	X	X	X	X	X	X
COT2202-3	Kidder							X		X	X	X	X	X	X	X
COT2203-1R	Sheridan									X	X	X	X	X	X	X
COT2203-2R	Sheridan									X	X	X	X	X	X	X
COT2301-1	Stutsman				X					X	X	X	X	X	X	X
COT2301-2	Stutsman				X					X	X	X	X	X	X	X
COT2301-3	Stutsman				X					X	X	X	X	X	X	X
COT2302-2R	Stutsman				X					X	X	X	X	X	X	X
COT2302-3R	Stutsman				X					X	X	X	X	X	X	X
COT2303-2	Kidder							X		X	X	X	X	X	X	X
COT2409-1R	Divide								X	X	X	X	X	X	X	X
COT2410-2	Sheridan									X	X	X	X	X	X	X
COT3201-2R	Burke									X	X	X	X	X	X	X
COT3201-3R	Burke									X	X	X	X	X	X	X
COT3202-1R	Burke									X	X	X	X	X	X	X
COT3202-2	Burke									X	X	X	X	X	X	X
COT3202-3R	Burke									X	X	X	X	X	X	X
COT3203-1R	Burke									X	X	X	X	X	X	X
COT3203-2R	Burke									X	X	X	X	X	X	X
COT3203-3R	Burke									X	X	X	X	X	X	X
COT3301-1	Divide								X	X	X	X	X	X	X	X
COT3301-2	Divide								X	X	X	X	X	X	X	X
COT3301-3	Divide								X	X	X	X	X	X	X	X
COT3302-2R	Divide								X	X	X	X	X	X	X	X
COT3302-3	Divide								X	X	X	X	X	X	X	X
COT3303-1	Divide								X	X	X	X	X	X	X	X
COT3303-2	Divide								X	X	X	X	X	X	X	X
COT3303-3	Divide								X	X	X	X	X	X	X	X
COT3409-2	Divide								X	X	X	X	X	X	X	X
COT3410-1R	Divide								X	X	X	X	X	X	X	X
NGP12A02-1R	Sargent							X		X	X	X	X	X	X	X
NGP12A02-2R	Sargent							X		X	X	X	X	X	X	X
NGP12A02-3R	Sargent							X		X	X	X	X	X	X	X
NGP12A03-1R	Sargent							X		X	X	X	X	X	X	X
NGP12A03-3R	Sargent							X		X	X	X	X	X	X	X
NGP12B01-1R	Ransom/Sargent	X						X		X	X	X	X	X	X	X
NGP12B01-2	Sargent							X		X	X	X	X	X	X	X
NGP12B01-3R	Sargent/Dickey							X		X	X	X	X	X	X	X
NGP12B02-1R	Sargent							X		X	X	X	X	X	X	X
NGP12B02-2R	Sargent							X		X	X	X	X	X	X	X
NGP12B02-3	Sargent							X		X	X	X	X	X	X	X
NGP13A01-1	Sargent							X		X	X	X	X	X	X	X
NGP13A01-3	Sargent							X		X	X	X	X	X	X	X
NGP13A02-1R	Sargent							X		X	X	X	X	X	X	X

Table B2. Continued.

Wetland ID	County	60	61	62	64	65	67	68	69	03	04	05	06	07	09	10
NGP13A02-2	Sargent							X		X	X	X	X	X	X	X
NGP13A02-3	Sargent							X		X	X	X	X	X	X	X
NGP13A03-1R	Ransom	X						X	X	X	X	X	X	X	X	X
NGP13A03-2	Ransom	X						X	X	X	X	X	X	X	X	X
NGP13A03-3R	Ransom	X						X	X	X	X	X	X	X	X	X
NGP13B01-1	Barnes								X	X	X	X	X	X	X	X
NGP13B01-2	Barnes								X	X	X	X	X	X	X	X
NGP13B01-3R	Barnes								X	X	X	X	X	X	X	X
NGP13B02-1R	Barnes									X	X	X	X	X	X	X
NGP13B02-2	Barnes								X	X	X	X	X	X	X	X
NGP13B02-3	Barnes								X	X	X	X	X	X	X	X
NGP13B03-1	Stutsman				X					X	X	X	X	X	X	X
NGP13B03-2	Stutsman				X					X	X	X	X	X	X	X
NGP22A01-1R	Barnes									X	X	X	X	X	X	X
NGP22A02-1	Barnes					X				X	X	X	X	X	X	X
NGP22A02-2R	Barnes					X				X	X	X	X	X	X	X
NGP22A02-3	Barnes					X				X	X	X	X	X	X	X
NGP22A03-1	Steele					X	X			X	X	X	X	X	X	X
NGP22A03-2	Steele					X	X			X	X	X	X	X	X	X
NGP22A03-3	Steele					X	X			X	X	X	X	X	X	X
NGP22B01-1	Griggs						X			X	X	X	X	X	X	X
NGP22B01-2R	Griggs						X			X	X	X	X	X	X	X
NGP22B01-3R	Griggs						X			X	X	X	X	X	X	X
NGP22B02-1	Griggs					X	X			X	X	X	X	X	X	X
NGP22B03-1	Nelson						X			X	X	X	X		X	X
NGP22B03-2R	Nelson						X			X	X	X	X		X	X
NGP22B03-3R	Nelson						X			X	X	X	X		X	X
NGP23A01-3	Nelson						X			X	X	X	X		X	X
NGP23A02-1R	Nelson						X			X	X	X	X	X	X	X
NGP23A02-2	Nelson						X			X	X	X	X	X	X	X
NGP23B01-1	McHenry								X	X	X	X	X	X	X	X
NGP23B01-3R	McHenry								X	X	X	X	X	X	X	X
NGP23B02-1R	McHenry								X	X	X	X	X	X	X	X
NGP23B02-3R	McHenry								X	X	X	X	X	X	X	X
NGP23B03-1R	McHenry								X	X	X	X	X	X	X	X
NGP23B03-2R	McHenry								X	X	X	X	X	X	X	X
NGP23B03-3R	McHenry								X	X	X	X	X	X	X	X
NGP2409-2	Ransom/Sargent	X						X		X	X	X	X	X	X	X
NGP32A01-2R	Benson						X			X	X	X	X	X	X	X
NGP32A01-3	Benson						X			X	X	X	X	X	X	X
NGP32A03-1R	Benson						X			X	X	X	X	X*	X	X
NGP32A03-2R	Benson						X			X	X	X	X	X*	X	X
NGP32A03-3R	Benson						X			X	X	X	X	X*	X	X
NGP32B02-1R	Rolette			X						X	X	X	X	X	X	X
NGP32B03-1R	Bottineau		X						X	X	X	X	X	X	X	X
NGP32B03-2R	Bottineau		X						X	X	X	X	X	X	X	X
NGP33A01-1R	Ramsey						X			X	X	X	X	X*	X	X
NGP33A01-2	Ramsey						X			X	X	X	X	X*	X	X
NGP33A01-3	Ramsey						X			X	X	X	X	X*	X	X
NGP33A02-1	Walsh			X						X	X	X	X	X*	X	X
NGP33A02-2	Walsh			X						X	X	X	X	X*	X	X
NGP33A02-3	Walsh			X						X	X	X	X	X*	X	X
NGP33A03-1R	Ramsey						X			X	X	X	X	X*	X	X
NGP33A03-2	Ramsey						X			X	X	X	X	X*	X	X
NGP33B01-1	Benson						X			X	X	X	X	X	X	X
NGP33B01-2	Benson						X			X	X	X	X	X	X	X
NGP33B01-3	Benson						X			X	X	X	X	X	X	X
NGP33B02-1	Benson						X			X	X	X	X	X	X	X
NGP33B02-2	Benson						X			X	X	X	X	X	X	X
NGP33B02-3	Benson						X			X	X	X	X	X	X	X
NGP33B03-1	Pierce									X	X	X	X	X	X	X
NGP33B03-3R	Pierce									X	X	X	X	X	X	X
NGP3409-1R	Pierce									X	X	X	X	X	X	X
NGP3410-1	Pierce									X	X	X	X	X	X	X
NGP3410-2R	Burke									X	X	X	X	X	X	X
NGP3410-3	Barnes								X	X	X	X	X	X	X	X
RRV1201-1R	Richland									X	X	X	X	X	X	X

Table B2. Continued.

Wetland ID	County	60	61	62	64	65	67	68	69	03	04	05	06	07	09	10
RRV1201-2R	Richland									X	X	X	X	X	X	X
RRV1201-3	Richland									X	X	X	X	X	X	X
RRV1202-1R	Sargent							X		X	X	X	X	X	X	X
RRV1202-2	Sargent							X		X	X	X	X	X	X	X
RRV1410-1	Cass					X				X	X	X	X	X	X	X
RRV3301-2R	Grand Forks			X						X	X	X	X	X	X	X

Notes: We did not include any photographs where the wetlands were frozen and most photos (~90%) were taken during spring and summer. We also collected photos of the entire wetland catchments for available wet months (according to the Palmer Drought Severity Index) during the same time period. Photos from Earth Explorer were downloaded at the highest available resolution and some photos were provided to us by the USFWS as scanned, georeferenced digital photos with resolutions of ≤ 1 -m cell size. We collected printed photos from NRCS/FSA county offices, scanned them in at 600 dpi and saved them in a .tif file format. Most photos had a resolution of ≤ 1 -m cell size but some photos (<5% from USGS Earth Explorer) were only available with ~4-m cell size. All water surface areas in 2007/2008 ("07" column) were collected by interpreting water surface areas from Digital Elevation Models collected from 2007–2008 but those marked with "X*" were collected in May 2009.