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Climate Change Impacts on Freshwater Wetland Hydrology and Vegetation Cover Cycling Along a Regional Aridity Gradient

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Abstract. Global mean temperature may increase up to 6°C by the end of this century and together with precipitation change may steepen regional aridity gradients. The hydrology, productivity, and ecosystem services from freshwater wetlands depend on their future water balance. We simulated the hydrology and vegetation dynamics of wetland complexes in the North American Prairie Pothole Region with the WETLANDSCAPE model. Simulations for 63 precipitation × temperature combinations spanning 6°C warming and −20% to +20% annual precipitation change at 19 locations along a mid-continental aridity gradient showed that aridity explained up to 99% of the variation in wetland stage and hydroperiod for all wetland permanence types, and in vegetation cycling for semipermanent wetlands. The magnitude and direction of hydrologic responses depended on whether climate changes increased or decreased water deficits. Warming to 6°C and 20% less precipitation increased wetland water deficits and more strongly decreased wetland stage and hydroperiod from historic levels at low aridity, especially in semipermanent wetlands, where peak vegetation cycling (Cover Cycle Index, CCI) also shifted to lower aridity. In contrast, 20% more precipitation decreased water deficits, increasing wetland stage and hydroperiod most strongly in shallow wetlands at high aridity, but filling semipermanent wetlands and reducing CCI at low aridity. All climate changes narrowed the range of aridity favorable to high productivity. Climate changes that reduce water deficits may help maintain wetlands at high aridity at the expense of those at low aridity, but with warming certain, increased deficits are more likely and will help maintain wetlands at lower aridity but exacerbate loss of wetlands at high aridity. Thus, there is likely not a universally applicable approach to mitigating climate change impacts on freshwater wetlands across regional aridity gradients. Conservation strategies need to account for aridity-specific effects of climate change on freshwater wetland ecosystems.

Key words: ecosystem models; ecosystem services; grasslands; Prairie Pothole Region; precipitation gradient; wetland complexes; wetland conservation; WETLANDSCAPE.

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Introduction

Continuing accumulation of CO_2 and other greenhouse gases in the atmosphere is predicted to increase global mean temperature up to 6°C by the end of this century (IPCC 2013). Future precipitation change is less certain, but contrasts in mean annual precipitation between wet and dry regions may increase, which may steepen regional gradients in precipitation, temperature and evaporative demand, and aridity (Bonan 2002, IPCC 2013). A steeper aridity gradient will increase differences across regions in ecosystem water balances and their responses to warming and precipitation change. Water balances in wetter locations may become increasingly coupled to future warming, while water balances in drier locations become increasingly coupled to precipitation change. Increased responses to warming or precipitation change may push ecosystem water balance past functional and structural thresholds, particularly at the extremes of regional aridity gradients.

Freshwater wetland ecosystems are widespread across the globe (Deil 2005), and several aspects of their hydrologic regime, including water holding capacity, depth, and duration of inundation, are tightly coupled to precipitation and temperature variability (Keddy et al. 2009), particularly in dry climates (Kundzewicz et al. 2007). Variation in wetland hydrology affects primary and secondary productivity, diversity of wetland flora and fauna, and ecosystem goods and services including retention and purification of water (Gleason et al. 2011), carbon sequestration (Bridgham et al. 2006), and secondary productivity. Thus, future regional biodiversity and ecosystem goods and services provision from wetlands hinge on the effects of future warming and precipitation change on their water balance and its variation along regional aridity gradients (Johnson et al. 2010).

The Prairie Pothole Region (PPR) in the northern North American Central Plains grasslands (Bridgham et al. 2006) supports five to eight million complexes of wetland basins (Johnson et al. 2010), but wetland loss rates exceed 5000 ha/yr in areas suitable for row crop agriculture (Johnston 2013, Wright and Wimberly 2013). The PPR spans an aridity gradient (Appendix S1: Fig. S1) formed by a west-to-east increase in mean annual precipitation and a north-to-south increase in mean annual temperature and potential evapotranspiration (PET; Appendix S1: Fig. S2). The PPR provides a useful model for the impacts of climate change on freshwater wetland complexes across regional aridity gradients. The climate of the PPR has warmed during the 20th century, and western locations have become drier and eastern stations wetter, suggesting a steepening of the already-strong aridity gradient (Johnson et al. 2005).

Projected warming for the U.S. portion of the PPR has been forecast by a variety of models. Under the mid/high IPCC emission scenario, mean temperature is forecast to increase 2.9°C by 2049 (1981–2000 baseline) using a statistical downscaling approach (CGCM; Canadian Center for Climate Modeling and Analysis, Third Generation Coupled Global Climate Model 3.1). Dynamic downscaling produced a 3.8°C temperature increase (WRFc; Weather Research and Forecasting Model; Steen et al. 2014). These projected levels of warming are consistent with those of the Coupled Model Intercomparison Project Phase 5 (CMIP5) ensemble model experiments using the Representative Concentration Pathways—RCP2.6 and RCP8.5 used by the IPCC 5th Assessment report. However, some scenarios exceeded a 6°C increase (Ojima and Lackett 2002, Romero-Lankao et al. 2014). Projected warming will increase evaporation rates (IPCC 2013) and may exceed thresholds beyond which wetlands across the PPR would cease to undergo the decadal cycles of vegetation cover change from dry marsh to submerged wetland that characterize diverse and productive wetland complexes (Johnson et al. 2016).

To evaluate how warming and precipitation change may interact to affect the hydrology of wetland complexes in the PPR, we conducted model experiments simulating their hydrology and vegetation dynamics under 63 combinations of precipitation and warming at 19 locations in the PPR. These combinations included up to 6°C warming, bracketing the warming projections for the PPR (Hayhoe et al. 2010, Stoner et al. 2013), and from 20% increased to 20% decreased precipitation amounts, representing changes in water deficit judged likely to expose the boundaries on wetland hydrology and function in the climatically variable PPR. The model simulated the hydrology of three wetland permanence types, temporary basins holding water for only 1 or 2 months; seasonal basins, which are larger, deeper, and hold water for 2–3 months; and semipermanent wetlands, the deepest and most dynamic type (van der Valk and Davis 1978). For semipermanent wetlands, the model also estimated an index of vegetation cover cycling associated with wetland function and productivity (Johnson et al. 2010). We hypothesized that with increasing aridity, precipitation change will cause larger responses in wetland hydrology than will warming and that the responses to precipitation change at more arid locations would be greatest in semipermanent wetlands, the most permanent type.

PPR Climate and Hydrology

Aridity gradient

The PPR spans historic (1906–2005) mean annual precipitation (MAP) and temperature (MAT) from nearly 800 mm and 8°C in the southeast to <400 mm and <2°C in the northwest (Appendix S1: Fig. S2A). Temperatures vary from 40°C in summer to −40°C in winter; multiyear droughts occurred in the 1930s, 1950s, and 1990s. The entire region is in precipitation deficit, with annual PET (Blaney and Criddle 1962) ranging from 800 mm in the northwest to 1100 mm in the southeast (Appendix S1: Fig. S2B). Nineteen locations across the PPR were chosen to represent the regional aridity gradient (Appendix S1: Table S1). These locations had 100 yr of historic weather records available and were used in previous modeling analyses (Johnson et al. 2010).

Wetland hydrology metrics

Three metrics describe the major aspects of the hydrology of these wetlands—stage, the mean depth of water; hydroperiod, the proportion of the ice-free season when surface water is present; and for semipermanent wetlands, the Cover Cycle Index (CCI). The CCI quantifies the rate of vegetation change in semipermanent wetlands as they cycle from dense emergent cover with little or no standing water in dry years to high water and little emergent vegetation in wet years (van der Valk and Davis 1978). The CCI combines the average of the proportion of time spent in the hemi-marsh state of the cover cycle and the number of cover cycles occurring over a 100-yr simulation and is strongly correlated with the primary and secondary productivity of semipermanent wetlands (Johnson et al. 2010).

Modeling approach

We simulated wetland hydrology with WETLANDSCAPE (WLS) (Johnson et al. 2010), a process-based, deterministic model tested and parameterized at two long-term study sites in the PPR. WLS simulates wetland surface water, groundwater, and vegetation dynamics of semipermanent, seasonal, and temporary permanence types and has been successfully applied across the PPR (Johnson et al. 2005, 2010).

Wetland hydrology and vegetation cycling were simulated at each of the 19 locations for temperature change in 1°C increments of warming from 0° to 6°C crossed with precipitation change in increments of 5% of annual precipitation amounts between −20% and +20%, for a total of 63 temperature × precipitation combinations. Precipitation change was adjusted on a percent rather than an absolute basis to create comparable changes in precipitation across sites with widely varying mean annual precipitation amounts. The combination of 0°C and 0% precipitation represented the historic climate. Each simulation yielded a 100-yr sequence of wetland depth, hydroperiod, and CCI at a 10-d time step for three parameterized replicate wetlands of each permanence type. Spillway depths and bathymetry of modeled wetland complexes were held constant across locations. Spillway depths averaged 0.56 m (temporary), 0.74 m (seasonal), and 1.4 m (semipermanent).

The warming and precipitation change scenarios were constructed using a stochastic weather generator, LARS-WG 5.5 (Semenov 2008). For each location, we calibrated the weather generator using the statistical properties of historic (1906–2005) daily precipitation and temperature data. The weather generator then applied the specified changes in temperature (1°–6°C) or precipitation amount (−20% to +20%) to adjust the temperature and precipitation distributions and generate 100-yr sequences of altered daily precipitation and temperature. We did not adjust for possible future changes in distributions and intensities of the climate variables.

Data analysis

At each of the 19 locations, stage, hydroperiod, and CCI were averaged across the three replicate wetlands of each permanence type over the 100-yr simulation runs. To quantify the magnitude and direction of warming and precipitation effects on hydrology and vegetation cover cycling, we calculated indices of warming and precipitation sensitivity for stage, hydroperiod, and CCI. Warming sensitivity of these metrics was calculated at each level of precipitation from their change per degree of warming, expressed as a ratio of their change at historic precipitation (0%). Similarly, precipitation sensitivity was calculated at each level of warming from their change with precipitation, expressed as a ratio with the change at historic temperature (0°C). Change was estimated from the slopes of exponential functions fit across the seven levels of warming and nine levels of precipitation amount. We focused on warming and precipitation sensitivities at the extremes of precipitation change (−20% and +20% precipitation) and precipitation sensitivity at maximum warming (6°C) to reveal potential boundary conditions on wetland hydrology and function under increased and decreased water deficits. The warming and precipitation sensitivities for the other levels of precipitation change and warming are shown in Appendix S1: Figs. S3–S5.

We evaluated linear or nonlinear change in wetland hydrology metrics and warming and precipitation sensitivity as functions of historic aridity and stage at each location. We chose historic aridity rather than aridity expected for each warming/precipitation combination to provide a standard frame of reference across the scenarios. Aridity was quantified with an index (Eq. 1) calculated from the ratio of MAP to PET, adjusted so that smaller values of the ratio indicate less precipitation deficit.

$$1 - (\mathrm{MAP}/\mathrm{PET}) \tag{1}$$

We fit linear, quadratic, Gaussian, and exponential functions, and the best fit equation was judged by examination of R^2 values and residuals.

Results

Hydrology in the historic climate

Wetland stage decreased exponentially with increasing aridity under the historic climate. At low-aridity locations, stage averaged >1.3 m in semipermanent wetlands, near their maximum depth, but reached only ~18 cm for temporary wetlands, well below their maximum (Fig. 1a, c). Stage decreased to <15 cm for all wetland permanence types in the driest locations ($R^2 > 0.87$, $P < 0.0001$, Fig. 1a–c; Appendix S1: Tables S2 and S3). Hydroperiod in semipermanent wetlands at low-aridity locations was 100%, indicating inundation for the entire ice-free period (Fig. 2c). Hydroperiod was < 100% at low-aridity locations in seasonal and temporary wetlands (Fig. 2a, b). Hydroperiod declined to 25% or less of the ice-free period for all permanence types at more arid locations ($R^2 > 0.88$, $P < 0.0001$, Fig. 2a–c; Appendix S1: Tables S2 and S3).

The historic precipitation sensitivities of stage and hydroperiod were always positive, denoting increased stage and hydroperiod with increased precipitation (Appendix S1: Fig. S3). Likewise, historic warming sensitivities were always negative, denoting reduced stage and hydroperiod with warming (Appendix S1: Fig. S4). Historic precipitation and warming sensitivities were greatest in intermediate levels of aridity for all permanence types.

The CCI for semipermanent wetlands under the historic climate peaked at intermediate levels of aridity ($R^2 = 0.53$, $P = 0.0009$, Fig. 3a), coincident with the historic peak climate sensitivities for stage and hydroperiod. Peak CCI exceeded 0.4, the threshold value indicating high rates of cover cycling. The historic precipitation sensitivity of CCI switched from negative to positive with increasing aridity (Appendix S1: Fig. S5a), indicating that higher precipitation reduced CCI at low-aridity locations and increased CCI at high-aridity locations. In contrast, warming sensitivity switched from positive to negative values with increasing aridity (Appendix S1: Fig. S5b), indicating that warming increased CCI at low-aridity locations while decreasing CCI at high-aridity locations.

Warming and precipitation change

The magnitude of stage and hydroperiod responses to warming and precipitation changes along the aridity gradient depended on their effect on water deficit. The aridity index explained 37–99% of the variation in warming and precipitation sensitivity of stage and hydroperiod (Figs. 4 and 5; Appendix S1: Table S3). Across permanence classes, warming to 6°C reduced stage and hydroperiod compared to historic levels across the aridity gradient (Figs. 1d–f and 2d–f), indicating increased water deficit. Decreases in stage and hydroperiod were greatest at low-aridity locations and corresponded with increases in the precipitation sensitivity of stage and hydroperiod in semipermanent (Figs. 4f and 5f) and to a lesser extent in seasonal and temporary wetlands (Figs. 4d, e and 5d, e).

The precipitation sensitivity of wetland stage at 6°C increased as stage approached maximum

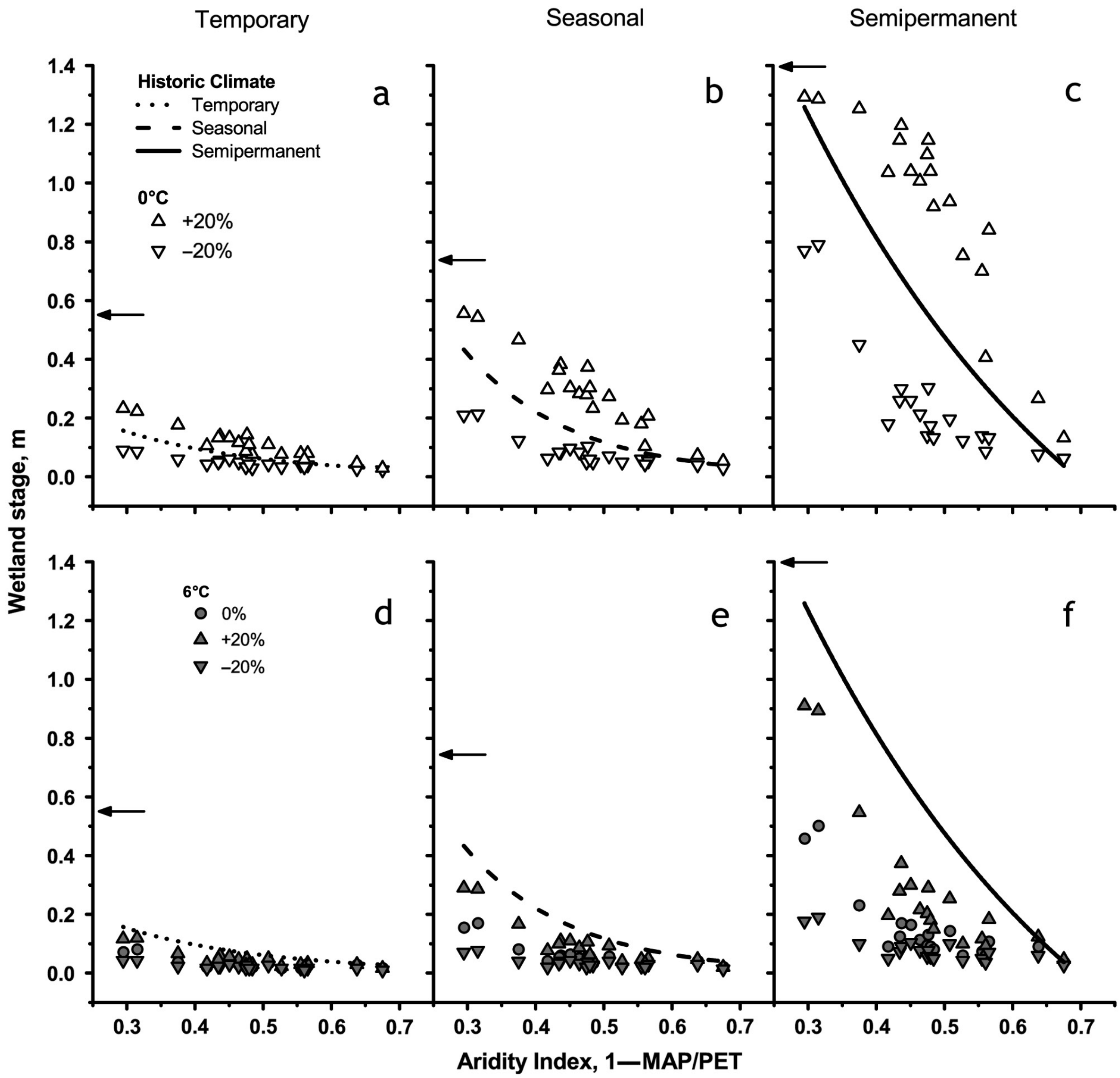

Fig. 1. Wetland mean stage (m) for the three wetland permanence types under maximum precipitation changes with no warming (a–c) and with 6°C warming (d–f) as a function of aridity index at 19 locations in the Prairie Pothole Region. Reference lines indicate mean stage under the historic climate. Arrows denote the maximum stage for each permanence type. For standard errors of the mean, see Appendix S1: Table S4.

levels (Fig. 6a). This was most evident in deeper semipermanent wetlands at low-aridity locations (Fig. 4f), because 6°C warming reduced stage below the maximum (Fig. 1f), allowing for more variation with precipitation change than when wetlands are full (Fig. 1c). The precipitation sensitivity of hydroperiod exhibited similar trends as the precipitation sensitivity of stage, increasing 60-fold in semipermanent wetlands at low aridity (Fig. 5f; Appendix S1: Fig. S3). With increasing aridity, the precipitation sensitivity of stage and hydroperiod decreased (R^2 0.62–0.99, $P < 0.0002$; Appendix S1: Table S3), falling below historic sensitivity at intermediate aridity locations (Figs. 4d–f and 5d–f), where low stages begin to limit further variation in stage with precipitation change (Fig. 6a).

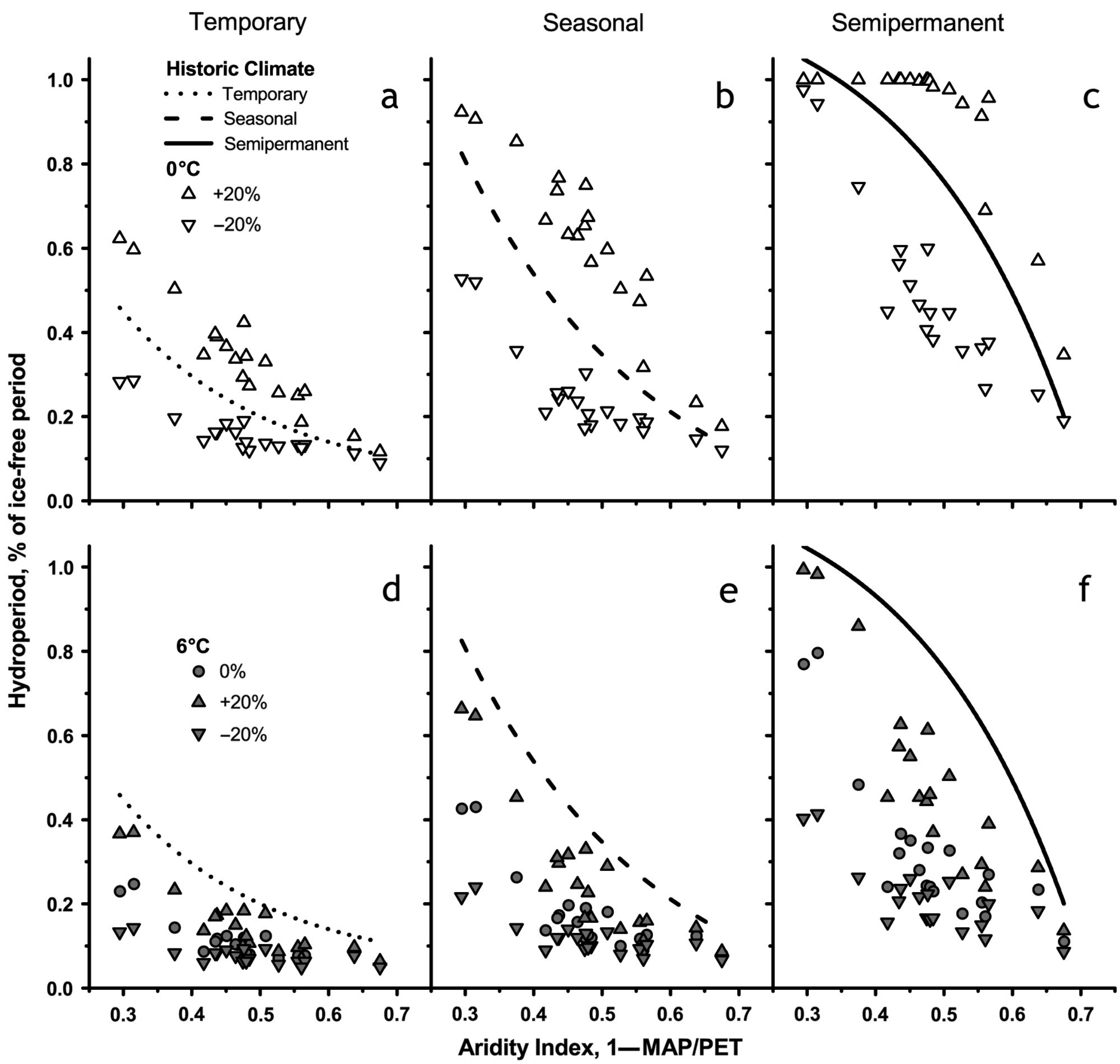

Fig. 2. Wetland hydroperiod (% of the ice-free period) for the three wetland permanence types under maximum precipitation changes with no warming (a–c) and with 6°C warming (d–f) as a function of aridity index at 19 locations in the Prairie Pothole Region. Reference lines indicate mean hydroperiod under the historic climate. For standard errors of the mean, see Appendix S1: Table S4.

The warming sensitivity of stage and hydroperiod varied with aridity in opposite ways depending on precipitation amount. With −20% precipitation, stage and hydroperiod decreased from historic levels (Figs. 1a–c and 2a–c) by a similar amount as with 6°C warming and no precipitation change (Figs. 1d–f and 2d–f), indicating a similar increase in water deficit. The relationship of stage and hydroperiod to aridity was concave up at −20% precipitation (Figs. 1b, c and 2b, c), indicating that decreases in stage and hydroperiod were greater at low aridity than at high aridity in semipermanent and to a lesser extent seasonal wetlands. Warming sensitivity fell below historic levels at intermediate aridity in all permanence types (R^2 0.54–0.91, $P < 0.0008$, Figs. 4a–c and 5a–c; Appendix S1: Table S3, Fig. S4), where stages were around 40% of maximum (Fig. 6b). Unexpectedly, warming sensitivity of stage in temporary wetlands was greatest at the most arid locations (Fig. 4a).

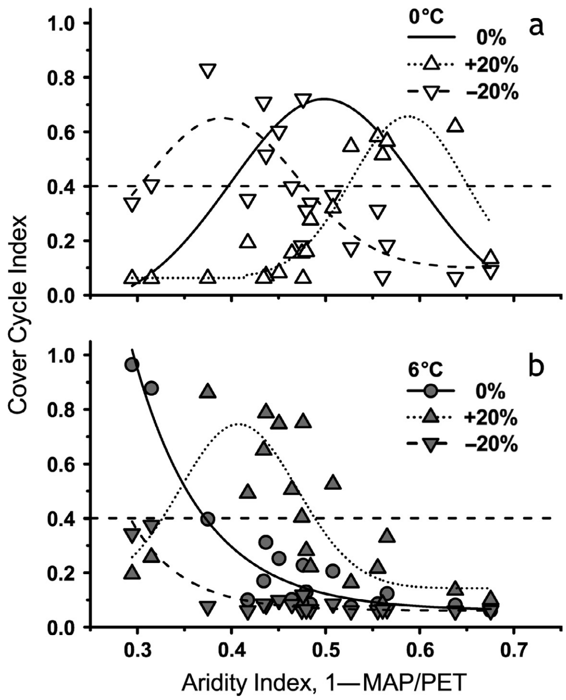

Fig. 3. Cover Cycle Index (CCI) of vegetation cover cycling in semipermanent wetlands at and −20, 0, and +20% precipitation at (a) historic temperature (0°C warming) and (b) with 6°C warming as a function of the aridity index at 19 locations in the Prairie Pothole Region. Dashed lines at CCI = 0.4 denote the threshold CCI value for high wetland productivity. Curve fits: R^2 0.54–0.93, $P < 0.0001$; Appendix S1: Table S2.

In contrast, with +20% precipitation, stage and hydroperiod increased and the relationship of warming sensitivity to aridity and wetland depth was reversed compared to the pattern at −20% precipitation. The relation of stage and hydroperiod to aridity shifted to concave down, indicating that stage and hydroperiod increased less at low aridity, especially in semipermanent wetlands as they neared maximum depth (Figs. 1c and 2c). This reduced the warming sensitivity at low aridity in seasonal and semipermanent wetlands (Figs. 4b, c and 5b, c). Warming sensitivity increased with greater aridity in seasonal and semipermanent wetlands (Figs. 4b, c and 5b, c; R^2 0.37–0.86, $P < 0.01$, Appendix S1: Table S3, Fig. S4b–f), indicating greater increases in stage in wetlands where responses were historically limited by low stage and short hydroperiod.

The aridity index explained 60–73% of the variation in the climate sensitivities of CCI ($P < 0.003$; Appendix S1: Table S3). Increased water deficit arising from 6°C warming and −20% precipitation shifted peak CCI to lower aridity locations than under the historic climate (Fig. 3; Appendix S1: Fig. S5). With +20% precipitation, reduced water deficit shifted peak CCI to high aridity at 0°C (Fig. 3a), but when combined with 6°C warming did not restore CCI to its historic peak (Fig. 3b). All combinations of warming and precipitation change narrowed the range of aridity index values in which CCI exceeded the 0.4 threshold for higher vegetation cycling. In all warming and precipitation change scenarios considered, 93% of the variation in CCI was predicted by stage (Fig. 7). Less extreme combinations of temperature and precipitation would also fall along this curve (data not shown). Thus, movements of peak CCI along the aridity axis with warming and precipitation change were almost entirely explained by changes in the depth of these wetlands.

Discussion

We predicted that wetland warming and precipitation sensitivity would increase at higher aridity with climate changes that decrease water deficits, while conversely, wetland warming and precipitation sensitivity would increase at lower aridity with climate changes that increase water deficits. The results from simulations of wetland hydrology and vegetation dynamics based on 63 combinations of temperature and precipitation levels were consistent with these predictions. They show that changes in the warming and precipitation sensitivity of wetland stage and hydroperiod along the PPR aridity gradient increased where climate changes increased the depth of historically dry wetlands or decreased the depth of historically deep wetlands. PPR wetland complexes are vulnerable to sizeable changes in productivity and distribution from climate change and have already been influenced by climate changes to date (Johnson et al. 2010, Werner et al. 2013). This study presents the first detailed analysis of the variation in precipitation and warming sensitivity as a function of aridity for the PPR. These results are important because they define boundary conditions on wetland responses to climate drivers associated

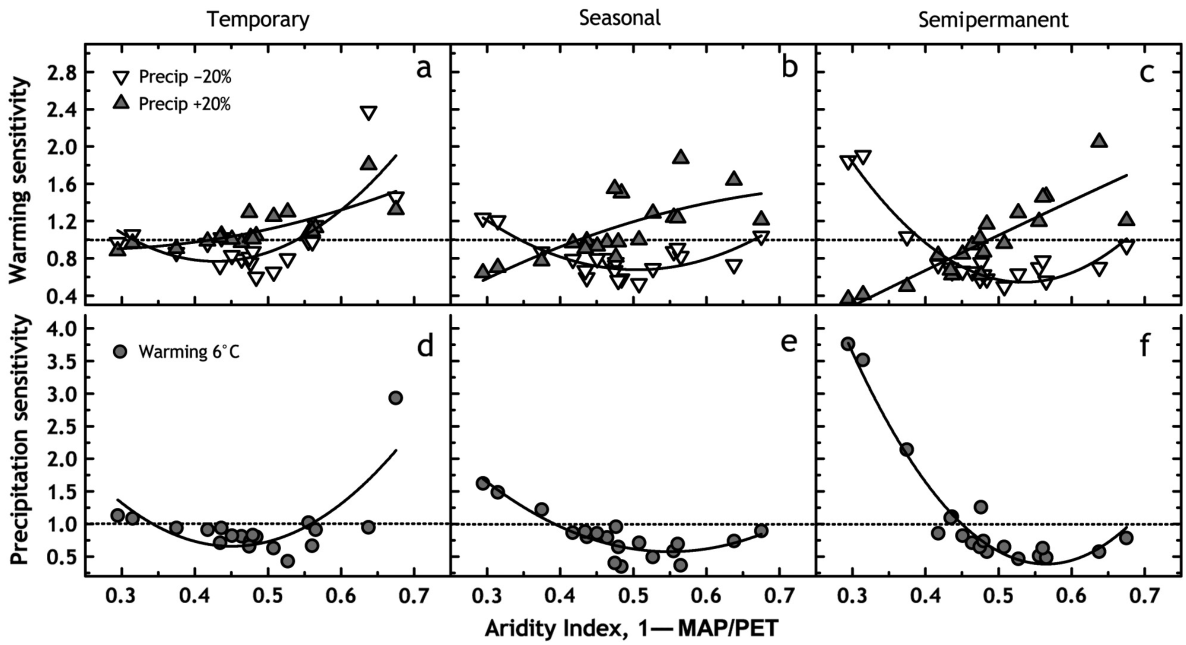

Fig. 4. Warming sensitivity (a–c) and precipitation sensitivity (d–f) of wetland stage in temporary, seasonal, and semipermanent wetlands as a function of historic aridity at 19 locations across the Prairie Pothole Region. Warming and precipitation sensitivities are expressed as a ratio of their historic (0°C, 0% precipitation) sensitivities, and 1.0 (dotted lines) represents no difference from historic sensitivities.

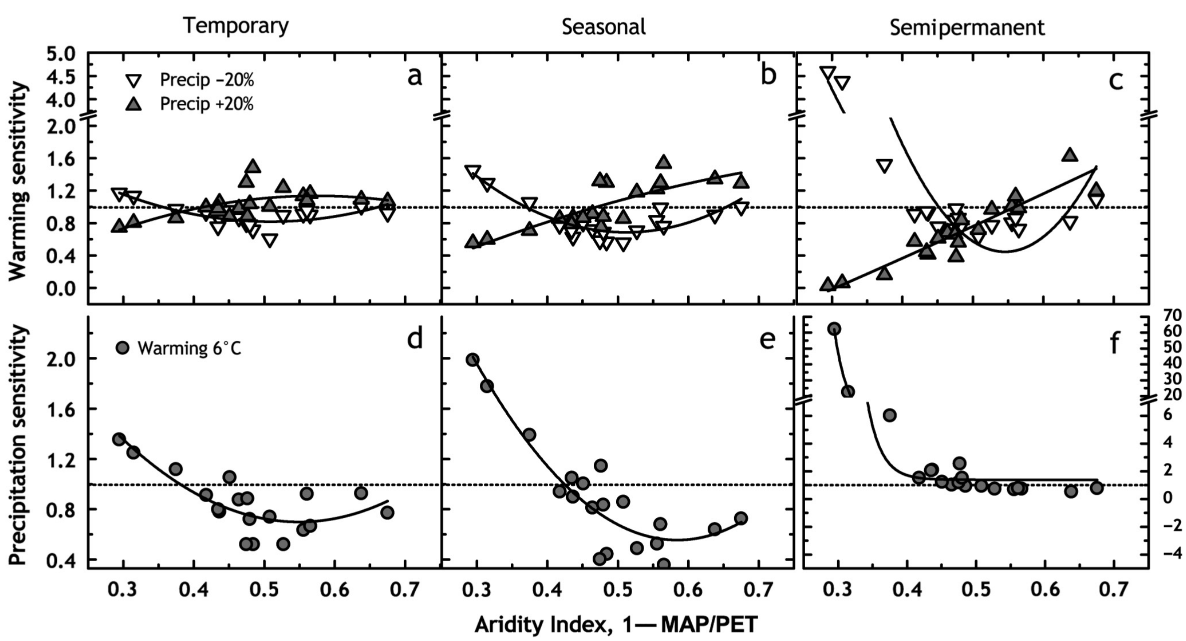

Fig. 5. Warming sensitivity (a–c) and precipitation sensitivity (d–f) of wetland hydroperiod in temporary, seasonal, and semipermanent wetlands as a function of historic aridity at 19 locations across the Prairie Pothole Region. Warming and precipitation sensitivities are expressed as a ratio of their historic (0°C, 0% precipitation) sensitivities, and 1.0 (dotted lines) represents no difference from historic sensitivities.

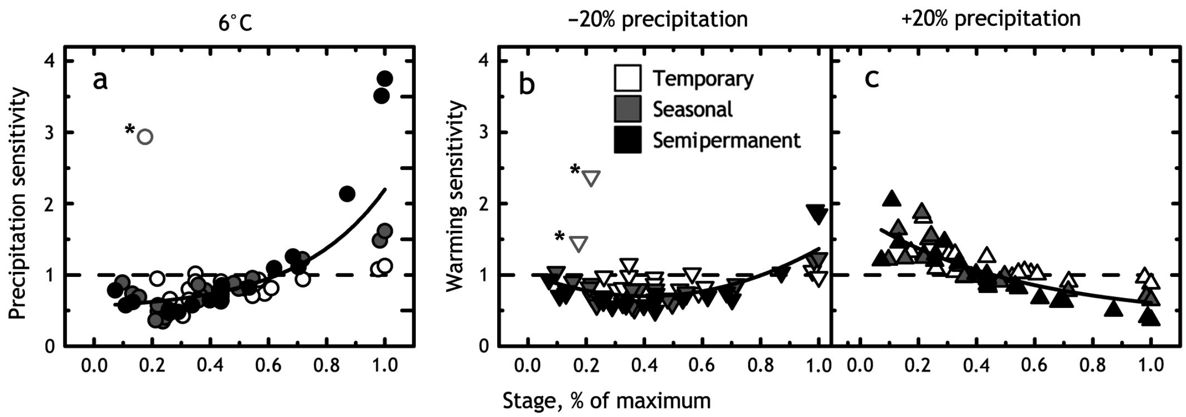

Fig. 6. Precipitation sensitivity (a) and warming sensitivity (b, c) as a function of stage in temporary, seasonal, and semipermanent wetlands in the Prairie Pothole Region of North America. Points marked by asterisks were omitted from curve fitting (Appendix S1: Table S2).

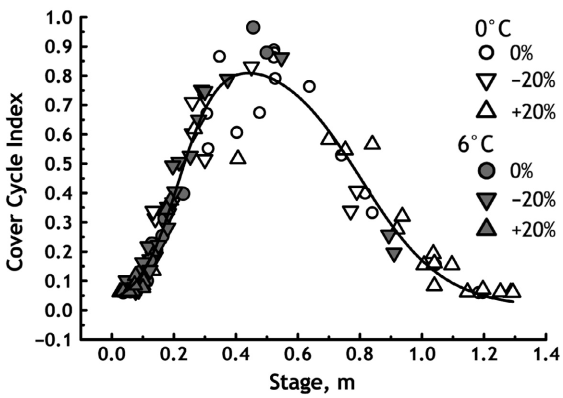

Fig. 7. Cover Cycle Index as a function of stage in semipermanent wetlands at 0° or 6°C and −20%, 0% or +20% precipitation change at 19 locations across the Prairie Pothole Region. Curve is a Gaussian fit across all temperature and precipitation levels (R^2 = 0.93, F = 662.9, P < 0.0001).

with wetland depth. Understanding these boundary conditions is crucial to predicting the structure and function of wetland complexes in future climates.

Warming to 6°C and 20% less precipitation each resulted in a steeper aridity gradient and the resulting increased evaporation increased wetland water deficits (Poiani et al. 1996). The reductions in depths and hydroperiods in wetlands at low-aridity locations were equivalent to a roughly 50% increase in aridity. This reduced wetland depth and hydroperiod to levels typical of less permanent wetlands under 20% more precipitation. The combination of 6°C warming and 20% less prediction caused even more drastic increases in water deficit and larger decreases in depth and hydroperiod, resulting in semipermanent wetlands becoming hydrologically seasonal, seasonal wetlands similarly becoming temporary, and temporary wetlands existing for <5% of the ice-free period across nearly the entire aridity gradient.

In contrast, 20% more precipitation resulted in a shallower aridity gradient and reduced water deficits, translating into increased depths and longer hydroperiods. With no warming, this raised temporary and seasonal wetland hydrology toward that of the next more permanent type. For semipermanent wetlands, this resulted in continuous inundation for the entire ice-free period across the majority of the aridity gradient and maximum stage values for wetlands at low-aridity locations. Critically, 6°C warming more than offset the effects of 20% more precipitation, and stage and hydroperiod was reduced below historic levels across the aridity gradient for all permanence types. Thus, under the 6°C warming expected by the end of the 21st century, precipitation would need to increase by more than 20% to maintain historic wetland depths and hydroperiods across the PPR aridity gradient, exceeding previous estimates (Poiani and Johnson 1993, Johnson et al. 2005).

Climate changes had the greatest impacts on wetland hydrology where they removed structural constraints on wetland depth. The clearest example was in semipermanent wetlands at low-aridity locations, which historically reached maximum stage and hydroperiod. With increased water deficit arising from 6°C warming and 20% less precipitation, stage and hydroperiod were reduced in these relatively deep wetlands, where both precipitation and warming sensitivity are high. However, the benefit of lowered stage and hydroperiod for low-aridity semipermanent wetland fell in a narrow range of aridity, especially with 6°C warming, and this beneficial aridity range is shifted toward locations that were historically less arid, where conversion to agricultural land uses reduces wetland area (Bartzen et al. 2010). Wetlands at locations with intermediate levels of aridity were historically the most productive (Johnson et al. 2005).

In contrast, the decreased water deficit resulting from 20% more precipitation increased wetland stage in the historically shallow and short-lived wetlands at high aridity. The greater depths buffered arid wetlands against increased temperatures and increased their precipitation sensitivity, resulting in increased vegetation cover cycling in arid semipermanent wetlands, suggesting their primary productivity will increase. However, the gains in arid wetlands from 20% more precipitation were offset by increased constraints on low-aridity semipermanent wetlands, which were inundated for the entire ice-free season over half the aridity gradient, reducing their warming sensitivity and cover cycling. The likely consequence is reduced productivity in the remaining wetlands at low aridity, exacerbating the negative effects of losses to agricultural land conversion (Bartzen et al. 2010).

The differential changes in the hydrology and productivity among wetland permanence types along the PPR aridity gradient have important functional consequences for wetland complexes. Climate changes that increase water deficit would likely increase the productivity of semipermanent wetlands at low aridity, because their greater warming and precipitation sensitivity would result in increased vegetation cover cycling. Concurrently, lower depths and hydroperiod may reduce the total area of wetland complexes at low aridity, while also amplifying the existing loss of wetland area at high aridity in the PPR (Werner et al. 2013). Reduced water deficit will likely reverse these effects, increasing wetland area and productivity at high aridity, while reducing the productivity of semipermanent wetlands at low aridity. Whether water deficit increases or decreases, the aridity range supporting high wetland productivity becomes narrower.

Shifts in the hydrology, structure, and vegetation dynamics among permanence types have important consequences for organisms in wetland complexes. Landscapes under the influence of a semiarid climate, dominated by abundant, heterogeneous wetland types, set the stage for dynamic wetland complexes that are biologically diverse and highly productive. The multiyear cycling of wetlands from drawdown to prolonged flooding will drive major shifts in wetland, influencing biodiversity in these wetland complexes. Wetlands in the PPR of North America provide critical habitat for migratory waterfowl (Walker et al. 2013), shorebirds (Skagen et al. 2008), and amphibians (Lehtinen et al. 1999). Changes affecting temporary wetlands will alter habitat availability for animals with short life cycles such as aquatic invertebrates, a key food source for higher trophic levels. Similarly, changes affecting seasonal wetlands will alter habitat for marsh vegetation and amphibians, for which seasonal wetlands provide a sufficiently long hydroperiod to successfully reproduce. Changes affecting semipermanent wetlands will impact organisms requiring longer periods of inundation and cycling between lake and marsh states, including marsh vegetation and aquatic vegetation, which in turn provide nesting habitat for waterfowl (Johnson et al. 2010).

Changes in water deficit will likely affect the ability of wetland-dependent species to disperse between patches of suitable habitat (McIntyre et al. 2014). The presence of all permanence types in wetland complexes provides critical habitat connectivity needed by low mobility organisms like amphibians and brings together lower trophic levels needed to support higher-order consumers such as waterfowl. The narrowing of favorable aridity zones and losses of wetland area at the extremes will mean fewer wetland complexes containing all permanence types, smaller refugia, and less critical habitat for wetland-dependent species during unfavorable times.

The combination of temperature and precipitation change representing the threshold for functional change in these wetlands depends in part on the timing of precipitation change. Precipitation change during spring has greater effects on wetland hydrology than change during summer, fall, or applied uniformly during the year (Poiani et al. 1995), as we did here. Thus, our estimates of the precipitation sensitivity of wetland hydrology are conservative and would be higher if precipitation change is concentrated in spring. This also means that wetlands will become increasingly sensitive to intra-annual variability in precipitation in future warmer climates.

Conclusions

The response of wetland complexes to climate changes depends on their climatic setting. Predictions about how wetlands will respond must take into account background levels of water deficit. Our simulation experiments demonstrated that when water deficits increased, benefits accrued to wetlands at low aridity, and when water deficits decreased, they accrued to wetlands at high aridity, although the favorable ranges of aridity narrowed for all wetland permanence types. Conservation strategies to mitigate potential deleterious effects of climate change on freshwater wetland ecosystems need to account for variation in wetland response along regional aridity gradients. Wetlands in one part of an aridity gradient respond differently than wetlands in other parts, so a "one size fits all" conservation approach will have limited regional benefit.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1504/supinfo