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ORIGINAL ARTICLE

Impacts of climate change on land-use and wetland productivity in the Prairie Pothole Region of North America

Benjamin S. Rashford · Richard M. Adams · JunJie Wu · Richard A. Voldseth · Glenn R. Guntenspergen · Brett Werner · W. Carter Johnson

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Abstract Wetland productivity in the Prairie Pothole Region (PPR) of North America is closely linked to climate. A warmer and drier climate, as predicted, will negatively affect the productivity of PPR wetlands and the services they provide. The effect of climate change on wetland productivity, however, will not only depend on natural processes (e.g., evapotranspiration), but also on human responses. Agricultural land use, the predominant use in the PPR, is unlikely to remain static as climate change affects crop yields and prices. Land use in uplands surrounding wetlands will further affect wetland water budgets and hence wetland productivity. The net impact of climate change on wetland productivity will therefore depend on both the direct effects of climate change on wetlands and the indirect effects on upland land use. We examine the effect of climate change and land-use response on semipermanent wetland productivity by combining an economic model of agricultural land-use change with an ecological model of wetland dynamics. Our results suggest that the climate change scenarios evaluated are likely to have profound effects on land use in the North and South Dakota PPR, with wheat displacing other crops and pasture. The combined pressure of land-use and climate change significantly reduces wetland productivity. In a climate scenario with a +4 °C increase in temperature, our model predicts that almost the entire region may lack the wetland productivity necessary to support wetland-dependent species.

Keywords Climate change · Wetland modeling · Cover cycle · Hydroperiod · Land-use change

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B. S. Rashford (✉)
Department of Agricultural and Applied Economics, University of Wyoming, Dept. 3354, 1000 E. University Ave., Laramie, WY 82071, USA
e-mail: brashfor@uwyo.edu

R. M. Adams · J. Wu
Department of Applied Economics, Oregon State University, Corvallis, OR 97331, USA
e-mail: richard.adams@oregonstate.edu

J. Wu
e-mail: junjie.wu@oregonstate.edu

R. A. Voldseth
School of Natural Resource Sciences, North Dakota State University, Dept. 7680, Fargo, ND 58108, USA
e-mail: richard.voldseth@ndsu.edu

G. R. Guntenspergen
US Geological Survey, Patuxent Wildlife Research Center, 12100 Beech Forest Road, Suite 4039, Laurel, MD 20708, USA
e-mail: glenn_guntenspergen@usgs.gov

B. Werner
Environmental Studies Program, Centre College, Danville, KY 40422, USA
e-mail: brettwerner@gmail.com

W. CarterJohnson
Department of Natural Resource Management, South Dakota State University, Brookings, SD 57007, USA
e-mail: Carter.Johnson@sdstate.edu

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Introduction

Expansion of intensive agriculture over the past century has left an indelible mark on North American prairie wetland ecosystems. Over half of the historical wetlands in the Prairie Pothole Region (PPR) have been drained, and conversion of upland areas to crops has altered wetland productivity (Tiner 1984; Kantrud et al. 1989). Today, though largely protected from direct draining, PPR wetlands face the new threat of a changing climate. Because of their shallow, ephemeral nature, prairie wetlands are highly susceptible to changes in temperature and precipitation (Poiani et al. 1996; Johnson et al. 2004, 2010). The effect of climate change on prairie wetlands, however, will not only be expressed through natural processes, but also through changes in human activities. Agricultural land use, the predominant historical driver of wetland degradation, will not remain static as climate change affects crop yields and global commodity prices (Adams et al. 1990, 1998). The ultimate effect of climate change on prairie wetlands will therefore depend on the interplay between climate, upland land use, and wetland productivity.

A growing body of research has examined the influence of climate on wetland productivity in the PPR (Poiani et al. 1996; Sorenson et al. 1998; Johnson et al. 2004, 2005, 2010). Whether based on historical data or computer simulation models, this research concludes that climate change will have significant negative effects on wetland productivity (e.g., through changes in wetland water budgets, emergent cover dynamics, hydroperiods, and species composition). Climate drives surface processes, such as the hydrologic cycle, and hydrology is the most important factor controlling key wetland processes and services (Winter and Woo 1990). Wetland water depth and the frequency and duration of hydroperiod—the cycle of wetland drying and inundation—greatly influences vegetation cover-cycle dynamics and productivity of semipermanent wetlands (Swanson and Duebbert 1989; Johnson et al. 2010).

Ojima and Lackett (2002) used two coupled atmosphere–ocean general circulation models (Canadian Climate Centre CGCMI model from the Canadian Centre for Climate Modeling and Analysis and the UK Hadley Centre HADCM2 model from the Hadley Centre for Climate Prediction and Research) to provide scenarios of future climate averaged over all ten of the U.S. Great Plains states. The changes in annual temperature and precipitation projected for the northern Great Plains will affect wetland hydroperiod, ratio of emergent plant cover to open water, species composition, wetland permanence, and primary and secondary productivity (van der Valk 1989). Winter (2000) predicted that the surface area of seasonal and semipermanent wetlands in the PPR would be reduced by increased evapotranspiration and reduced summer soil moisture. With increased temperatures, summer evapotranspiration would put increasing demands on groundwater, resulting in earlier drying of wetlands. Such effects will hamper the ability of these wetlands to provide valuable ecosystem services, including waterfowl production for which the PPR is the most important breeding ground in North America (Sorenson et al. 1998).

Climate also affects wetland water budgets indirectly through its influence on land use and crop choice in adjacent uplands. A warmer and drier climate, for example, may cause farmers to shift crops or farming methods, which would affect runoff and groundwater recharge—two important components of wetland water budgets. Most previous studies of climate change and wetlands, however, do not explicitly consider the effects of upland land-use change on wetland productivity. The simulation analyses by Johnson and colleagues (see e.g., Poiani et al. 1996; Johnson et al. 2010) modeled wetland complexes within unmanaged grassland. Extensions of their modeling efforts have demonstrated that upland land use affects prairie wetland functions by altering hydrologic process and vegetation dynamics (Voldseth et al. 2007). More recently, Voldseth et al. (2009) explicitly modeled the effect of climate change on wetlands given alternative upland land uses, including cultivated crops. Their results indicate that the effects of climate change on wetlands depend on upland land use and suggest that managed cover (i.e., grazed grassland or crops) could mitigate some degree of climate warming by maintaining wetland water levels.

The previous research establishes potential effects of both climate change and land use on prairie wetland productivity. A key unanswered question is how land use in the PPR is likely to evolve in response to climate change, and thus, how wetlands will actually be affected on a regional scale by the joint impacts of climate and land-use change. Since much of the PPR is privately owned and used for agricultural production (Kantrud et al. 1989), land-use change will reflect changes in the economic incentives faced by producers (Rashford et al. 2011). Climate change is generally predicted to have mixed effects on crop yields in North America, with some crops more affected (e.g., corn) than others (e.g., wheat) (Adams et al. 1998; Hertel et al. 2010). Differential yield effects can change the relative returns of alternative crops, inducing land-use change and impacting productivity of prairie wetland complexes within the agricultural matrix. The importance of price-induced changes in land use is demonstrated by the recent expansion of corn acreage in the Northern Plains in response to rapid increases in prices (Westcott 2007). Thus, it is important that human response to climate change, such as changes in crop choices, is explicitly incorporated into

any assessment of the resiliency of PPR wetlands to climate change.

We expand the literature by jointly modeling the effects of climate change on land use and wetland productivity. We do so by combining results from an econometric model of land use in the PPR of North and South Dakota and a process-based wetland simulation model developed for semipermanent prairie wetlands. Our approach allows us to consider climate and land-use effects on wetlands on a broad regional scale and therefore establishes potential future states of wetlands across much of the PPR. A better understanding of how and where prairie wetlands will be most affected by the interaction between climate and land-use change is a necessary starting point in determining how to effectively mitigate climate change impacts.

Methods

Model overview, study area, and climate scenarios

We modeled the effect of climate change and land use on wetland productivity in the Prairie Pothole Region (PPR) of North and South Dakota, USA (Fig. 1). Our modeling process used a simulation procedure to integrate the results of an econometric land-use model (Wu et al. 2004) and a wetland simulation model, WETLANDSCAPE (Johnson et al. 2010). In simple terms, our modeling process involved (1) estimating an econometric model to predict land use (i.e., probability of observing specific agricultural uses) under alternative climate scenarios, (2) estimating wetland productivity given alternative climate scenarios and upland land uses, and (3) combining the results from the two models to predict the joint effect of climate and land-use change on wetland productivity. Since the land-use and wetland simulation models used different data and scales, we explain each in turn below and then describe their integration into our assessment model.

Land-use model

We predicted land use using a multinomial logit model of parcel-level crop choice previously developed for the U.S. Northern Plains. The methods and data used followed Wu et al. (2004), who estimated a similar model for the corn belt. The land-use model predicts the probability of observing a parcel in a specific use as a function of economic, crop, landscape, and weather characteristics according to the logit probability function:

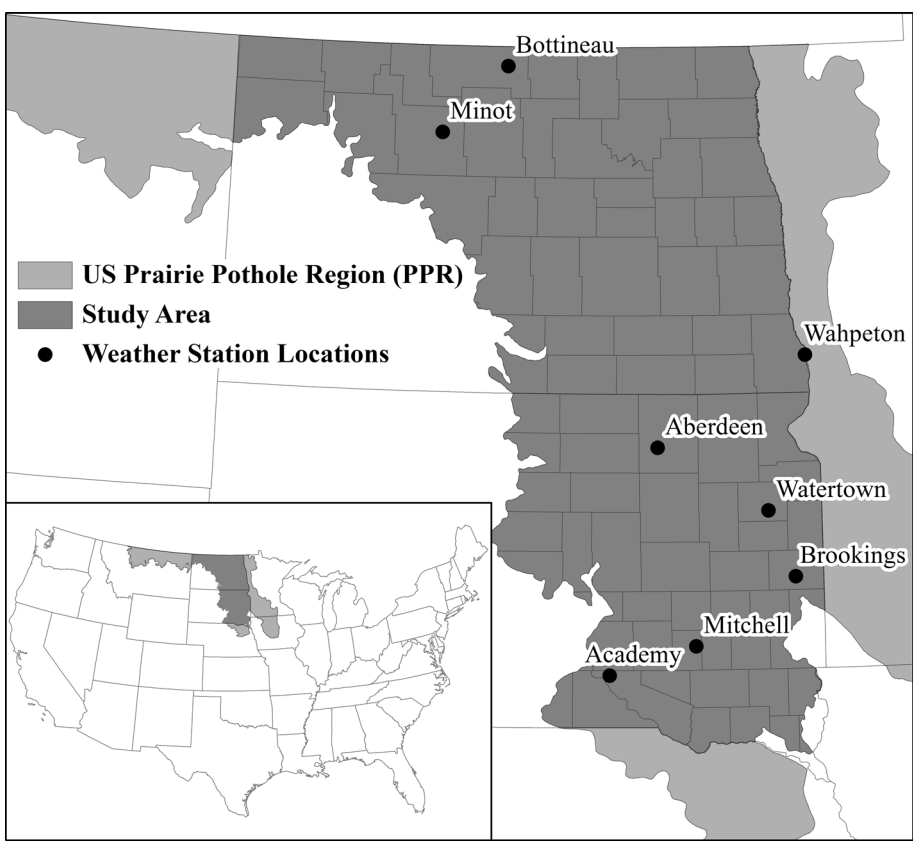

Fig. 1 Map of the Prairie Pothole Region in North and South Dakota (USA), including weather station locations used in the analysis

$$p_{ij} = \frac{\exp\left(\beta_j' x_{ij}\right)}{1 + \sum_j \exp(\beta_j' x_{ij})} \quad (1)$$

where p_{ij} is the probability parcel that i is in use j, x_{ij} is a vector of explanatory variables for parcel i, use j, and β_j is a vector of coefficients to be estimated. Logit models have been shown to outperform other flexible forms and have therefore been widely used to model agricultural land use (see e.g., Wu and Segerson 1995; Wu and Tanaka 2005; Rashford et al. 2011).

We estimated the land-use model using data from the National Resources Inventory (NRI) for the prairies states of ND, SD, and NE. The NRI is a scientifically based longitudinal survey of soil, water, and land use covering the period 1982–1997. Though somewhat dated, the NRI sample remains the best data set for modeling parcel-level crop choice. More recent NRI sampling periods only provide aggregate land-use observations (i.e., they no longer provide the parcel-level data required to estimate the land-use model). Alternative data sets that include more recent observations are either aggregated and thus cannot be used for parcel-level modeling (e.g., county-level USDA data), or have high crop-level misclassification error rates (e.g., satellite imagery data), which lead to biased parameter estimates and predictions in logit land-use models (Hausman et al. 1998). Previous research also successfully demonstrates that land-use models estimated with the 1982–1997 NRI sample can accurately forecast future land use in the PPR (Rashford et al. 2011).

The data included 48,403 sampled parcels in the three states and 39,215 sampled parcels in the PPR region of North and South Dakota. We used the NRI data to define land-use categories for five primary crops in the region according to the NRI data: corn, soybeans, wheat, hay, and sorghum. Pasture and rangeland uses were implicitly modeled as the residual category. Explanatory variables used in the land-use model (i.e., x_{ij}) were consistent with previous literature (see e.g., Wu et al. 2004). These variables capture the impacts of cropping history, input and output prices, yield, land characteristics, and weather on land-use choice (see Appendix for a detailed description of variables and associated summary statistics).

The parameter estimates from the land-use model allow us to predict land use at each NRI parcel given alternative assumptions about future climate and economic conditions. To predict land use under climate change, we needed to generate future values of the weather variables used in the land-use model. Since some of the information for these variables was generated in the wetland model, we next describe that model and then describe the simulation procedure used to integrate the two models.

Wetland model

We used the model WETLANDSCAPE (WLS) to determine the combined impact of climate and land use on wetland productivity. WLS operates on a 10-day time step and is a climate-driven, process-based, deterministic simulation model that simultaneously simulates wetland surface water, groundwater, and vegetation dynamics of a wetland complex (Johnson et al. 2010). The WLS surface hydrology and soil processes are based on the EPIC Model (Williams 1995), ceasing to operate during frozen winter months and using runoff curve numbers that are dynamically adjusted in response to soil moisture and frost conditions. The model was parameterized and tested at a long-term monitoring site in eastern South Dakota named Orchid Meadows (OM), which consists of 83.4 ha of rolling grassland with 10 wetlands. The wetlands at OM include temporary, semipermanent and seasonal wetland permanence classes (see Stewart and Kantrud 1971 for a description of permanence classes). This site is representative of highly productive PPR grassland; however, the range of wetland basin morphometry from this site is less than the range across all of the PPR. One hundred years of weather data from multiple weather stations across the PPR were used to inform and validate the WLS model. Previous research has demonstrated the validity of using weather data from multiple locations to capture spatial variability in wetland dynamics (Johnson et al. 2005). One 100-year simulation was run for the historic and three climate scenarios at each location.

We used WLS to simulate the temporal and spatial effects of climate change on wetland functions by using historic and projected weather data at eight weather stations spatially distributed across the North and South Dakota portion of the PPR (Fig. 1). For each weather station, we used the graphical output from the IPCC Fourth Assessment Report (Christensen et al. 2007) on regional yearly averages of temperature and precipitation projections to interpolate projections to the northern Great Plains of the USA. The A1B emission scenario describes a future world of very rapid economic growth followed by rapid introductions of new and more efficient technology—it represents a high emission storyline. Our +4 °C temperature and +4 °C and +10 % precipitation scenarios represent this scenario. Our use of the +2 °C temperature scenario represents a midvalue between the historical and the IPCC fourth assessment A1B scenario. The United States National Climate Assessment offers a more recent analysis of future climate scenarios in the Northern Great Plains (Melillo et al. 2014). The climate framework is based on climate model simulations using the high (A2) and low (B1) SRES emission scenarios and uses

dynamically downscaled climate model simulations (Kunkel et al. 2013). The range of projections from this most recent analysis spans our future climate scenarios and suggests that our higher mean annual temperature and precipitation scenarios for North and South Dakota are conservative. We used the delta method (Giorgi and Mearns 1991) to apply each scenario to each weather station. This method adds coarse-scale climate predictions to historical data sets of high-resolution observations. One of the limitations of this method is that it assumes no changes in climatic variability are expected in the future, as this variability is inherited from the current climate regime.

Given climate projections for each weather station, the model for the OM site was essentially "transported" to each station and then we performed simulations with the climate data for each location. WLS also simulates the effect of upland land use by altering upland runoff, infiltration, and evapotranspiration rates to correspond with alternative land covers (Voldseth et al. 2009). We therefore ran WLS simulations at each weather station under each of the uses included in the land-use model.

For each site, land use and climate scenario, WLS generated two measures of semipermanent wetland productivity: cover-cycle index and hydroperiod. The cover-cycle index (CCI) describes the frequency and speed at which semipermanent prairie wetlands transition through the four cover-cycle stages: (1) dry stage with dense emergent vegetation, (2) regeneration stage with re-flooding and vegetative propagation, (3) degenerative stage with rising water levels and emergent vegetation in decline, and (4) lake stage with high water and little emergent vegetation (van der Valk and Davis 1978). The speed of the cover cycle and the number of switches between cover-cycle stages over time are positively correlated with wetland productivity and biodiversity (Johnson et al. 2010; Werner et al. 2013). In addition to the CCI, we also estimated wetland hydroperiod—the length of time a wetland is inundated with water. Many wetland-dependent species require a minimum number of days of wetland inundation within a home wetland or across a wetland complex to complete their seasonal life cycle (Johnson et al. 2010). A hydroperiod of 100 days generally corresponds to the median value for many PPR vertebrates, including waterfowl (Bellrose 1980) and amphibians (Wagner 1997). However, some waterfowl species, such as pintails, require as few as 70 days, while others, such as canvasbacks, require as many as 130 days (Bellrose 1980; Austin and Miller 1995).

In addition to measures of semipermanent wetland productivity, we also used WLS to inform the land-use modeling component of the integrated model described below. Specifically, we used WLS to determine the mean temperature, mean precipitation, and standard deviation of precipitation during the corn and wheat growing season, and the mean and standard deviation of snow precipitation. This was necessary since climate change could affect the timing and length of crop growing seasons (Dunnell and Travers 2011). Thus, using historical growing season dates to determine future weather variables could systematically misrepresent actual growing conditions and bias the land-use predictions. WLS determines the growing season as the annual date range (average over a 100-year simulation) when crop leaf area index is continuously greater than zero. Winter dates are determined by when WLS projects that precipitation falls as snow. Thus, given the growing season and winter dates determined by WLS for each climate scenario and weather station location, we calculated the weather variables necessary to project land use.

Simulating land use and wetland productivity with climate change

The land-use model generated a parameterized function to predict the probability that each of the 39,215 parcels in the ND and SD PPR is observed in each alternative use (i.e., corn, soybeans, wheat, hay, sorghum, and pasture/rangeland) given economic and weather conditions. WLS produced estimates of wetland CCI and hydroperiod at eight weather stations across ND and SD for each possible combination of climate (historical, +2, +4, and +4 °C with +10 % precipitation) and land use. Combining the results from these models to project wetland productivity resulting from climate and land-use change required several steps.

First, to make the wetland simulation spatially consistent with the land-use model, we used the spline procedure in ArcGIS (version 10) to extrapolate wetland productivity and climate measures from the eight weather stations used in the WLS simulations to each county in the region.[1] Second, we updated the economic variables in the land-use model by collecting output and input price variables for 2008. Next, we used the county-level climate measures (e.g., average temperature during the corn growing season) and updated economic variables to predict land-use probabilities at each NRI parcel under each climate scenario according to:

$$\hat{p}_{ijk} = \frac{\exp\left(\hat{b}_j' x_{ijk}\right)}{1 + \sum_j \exp\left(\hat{b}_j' x_{ijk}\right)}, \tag{3}$$

where $\hat{p}_{ijk}$ is the predicted probability that parcel i is in land use j given climate scenario k, $\hat{b}_j'$ is a vector of estimated coefficients from the land-use model, and x_{ijk} is a vector of explanatory variables for use i, parcel j, and climate

[1] We used the regularized spline option with a weight of 0.1 and six input points. Experimentation with other weights and input points did not produce meaningfully different county-level estimates.

scenario k. This approach represents a retrospective simulation—it predicts the likely distribution of land uses given 2008 prices and each future climate scenario. Holding prices fixed under alternative climate scenarios may seem restrictive since climate change is expected to influence global commodity prices (Easterling et al. 2007). The effect of climate change on prices, however, is highly uncertain and depends on global adaptation and mitigation policies. Moreover, changes in relative prices (e.g., corn relative to wheat) not absolute prices drive land-use change, and given the high correlation between crop prices, relative prices are fairly stable through time (USDA 2013).

Given land-use probabilities, we calculated the expected CCI and hydroperiod on each parcel according to:

$$E[\mathrm{CCI}_{ik}] = \sum_j \hat{p}_{ijk}\mathrm{CCI}_{ijk}, \tag{4}$$

where subscripts are defined above, and CCI values are replaced by hydroperiod values to calculate expected hydroperiod. Finally, we aggregated wetland productivity measures to the county level using a weighted average across all parcels in a county with weights corresponding to each parcels expansion factor (i.e., each parcel is weighted according to the proportion of the county it represents). Aggregating to the county level acknowledges that we do not know the exact location of individual parcels, nor the actual distribution of wetlands across parcels. The productivity measures reported below should therefore be interpreted as the productivity level likely to occur for wetlands within the agricultural matrix given an assumed prevailing climate.

Results

Land-use model

The land-use model generally fits the observed land-use data well and behaves as expected (see Appendix Table A2 for individual parameter estimates and significance). Estimated elasticities are generally consistent with economic theory, suggesting the model accurately reflects the incentives faced by landowners in the PPR (Appendix Table A3). Own-price elasticities (e.g., price of corn in the corn equation) are all positive, implying the probability of observing a given use increases when its price increases relative to other uses. Cross-price elasticities are generally negative, indicating that the probability of a given use decreases when the price of competing uses increase (e.g., corn vs. soybeans). A few of the cross-price elasticities, however, are positive, indicating that the probability of a given use increases when the price of competing uses increase. Such counterintuitive results could suggest that some crops are more complimentary than others. Elasticities of the land characteristics indicate, as expected, that high-quality land is more likely to be planted to high-value crops. Elasticities of the weather variables indicate that alternative crops are likely to respond differently to climate changes. For example, increases in average maximum temperature and precipitation during the summer growing season tend to favor wheat and sorghum over other crops, which is generally consistent with the relative responses of alternative crops found in previous studies (Lobell and Field 2007; Tebaldi and Lobell 2008).

Wetland model

WETLANDSCAPE results indicate that semipermanent wetland productivity, as measured by hydroperiod and CCI, varies systematically across upland land uses, weather stations, and climate scenarios. Hydroperiod and CCI generally decrease across all uses and climate scenarios moving from the southeast to the northwest (Appendix Figure A3). On average, wetlands in the southeast portion of the study region tend to have hydroperiods of at least 100 days under most land uses and climate scenarios; however, in the most extreme scenario (+4 °C and wheat/hay), hydroperiods in the southeastern locations generally fail to reach 80 days. In contrast, wetlands in the northwest fail to achieve 100-day hydroperiods under any land use–climate scenario combinations, and only achieve 80-day hydroperiods given the historical climate and land use in pasture. Recall that 100 days are median number of days required by most wetland-dependent species in the region, and that less than 80 days will likely impact all but the least sensitive species. CCI has similar trends over space and climate scenarios, ranging from a maximum of 0.98 in Academy, SD (historical climate, pasture) to a minimum of 0.21 Bottineau, ND (+4 °C, wheat). Across land uses, hydroperiod consistently decreases from low-intensity agriculture (i.e., pasture) to intensive crops, with wheat generally producing the lowest hydroperiods across locations and climate scenarios (Table 1). CCI, however, is less consistent across uses. In many location and climate scenarios, CCI is higher under intensive cropping uses as crops improve wetland inflows, increasing cover-cycle transitions (see Voldseth et al. 2007).

Climate change effects on land use and semipermanent wetland productivity

Given historical climate and 2008 economic conditions, the land-use simulations depict a landscape consistent with what is currently observed in the North and South Dakota portions of the PPR (e.g., state-level total cropland is predicted within 10 % of what is actually observed). The

Table 1 Average cover-cycle index and hydroperiod by climate scenario

	Land use			
	Pasture	Corn	Soybean/sorghum	Wheat/hay
Hydroperiod[a]				
Historical	113.51	107.94	105.63	104.35
+2 °C	97.10	89.98	87.82	85.12
+4 °C	83.92	76.93	76.08	70.25
+4 °C and 10 % precipitation	102.43	94.61	92.83	87.65
Cover-cycle index[b]				
Historical	0.72	0.73	0.74	0.73
+2 °C	0.76	0.72	0.70	0.71
+4 °C	0.51	0.46	0.44	0.43
+4 °C and 10 % precipitation	0.80	0.73	0.73	0.72

[a] Hydroperiod is the average annual number of days a wetland is inundated

[b] Cover-cycle index is an index of wetland productivity related to the speed and frequency with which wetlands cycle through vegetation cover stage. Higher cover-cycle index values indicate more dynamic and productive wetland conditions

region's agricultural land is dominated by wheat (48 %) and pasture (30 %), with relatively little land in corn (13 %), hay (6 %), soybeans (2 %), or sorghum (<1 %). The alternative uses, however, are unevenly distributed across the region. Corn and soybeans are concentrated in the southeast and along the eastern border of the region, where climatic conditions have been historically conducive. Wheat is concentrated in ND with greatest concentration along the western boundary of the PPR. Pasture is distributed widely, occupying historically less productive land; however, pasture area is lowest in counties dominated by corn and soybeans.

Predictions of land use given alternative climate scenarios indicate that climate change may have profound effects on the distribution of agricultural land use in the region. Wheat is predicted to substantially increase under each climate scenario (Fig. 2). The majority of the increase in wheat results from reallocating land historically used for pasture or, to a lesser extent, corn. The latter conversions may largely be a result of the 2008 price scenario we used, since 2008 was a relatively high-price year for wheat. The reallocation of land under climate change also affects the spatial distribution of dominant agricultural uses. As

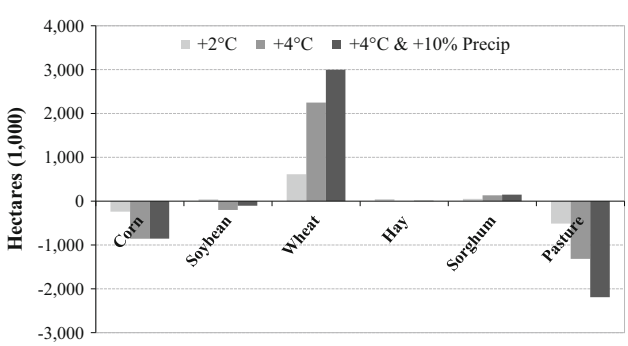

Fig. 2 Change in area (1,000 ha) by use predicted in the North and South Dakota portion of the Prairie Pothole Region for three future climate scenarios (+2, +4, and +4 °C with +10 % precipitation)

temperature increases from historic to +4 °C, wheat production intensifies in the northwest and expands on the western SD boundary of the PPR. There is, however, spatial heterogeneity in predicted land use. Although wheat area increases in total across the climate scenarios, for example, wheat acreage decreases in eastern ND in the +2 °C scenario as corn and soybeans are able to shift northward. As noted previously, much of the reallocation of land involves a decrease in pasture area (Fig. 3). With the exception of a few northeastern ND counties in the +2 °C scenario, pasture area systematically decreases in all counties, with the highest percentage losses in the northwest.

The combined impact of climate and land-use change indicates that PPR wetlands will be less productive with a warming climate. CCI and hydroperiod are lower than historical in all climate scenarios. With historic climate conditions and land use, the majority of the region's wetlands in the agricultural matrix are relatively productive (CCI > 0.43) and have expected hydroperiods greater than or equal to the 80 days necessary to meet waterfowl requirements (Figs. 4, 5). As climate warms, the areas likely to contain productive wetlands migrate to the southeast. In the +4 °C scenario, our models project that essentially the entire PPR in ND will have much less productive wetlands than have been observed historically.

The indirect effects of land-use change generally exacerbate the effect of climate change on wetland process. CCI and hydroperiod are nearly always lower (i.e., less productive wetlands) when land-use change is taken into account. The indirect effects, however, are small relative to the direct effects. On average across the region, land-use change reduces CCI by 0.001–0.02 and hydroperiod by 0.5–2 across climate scenarios. In specific locations, however, the indirect effects of land-use change can be significant. In counties predicted to lose substantial pasture area, for example, ignoring land-use change underestimates climate change effects on wetlands by as much as 10 %.

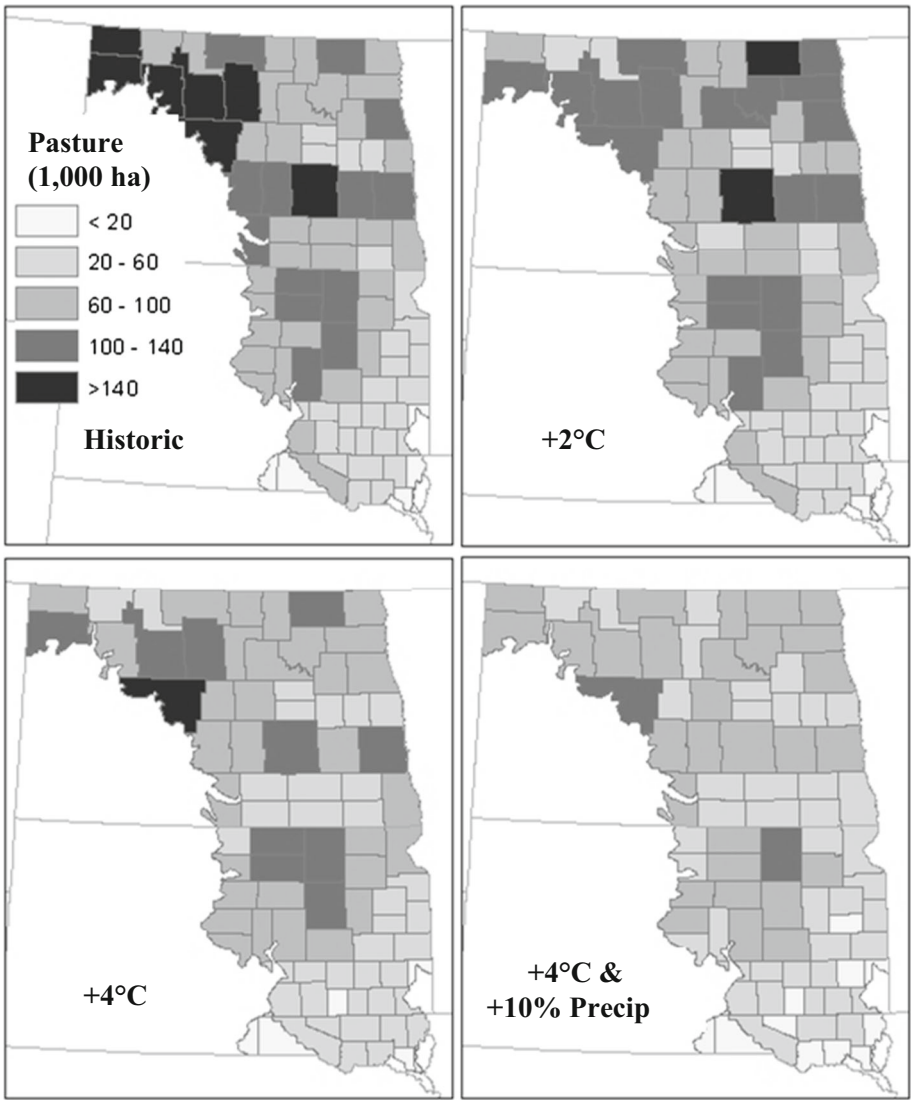

Fig. 3 Pasture area (1,000 ha) by county for four climate scenarios

Discussion

The warmer temperatures expected to prevail in the prairies of North America will affect the economic incentives facing private agricultural producers. Past research has generally concluded that yields for the primary crops currently grown in the northern prairies will likely decrease, with the largest effects on corn (see e.g., Adams et al. 1998; Hertel et al. 2010). Our land-use model used average temperature and precipitation to capture weather-related impacts on crop choice. Though our data set only covered a relatively short time period (1981–1997), our results are consistent with past literature. Parameter estimates on the weather variables (Appendix Table A2) indicate that corn and soybeans are more sensitive than wheat to increases in temperature. As a result, we predict a future PPR landscape with less crop heterogeneity and substantially more area planted to wheat.

If warmer temperatures are accompanied by increases in precipitation, the reallocation of land to wheat production is even more extreme. Despite increased precipitation, corn and soybean area decreases because of negative temperature effects. Wheat, with less temperature sensitivity, can take advantage of the increased moisture. As a result, we predict significant conversion on the extensive margin as it becomes relatively profitable for producers to grow wheat on historically less productive pastureland. Conversions on the extensive margin likely pose the greatest threat to wetland-dependent biodiversity, since wetlands surrounded by grassland (e.g., pasture) are historically the most productive for wildlife, especially breeding waterfowl (Klett et al. 1988).

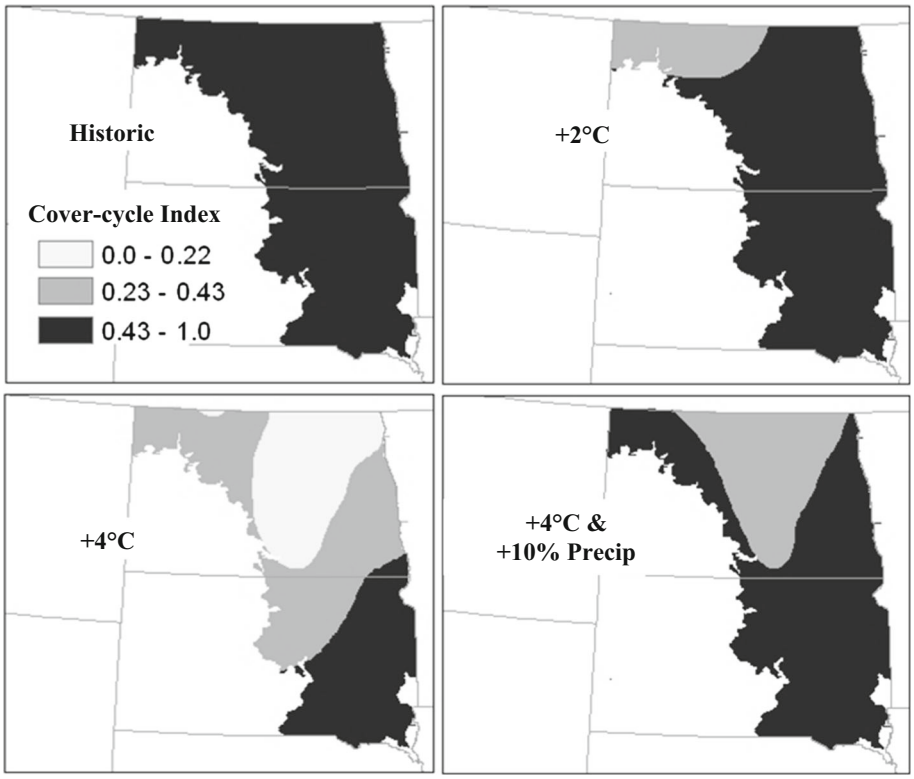

Fig. 4 Cover-cycle index given four climate scenarios (historical, +2, +4, and +4 °C with +10 % precipitation) and predicted land-use change for the prairie pothole region of North and South Dakota. Cover-cycle index is an index of wetland productivity related to the speed and frequency with which wetlands cycle through vegetation cover stage

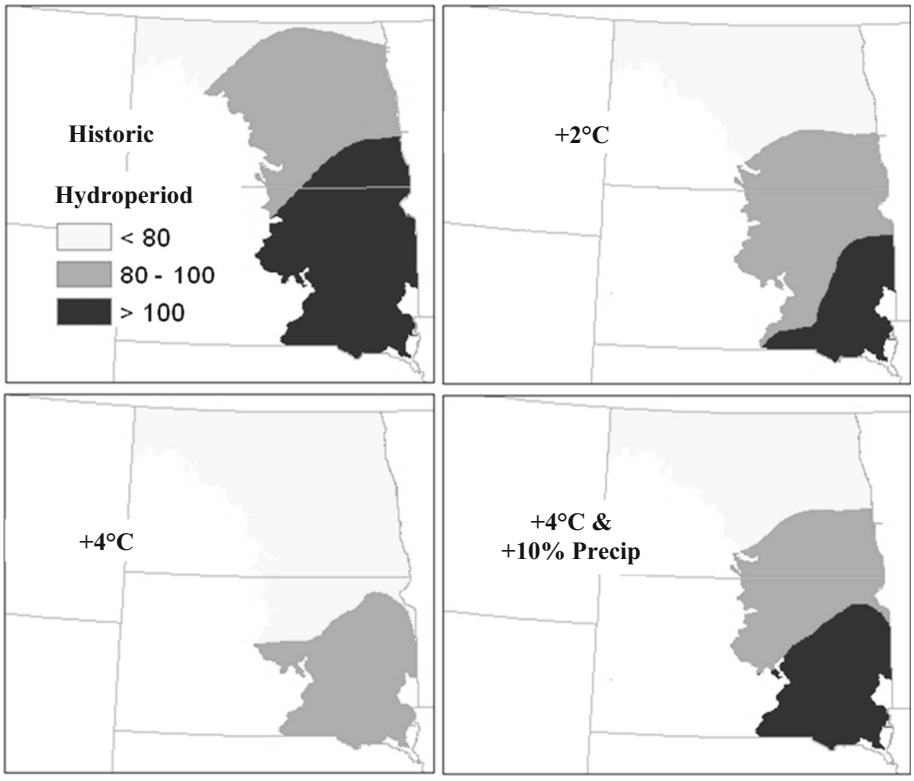

Fig. 5 Hydroperiod given four climate scenarios (historical, +2, +4, and +4 °C with +10 % precipitation) and predicted land-use change for the prairie pothole region of North and South Dakota. Hydroperiod is the average annual number of days a wetland is inundated

Previous work by Johnson et al. (2004, 2005, 2010) has concluded that climate change could have significant negative effects on prairie wetland productivity. These studies, however, primarily considered wetlands in unmanaged grassland. Thus, these estimates likely reflect climate impacts on the most pristine wetland complexes in the PPR. Many PPR wetlands are interspersed in the agricultural matrix and therefore are affected by upland agricultural land uses. Our model, though not directly comparable with previous analyses due to scale differences, accounts for the combined effect of climate and upland land-use change on semipermanent wetland productivity.

Given expansive crop production in the PPR, wetlands are generally less productive and more sensitive to climate change than if the wetland complex was dominated by grassland (Fig. 6). Both the cover-cycle index and hydroperiod are lower in every climate scenario when land-use response is properly accounted for. Wetland productivity also decreases with climate change by a greater magnitude when the landscape includes intensive crops. Hydroperiod in the +2 °C scenario given predicted land use, for example, decreases on average by seven additional days compared with a landscape dominated by pasture.

Although wetlands within cropland are generally less productive than those in sustainably grazed pasture, the difference is relatively small. With significant warming (i.e., +4 °C), semipermanent wetlands are relatively unproductive on average (CCI < 0.44; hydroperiod <80 days)

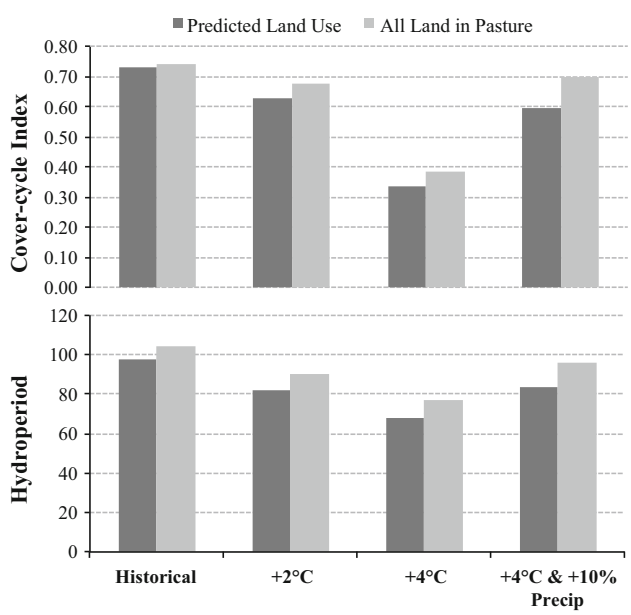

Fig. 6 Comparison of cover-cycle index (*top*) and hydroperiod (*bottom*) given four climate scenarios (historical, +2, +4, and +4 °C with +10 % precipitation) and two alternative land-use assumption: predicted land use given climate change, and all land in pasture

regardless of upland land use. What is the ecological significance of this? Recall that a 100-day hydroperiod is typically required for most dabbling ducks to fledge their offspring (Bellrose 1980) and for many amphibians to complete reproduction (Wagner 1997). Over time, an increase in the number of seasons when hydroperiod is less than these life cycle requirements could pose a serious threat to the sustainability of these populations. Additionally, conservation programs, such as the Cropland Retirement Program and Grassland Reserve Program, which have successfully increased waterfowl production in the PPR with regard to nesting habitat (Reynolds et al. 2001), may be insufficient to maintain the region's waterfowl productivity in a warmer climate. The availability of upland cover can only mitigate climate impacts on waterfowl if (or when) water is available—thus, the boom-and-bust cycle of waterfowl production in the PPR is likely to remain, or become more extreme, with or without conservation of upland cover.

Sorenson et al. (1998) used data on historic waterfowl populations and drought to estimate the potential impacts of climate change on waterfowl breeding populations in the PPR. Their model predicts population levels 30–70 % lower than historical averages with temperature increasing from 1.5 to 4 °C. Our predictions for lower wetland productivity support the prediction of lower waterfowl populations under the climate change scenarios evaluated here. Sorensen et al.'s estimates, however, may be conservative because they did not explicitly consider land-use change. Our prediction that significant pastureland could be converted to crops with climate change suggests that waterfowl production may be further limited by insufficient upland nesting cover. It is also possible that climate change will shift productive waterfowl breeding habitat further north. Research in the Canadian PPR, however, indicates that adequate breeding habitat is unlikely to exist even in the most northern extremes of the PPR (Johnson et al. 2010; Withey and van Kooten 2011).

Our model assumes that the relative returns to alternative uses remain approximately constant with climate change. Since climate change will affect global agricultural yields, the relative supply of agricultural commodities, and hence their relative prices, may change. Many studies suggest that yields in North America will change for the primary crops in the PPR; concurrently, commodity prices will change in response to changes in regional and global supplies (Adams et al. 1998; Hertel et al. 2010). It is thus unclear how the incentives faced by producers in the PPR will evolve under climate change—constant relative returns may be as likely as any other scenario. Nonetheless, if relative returns do change substantially with climate change, land use and wetland productivity outcomes could be different than our current model predicts. Additionally,

federal farm policy is currently shifting toward more crop insurance-based subsidies (ERS 2014), which will also have implications for the relative returns of alternative land uses. Moreover, federal policies to curb climate change, such as ethanol mandates or subsidies for terrestrial carbon sequestration, could also lead to different implications for land use and wetland productivity in the PPR, as evidenced by recent increases in corn acreage in the PPR.

Conclusions

The interaction between climate change and human-induced land-use change is likely to substantially reduce the productivity of prairie wetlands, including their ability to support wildlife. Our results suggest that climate change is likely to have profound effects on land use in the PPR. The combined pressure of land-use and climate change may, in turn, significantly reduce wetland productivity. In a climate scenario with a +4 °C increase in temperature, our model predicts that almost the entire region may lack the wetland productivity necessary to support historically prairie wetland-dependent species. More research is needed to determine how to strategically manage wetland complexes in a warmer climate to support targeted species, such as waterfowl. For example, our model in the PPR indicates wheat production will increase with climate change. Incentives for private landowners to plant winter wheat, which provides better waterfowl nesting habitat (Duebbert and Kantrud 1987), instead of spring wheat, may help mitigate climate impacts on waterfowl. The interaction between land-use and climate change, however, increases the uncertainty regarding where and when productive wetland complexes will be formed, which creates challenges for future wetland conservation efforts. Landscape-level conservation may therefore need to be spatially and temporally flexible in order to adapt to changing climate and land-use realities.

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