12-2016

Interannual Water-level Fluctuations and the Vegetation of Prairie Potholes: Potential Impacts of Climate Change

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Keywords

Climate change, Harmonic hydrologicalmodels, Plant communities, Prairie pothole region, Wet–dry cycle, Wetlands

Disciplines

Climate | Ecology and Evolutionary Biology | Hydrology | Plant Sciences | Statistical Models

Comments

This article is published as van der Valk, Arnold, and David M. Mushet. "Interannual water-level fluctuations and the vegetation of prairie potholes: Potential impacts of climate change." *Wetlands* 36 (2016): 397-406. doi: 10.1007/s13157-016-0850-8.

Wetlands (2016) 36 (Suppl 2):S397–S406
DOI 10.1007/s13157-016-0850-8

ORIGINAL RESEARCH

Interannual Water-level Fluctuations and the Vegetation of Prairie Potholes: Potential Impacts of Climate Change

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Received: 15 January 2016 / Accepted: 1 November 2016 / Published online: 14 November 2016

Abstract Mean water depth and range of interannual water-level fluctuations over wet-dry cycles in precipitation are major drivers of vegetation zone formation in North American prairie potholes. We used harmonic hydrological models, which require only mean interannual water depth and amplitude of water-level fluctuations over a wet–dry cycle, to examine how the vegetation zones in a pothole would respond to small changes in water depth and/or amplitude of water-level fluctuations. Field data from wetlands in Saskatchewan, North Dakota, and South Dakota were used to parameterize harmonic models for four pothole classes. Six scenarios in which small negative or positive changes in either mean water depth, amplitude of interannual fluctuations, or both, were modeled to predict if they would affect the number of zones in each wetland class. The results indicated that, in some cases, even small changes in mean water depth when coupled with a small change in amplitude of water-level fluctuations can shift a prairie pothole wetland from one class to another. Our results suggest that climate change could alter the relative proportion of different wetland classes in the prairie pothole region.

Keywords Climate change · Harmonic hydrological models · Plant communities · Prairie pothole region · Wet–dry cycle · Wetlands

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Introduction

Although pioneering wetland ecologists recognized a variety of environmental factors (soil characteristics, wave action, turbidity, etc.) that could affect wetland plant distributions, they stressed the overriding importance of water depth (see the classic paper of Spence (1967)). Paul Keddy and coworkers (Keddy and Reznicek 1986; Hill et al. 1998; Keddy and Fraser 2000) were among the earliest wetland ecologists to recognize that, in addition to water depth, range of interannual water-level fluctuations was also a major driver of species diversity and the formation of vegetation zones in a wetland (van der Valk et al. 2015). Keddy's studies and models of shoreline vegetation of lakes and rivers showed that as the range of water-level fluctuations increased species richness increased until "hypervariable" fluctuations occurred. Hypervariable fluctuations are water-level fluctuations so large that they exceeded the tolerances of wetland species (Hill et al. 1998). Less than hypervariable fluctuations allowed a variety of wetland species (submersed aquatics, floating-leaved species, emergents, wet-meadow species, etc.) that dominate different kinds of wetland communities to find suitable habitats (hydrologic regimes) and form vegetation zones within a wetland. Conversely, as the range of interannual water-level fluctuations decreases, e.g., due to water-level regulation, some kinds of wetland species no longer find suitable habitats, and the number of vegetation zones a wetland supports diminishes. See also Riis and Dawes (2002) who investigated the relationships between wetland species diversity and short-term water-level fluctuations in New Zealand lakes.

Stewart and Kantrud (1971) developed a classification system for ponds and lakes (i.e., prairie pothole wetlands) of the glaciated prairie region of North America. Their system identified seven classes named Class I–VII, with each being defined by the occurrence of a specific vegetation zone in the deepest part of a wetland. Class I ponds consist of a single low-prairie zone throughout the basin and are no longer considered to be wetlands due to a lack of hydric soils. Class II ponds have a wet-meadow zone in their deepest point and are often termed "temporary wetlands." Likewise, Class III and Class IV ponds have shallow-marsh and deep-marsh vegetation zones in their deepest parts and are often termed seasonal and semi-permanent wetlands, respectively. Class V ponds and lakes have a permanent open-water zone as their deepest zone. Lastly, classes VI and VII are unique classes that represent alkali ponds/lakes and fens, respectively. The Stewart and Kantrud system has been widely used throughout the prairie pothole region and is the system we adopt here. However, since the temporary wetland, seasonal wetland, etc., nomenclature can be somewhat misleading, we refer to pothole wetland classes here by their specific class designations, i.e., Class II–V (Table 1). (See van der Kamp et al. (2016) in this issue for more information on the demarcation of various kinds of potholes).

Since the work of Stewart and Kantrud (1971) on the classification of prairie potholes (Table 1), it has been recognized that the number of vegetation zones in prairie pothole wetlands is a function of the maximum realized water depth in a pothole during wet years. Stewart and Kantrud (1971) also recognized that water levels fluctuated significantly from year to year in a given pothole depending on total annual precipitation. During droughts, ponded water in all but the deepest pothole wetlands typically went dry. During periods with above normal rainfall, water depths reached their maxima, and these high water levels can drown out some vegetation (zones) normally found in shallow water. Changes in the vegetation structure (zonation) in prairie pothole wetlands caused by interannual changes in annual precipitation are called vegetation cover cycles. Interannual periods of alternating below normal and above normal annual precipitation are called wet–dry cycles. Wet–dry cycles can equally well be called dry–wet cycles. Their start and end can be either a year with the lowest annual precipitation and end in the year prior to the next year with the lowest annual precipitation in a series or with a year with the highest annual precipitation and end in the year prior the next year with the highest annual precipitation in a series. In either case, the significant range in annual precipitation over a cycle is due to some years of below normal precipitation (drought years) and some years of above normal precipitation ("deluge" years, see Winter and Rosenberry (1998)) during the cycle. Variation in annual precipitation during a cycle alters water depths in pothole wetlands, and these changes in water depths cause vegetation cover cycles. Vegetation cover cycles in deeper wetlands (Class IV and V) can have a number of stages or phases. Stewart and Kantrud (1971) recognized four phases in Class IV potholes: drawdown bare-soil, drawdown emergent, normal emergent, and open-water. Weller and Spatcher (1965) divided the vegetation cover cycle into five stages: dry marsh, dense marsh, hemi-marsh, open marsh, and open water. Later, van der Valk and Davis (1978) reduced the vegetation cycle to four stages: dry marsh, regenerating marsh, degenerating marsh, and open water.

How vegetation cover cycles could be affected by climate change has been examined by linking changes in precipitation during wet–dry cycles that result in mean annual ponded-water depth changes and then examining the predicted impacts of these hydrologic changes on the vegetation cover cycle. Information about the highly variable climate of the prairie pothole region and how it might be altered by climate change can be found in Johnson et al. (2005, 2010, 2015) and Millett et al. (2009). In their 2005 paper, Johnson et al. used a computer simulation of wetland P1 at the USGS Cottonwood Lake site in North Dakota to examine how changes in water level affected the vegetation in this Class IV pothole wetland (Winter 2003). Their vegetation simulation model, WETSIM was based on a vegetation cover-cycle model originally developed by Karen Poiani (Poiani and Johnson 1991, 1993; Poiani et al. 1996; Johnson and Poiani 2016). Later Johnson et al. (2010) simulated changes in the vegetation cycles of Class II, Class III and Class IV wetlands at the Orchid Meadows site in South Dakota (Johnson et al. 2010). In this later model, precipitation and temperature are linked to a basin hydrology model that is in turn linked to a vegetation cycle model. See Johnson and Poiani (2016) for a detailed account of the development of these models.

In these models, a series of empirically derived rules are used to link water depths to the cover cycle. For example, a Class IV wetland will switch from the hemi-marsh stage (about 50:50 emergent vegetation and open water) to the lake stage (mostly open water) if water depths become greater than 0.75 m for more than 2 years; and, if in the lake stage, it will

Table 1 Vegetation zones found in different classes of prairie pothole wetlands in the glaciated plains of North America according to Stewart and Kantrud (1971)

Wetland class	Wet meadow	Shallow marsh	Deep marsh	Open water
II—temporary pond	X			
III—seasonal pond	X	X		
IV—semi-permanent pond	X	X	X	
V—permanent pond/lake	X	X	X	X

For a list of plant species associated with each zone, see Stewart and Kantrud (1971) switch to the hemi-marsh stage if water levels drop to 0.50 m or less during the summer (Johnson et al. 2010). That changes in water depth over wet–dry cycles drive changes in the vegetation cover cycle of prairie wetlands has been recorded in many field studies (Weller and Spatcher 1965; Millar 1973; van der Valk and Davis 1978; Shay and Shay 1986; Euliss and Mushet 1996; Winter 2003) and demonstrated experimentally in a study in the Delta Marsh, Manitoba, Canada, in which water levels were manipulated over 10 years to drive a vegetation cover cycle (van der Valk et al. 1994; Murkin et al. 2000).

As noted, the potential impact of climate changes on vegetation cover cycles in prairie potholes has been investigated by Johnson et al. (2005, 2010). Their models suggested that predicted changes in rainfall and temperature could alter the hydrology of prairie potholes enough to change the rate of vegetation cover cycles and that in Class IV wetlands cover cycles might remain longer in either the lake stage (little or no emergent vegetation) or dry stage (no standing water). Johnson et al. (2005, 2010) do not explicitly address whether a wetland could permanently change its class, e.g., change from a Class IV to a Class III or V wetland, due to climate change, but only the characteristics of its cover cycle.

In this paper, we investigate a different approach to evaluating the potential impacts of climate change on prairie wetlands. Each class of prairie potholes has a characteristic mean water depth and range of water-level fluctuations over a wet–dry cycle. Any significant changes in either of these hydrological parameters in a pothole could have an impact on either its vegetation cycles or its vegetation structure (zonation). Our objective is to examine how sensitive each class of potholes is to climate change due to small changes in mean water depth and/or range of water-level fluctuations. Our overall approach involves three steps:

(1) to determine from field studies the mean water depths and ranges of interannual water-level fluctuations of the four most common classes of prairie potholes (Class II, Class III, Class IV, and Class V) recognized by Stewart and Kantrud (1971): it has not been established previously what the defining mean depths and ranges of water-level fluctuations are for these four classes;
(2) use data on interannual mean water depths and ranges of water levels to calibrate harmonic models of each class and use these models to examine how much a small increase or decrease in mean water depth and/or the range of water levels impact a pothole's vegetation cycles or structure; and
(3) examine the actual vegetation cover cycles and structure of a number of prairie potholes over two very different wet–dry cycles at the Cottonwood Lake site (Winter 2003) in North Dakota to determine if the responses of these wetlands to changes in mean interannual water depths and ranges of water-level fluctuations are consistent with the predictions of our harmonic models.

Specifically, we begin with a review of what is known about mean water depths and ranges of water-level fluctuations in prairie potholes. This is followed by a brief description of harmonic models and their previous use in assessing potential impacts of climate change on wetlands. We then use the mean water depth and ranges derived from the available field data to parameterize harmonic models for all four classes of prairie potholes and examine the sensitivity of each class to small increases and decreases in mean interannual depth and/or range of water-level fluctuations. Finally we use the data from Cottonwood to examine if the potholes at that site behaved as predicted by the harmonic models over two wet-dry cycles. This is followed by a discussion of our findings.

Hydrology of Different Classes of Prairie Potholes

Stewart and Kantrud (1971) did not define the various classes of prairie potholes by their maximum or mean water depth or range of water-level fluctuations over wet–dry cycles, but delimited them only by the type of vegetation found in the deepest part of the basin (Table 1). They did, however, compare their vegetation types with those previously recognized in an earlier national American wetland classification system developed by Martin et al. (1953), which used depth of water during the growing season to define freshwater wetland types. The "shallow fresh-water marsh" of Martin et al. (1953) is equivalent to the shallow-marsh zone in Stewart and Kantrud (1971), which dominates the deepest portions of Class III wetlands. According to Martin et al. (1953), shallow-marsh vegetation is flooded to a depth of up to about 0.15 m (6 in. during part of the growing season. By extension, the deep-marsh zone of Stewart and Kantrud (1971) corresponds most closely to the deep, fresh marshes of Martin et al. (1953), which are defined as being flooded from 0.15 m (6 in. to around 0.90 m (3 ft) during the growing season. Martin et al. (1953) do not set a minimum depth or range for open, fresh water, which corresponds most closely to the permanent open-water zone in Stewart and Kantrud (1971). However, Martin et al. (1953) did set a maximum water depth of about 1.80 m (6 ft) for this wetland type. Since open-water areas in potholes are in deeper parts of their basins than deep-marsh zones, maximum water depths must be deeper than in the deep-marsh zones, i.e., more than 0.90 m. In summary, what we can glean from Stewart and Kantrud (1971) and Martin et al. (1953) is that wet meadows have either saturated soils or shallow, seasonal standing water; shallow marshes are flooded during the growing season perhaps up to about 0.15 m or more; deep marshes are flooded during the growing season from 0.15 to 0.90 m, and open-water zones can have water depths of 0.90–1.80 m. Martin et al. (1953), however, did not take into account changes in water depths during wet–dry cycles or even seasonally. Stewart and Kantrud (1971) did recognize these and set the lower limit for water levels during drought years in wet meadows, shallow marshes, and deep marshes at 0 during drought years and greater than 0 for permanent open-water zones.

Studies of water-level fluctuations in Saskatchewan potholes at the St. Denis National Wildlife Area and other sites (Millar 1973; Conly and van der Kamp 2001; van der Kamp and Hayashi 1998, 2008) indicate that interannual water-level fluctuations in a Class III wetland (S109 at St. Denis) were about 1 m and in a Class V wetland (S50 at St. Denis) were about 2 m. Price (1993) provides 10 years of water-depth data on a larger sample of potholes in Saskatchewan that are similar in range to those reported by Conly and van der Kamp (2001) and van der Kamp and Hayashi (1998, 2008). Unfortunately, Price does not provide any data on their vegetation. However, Price (1993) does provide typical hydrographs for selected potholes (sloughs) representing different water regimes and provides information on their mean depth and the percent of the time that these potholes were dry during the study. His data indicate a Class II wetland (Fort Qu'Appelle G19) had a mean depth of only 0.06 m and an interannual range of water levels of 0.4 m. It was dry more than 50 % of the years. The representative Class III wetland (Wilkie G6) had a mean depth of 0.1 m and a range of water levels of 0.6 m. It was dry between 26 and 50 % of the time. The Class IV wetland (Saskatoon G12) had a mean depth of 0.3 m and an interannual range of water levels of 0.9 m. It was dry between 1 and 25 % of the time. Price (1993) included two Class V wetlands (Melford G1 and Wilkie G9) that varied in the magnitude of their interannual water-level ranges. Melford G1 had a mean depth of 0.7 m and an interannual range of water levels of 1 m. It never went dry during the study period. Wilkie G9 had a mean depth of 1.2 m and interannual water-level fluctuation was 3.2 m. During most of the study period the water level in Wilkie G9 was increasing. The major source of water for all these wetlands was snowmelt.

Johnson et al. (2004) provide detailed data on the surface and groundwater hydrology of wetlands during a 3-year drought period (1987–1989) and an unusually wet period (1993–1995) at the Orchid Meadows site in Deuel County, South Dakota. Annual and interannual surface water hydrographs for selected Class II, Class III and Class IV wetlands are provided in Figs. 6–9 of their publication. The interannual ranges of surface water-level fluctuation in these three types of wetlands were estimated to be 0.25–0.30 m, 0.50–0.55 m, and ca. 1.00 m for Class II, Class III and Class IV wetlands, respectively. These interannual ranges are similar to those reported by Price (1993) and Conly and van der Kamp (2001).

A site at which both water levels and vegetation have been monitored for many years is the Cottonwood Lake Area in North Dakota (Winter 2003). Long-term data on the water levels and the vegetation of 16 potholes spanning two wet–dry cycles (1988–2001 and 2002–2012; Mushet unpublished data) are available from this site. (Data for the Cottonwood Lake Area site are available on the Missouri Coteau Wetland Ecosystem Observatory website.) We used data from this site to examine their mean water depths and the ranges of interannual water-level fluctuations and to relate these to the vegetation found in them. The wet–dry cycles that we delimited are based on rainfall patterns at Jamestown, ND (Fig. 1). These cycles begin with the onset of a year with lowest annual precipitation and run till the year prior to next year with the lowest annual precipitation in the series. These 16 wetlands at Cottonwood Lake were originally classified into two classes, Class IV (P1, P2, P3, P4, P6, P7, P8, P11) and Class III (T1, T2, T3, T4, T6, T7, T8, T9) potholes. Unfortunately, no Class II wetlands were monitored at this site. During high water periods, however, some of these wetlands overflowed and became connected, e.g., T1 and T3 with P1, and P2 with P4 (Winter 2003). The 2002–2012 wet–dry cycle was not as extreme in terms of water-level fluctuations as the 1988–2001 cycle or a previous (1979–1987) cycle. In fact, it is possible that the 2002–2012 cycle was not yet over. It is only possible to delimit definitively wet-dry cycles *post hoc*. Because of the limitations of the Cottonwood Lake vegetation data set, only the most recent two cycles could be considered. During the 1979–1987 cycle, the mean range of water-level fluctuations in the potholes was 0.76 m. During the 1988–2001 cycle, it was 1.85 m. During the 2002–2012 cycles, it was 1.02 m. Thus the 2002–2012 cycle could be characterized as "normal" while the previous two cycles as drier and wetter than normal, respectively. This is consistent with the rainfall pattern at Jamestown (Fig. 1). From 1976 to 1987, mean annual rainfall was 5 % lower than during the 2002–2012 wet–dry cycle while during the 1988–2001 cycle it was about 10 % higher. Overall, the mean range of water-level fluctuations was 1.21 m.

On the basis of the available field data, it is possible to estimate the mean water depth of an ideal or typical Class II (temporary), Class III (seasonal), Class IV (semi-permanent), and Class V (permanent) prairie pothole (Table 2) from the data in Price (1993), Conly and van der Kamp (2001), Johnson et al. (2004), and the data from Cottonwood Lake area wetlands. Although these sites have different climates (rainfall, temperature, evapotranspiration, etc.), it is the annual maximum water depth and interannual mean water depth of a pothole that determines its class. Consequently, regardless of location the mean interannual water depth and range of water-level fluctuations over a wet–dry cycle of each class are assumed to be the same over the entire prairie pothole region.

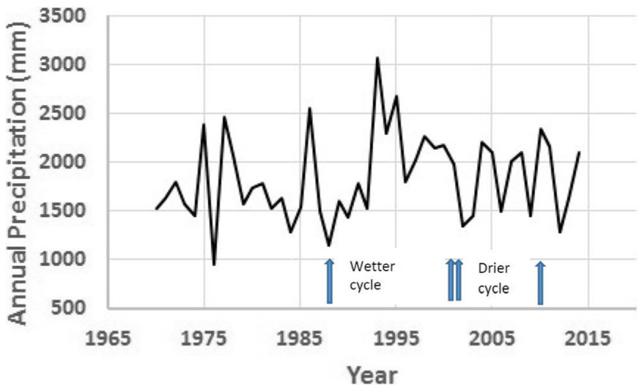

Fig. 1 Annual precipitation at the Jamestown Municipal Airport, North Dakota, from 1965 to 2014. Changes in hydrology and vegetation structure during two wet-dry cycles were examined at Cottonwood Lake: 1988–2001 (wetter than normal) and 2002–2012 (drier than normal)

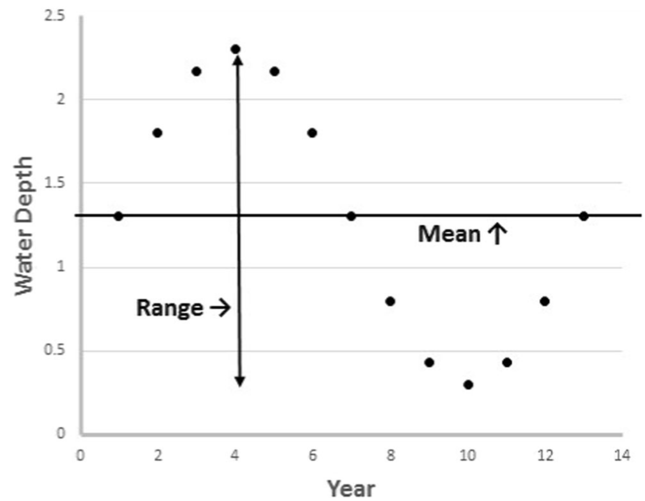

Fig. 2 Interannual water-level fluctuations can be modeled using a sine curve (water depth = (mean interannual water depth + amplitude of interannual water-level fluctuation) x Sin(year converted to radians). Only mean water level, amplitude (half the range) of water-level fluctuation over a wet-dry cycle, and year during the cycle (converted to phase angle in radians) are needed to parameterize this simple model

As expected, Class II wetlands have the lowest mean depth and range of interannual water levels, followed by Class III wetlands. Class IV wetlands and Class V wetlands/Lakes, however, are harder to distinguish by their hydrology. Both show large and overlapping ranges of interannual mean water depths as well as interannual water-depth fluctuations (Table 2). The major difference between these two classes is whether they go dry for 1 year or more years during a wet–dry cycle. Class V wetlands and lakes do not, and thus are often in the open-water stage of the vegetation cover cycle. Whether a given wetland is Class V is very much dependent on the differences between the driest years of a wet–dry cycle or the severity of the dry part of a wet-dry cycle.

Harmonic Models

Interannual fluctuations in water depth in wetlands can be modeled using harmonic models that require only their mean water depths plus a finite number of sine curves that describe annual and interannual fluctuations in their water depths (Fig. 2). Typically, a sine curve describing seasonal variation in water levels in a given year is superimposed on a sine curve describing much larger interannual changes in water level caused by wet–dry cycles (Richter et al. 1996; van der Valk 2005; van der Valk et al. 2015). Each sine curve represents a harmonic in a hydrological time series of water depths plotted against time. Both the annual and interannual harmonics (sine curves) can be quantified using the annual or interannual mean water depth and the annual or interannual amplitude (A) or range (R, where R = 2A) of water-level fluctuations over a wet–dry cycle. Because our focus is on potential major changes in pothole vegetation cycles or structure caused by climate change, only interannual fluctuations in water depths will be considered. The range of interannual water level is defined as the highest water level - lowest water level recorded over a wet–dry cycle. If the wetland pond goes dry during an interannual cycle, its lowest water level is zero.

The use of harmonic models as a tool to investigate potential impacts of climate change on wetlands has only recently been investigated. In an examination of the potential impacts of climate change on the Florida Everglades, van der Valk et al. (2015) proposed that the number of vegetation types (zones) in a wetland is primarily a function of the range of water-level fluctuations over a wet–dry cycle. (Because of its flat topography and because its water levels are controlled by a series of dikes and water control structures, the mean interannual water depth of the Everglades was unlikely to change due

Table 2 Estimated interannual mean water depths, ranges of interannual water-level fluctuations, and minimum water depth during a wet–dry cycle in different wetlands classes (Stewart and Kantrud 1971) of prairie potholes

Wetland class	Mean water depth (m)	Range of water depths (m)	Minimum water depth (m)
II—temporary pond	0.05–0.15	0.2–0.4	0
III—seasonal pond	0.2–0.4	0.4–0.8	0
IV—semi-permanent pond	0.5–3	0.9–4	0
V—permanent pond/lake	0.5–3	1.2–4	>0

Estimates derived from all known published and unpublished field studies to climate change.) Once this range of water-level fluctuations was known, it was possible to use a harmonic model to predict if climate change would alter the vegetation structure of the Everglades by determining if climate change could significantly alter the baseline (historic) range of interannual water-level fluctuations. In south Florida, as in the prairie pothole region, there are years with below normal precipitation and years with above normal precipitation that over a period of 15 to 20 years can result in water-level fluctuation of about 1.5 m in the deepest part of the Everglades (van der Valk et al. 2015). If the range of water-level fluctuations either increases or decreases more than 0.25–0.30 m in the Everglades during wet–dry cycles, the number of vegetation types or zones in the Everglades would change (van der Valk et al. 2015). This study found that climate change could alter the number of vegetation types found under the more extreme climate-change scenarios predicted for South Florida.

In order to develop harmonic models of different classes of prairie potholes, it is necessary to establish the mean water depths and amplitudes (one half of their ranges) of water-level fluctuations for each of the four classes of potholes recognized by Stewart and Kantrud (1971) under current climatic conditions. Mean water depths and ranges of water-level fluctuations in prairie potholes are influenced by a number of factors: topographic position; surface runoff (catchment size and other characteristics); land use in catchment; groundwater gradients; evaporation and/or evapotranspiration; and seasonal, annual, and interannual precipitation patterns). In this paper, we explore only how an idealized class II, III, IV, and V pothole would respond to changes in mean water depth and the range of water-level fluctuations over a wet–dry cycle and thus ignore these contingent factors, except for our case study at the Cottonwood Lake Site. Any application of this type of model to an actual wetland would, of course, have to take these into account.

As noted, the model of interannual water-level fluctuations in Fig. 2 requires only two inputs, the interannual mean and amplitude of water-level fluctuation over a wet-dry cycle. We examined the impact of small increases or decreases, i.e., within the range found in a given class, in the interannual mean water depth and range of water levels (Table 2). We used the field data summarized in Table 2 to parameterize harmonic models for baseline years for all four classes of potholes. The six scenarios that we investigated include three in which rainfall is assumed to increase over a wet-dry cycle due to climate change (wetter) and three in which it is assumed to decrease (drier) when compared to baseline conditions:

Wetter scenarios: (1) an increase in mean water depth and a smaller range of water-level fluctuations; (2) an increase in mean water depth and no change from the baseline range in water-level fluctuation; and (3) an increase in mean water depth and an increase in the range of water-level fluctuation.

Drier scenarios: (1) a decrease in mean water depth and a smaller range of water-level fluctuations; (2) a decrease in mean water depth and no change from the baseline range in water-level fluctuation; and (3) a decrease in mean water depth and an increase in the range of water-level fluctuation.

These are all hypothetical scenarios and are not based on any specific predictions of any climate change model. They were chosen because they cover a wide range of potential changes in pothole hydrology over wet–dry cycles. An increase in the range in water-level fluctuations over a wet–dry cycle represents climate change scenarios with more extreme variation in annual rainfall than during the baseline period. The reverse would be true for scenarios with a decrease in the range of water-level fluctuations. In evaluating the potential impacts of the various climate change scenarios, we used 1) the range of water depths over a wet–dry cycle above the soil surface, and 2) whether a wetland goes dry over the course of a wet-dry cycle. The specific parameters (means, ranges) for each scenario modeled are given in Tables 3, 4, 5, and 6.

Harmonic Model Results

Tables 3, 4, 5, and 6 summarize the results of the harmonic modeling of the baseline and two water-depth scenarios (wetter than baseline and drier than baseline) and three ranges of water-level fluctuation scenarios (smaller than baseline, baseline, and greater than baseline) for each class of prairie pothole. The least affected are Class II wetlands (Table 3). Only one scenario, increased mean water depth and increased range of water-level fluctuations, transformed Class II wetlands into another class of wetland, most likely Class III. However, because they do not completely dry out, the hydrological characteristics of the transformed wetland do not perfectly match those of Class III wetlands. Transformed Class II wetlands have mean water depths and ranges of water-level fluctuations that are too small (Table 2) for them to be classified as Class IV potholes. Class III wetlands (Table 4) were predicted to be transformed into Class IV wetlands under two scenarios: higher than baseline mean water depths and either baseline or greater than baseline ranges of water levels, i.e., under wetter conditions. Class IV wetlands (Table 5) are most likely to be impacted by climate change. In three scenarios, they are predicted to be transformed into Class V wetlands or lakes: (1) increased mean water depth and a reduced range in water-level fluctuations; (2) increased mean water depth and the baseline range of water-level fluctuations; and (3) decreased water depth and reduced range of water-level fluctuations. The latter occurs because with the smaller range in water-level fluctuations in this scenario, Class IV wetlands do not go dry in any year of a wet-dry cycle. The only potential transformations for Class V wetlands/lakes (Table 6), not surprisingly, was into Class IV wetlands. This is predicted to occur

Table 3 Predicted interannual range of water depth and class for Class II potholes by the harmonic model with increased (wetter than baseline) and decreased (drier than baseline) mean interannual water depths and three different interannual water-level fluctuations water (smaller than baseline, baseline, and greater than baseline)

Climate change wetland scenario	Mean interannual water depth (m)	Interannual range of water-level fluctuation (m)	Predicted interannual range of water depth >0 (m)	Baseline wetland class	Predicted post climate-change wetland class
Baseline	0.10	0.20	0.20	II	II
Wetter	0.15	0.10	0.20[a]	II	II
Wetter	0.15	0.20	0.25[a]	II	III
Wetter	0.15	0.30	0.30	II	II
Drier	0.05	0.10	0.10	II	II
Drier	0.05	0.20	0.15	II	II
Drier	0.05	0.30	0.20	II	II

[a] Minimum water depth >0 (m)

Table 5 Predicted range of water depth and class for Class IV potholes by the harmonic model with increased (wetter than baseline) and decreased (drier than baseline) mean interannual water depths and three different interannual water-level fluctuations water (smaller than baseline, baseline, and greater than baseline)

Climate change wetland scenario	Mean interannual water depth (m)	Interannual range of water-level fluctuation (m)	Predicted interannual range of water depth >0 (m)	Baseline wetland class	Predicted post climate-change wetland class
Baseline	1.0	2.0	2.0	IV	IV
Wetter	1.5	1.0	1.0[a]	IV	V
Wetter	1.5	2.0	2.0[a]	IV	V
Wetter	1.5	3.0	3.0	IV	IV
Drier	0.7	1.0	1.2[a]	IV	V
Drier	0.7	2.0	1.7	IV	IV
Drier	0.7	3.0	2.2	IV	IV

[a] Minimum water depth >0 (m)

under two scenarios: decreased mean water depths and baseline or increased ranges of water-level fluctuations.

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Table 7 summarizes the interannual mean and range of water levels during the 1988–2001 and 2001–2012 wet–dry cycles and the vegetation found in the deepest area during the corresponding vegetation cover cycle for 16 potholes at the Cottonwood Lake site. Vegetation data were only available from 1992–2001 for the 1988–2001 wet–dry cycle. This was not a problem for characterizing the vegetation cover cycle in each pothole during this wet–dry cycle because the wettest years of this cycle occurred during its last few years (Fig. 1). During the 1988–2001 wet–dry cycle all of these potholes went dry for one or more years. During the 2002–2012 cycle, only one of the wetlands earlier considered to be Class V dried, wetland P3. This is because they entered this cycle with high water levels. However, all of the wetlands considered originally to be Class II went dry with the exception of wetland T1. Wetland T1, while originally considered as a separate wetland than P1, is merged with P1 during most years and has a hydrology dominated by that of the much larger wetland. Thus, T1 is best considered as being part of P1 rather than as a

Table 4 Predicted interannual range of water depth and class for Class III potholes by the harmonic model with increased (wetter than baseline) and decreased (drier than baseline) mean interannual water depths and three different interannual water-level fluctuations water (smaller than baseline, baseline, and greater than baseline)

Climate change wetland scenario	Mean interannual water depth (m)	Interannual range of water-level fluctuation (m)	Predicted interannual range of water depth > 0 (m)	Baseline wetland class	Predicted post climate-change wetland class
Baseline	0.3	0.6	0.6	III	III
Wetter	0.4	0.4	0.4[a]	III	IV
Wetter	0.4	0.6	0.6[a]	III	IV
Wetter	0.4	0.8	0.8	III	III
Drier	0.2	0.4	0.4	III	III
Drier	0.2	0.6	0.5	III	III
Drier	0.2	0.8	0.6	III	III

[a] Minimum water depth >0 (m)

Table 6 Predicted interannual range of water depth and class by the harmonic model for Class V potholes with increased (wetter than baseline) and decreased (drier than baseline) mean interannual water depths and three different interannual water-level fluctuations water (smaller than baseline, baseline, and greater than baseline)

Climate change wetland scenario	Mean interannual water depth (m)	Interannual range of water-level fluctuation (m)	Predicted Interannual range of water depth >0 (m)	Baseline wetland class	Predicted Post climate-change wetland class
Baseline	1.5	2.0	2.0	V	V
Wetter	2.0	1.0	1.0	V	V
Wetter	2.0	2.0	2.0	V	V
Wetter	2.0	3.0	3.0	V	V
Drier	1.0	1.0	1.0	V	V
Drier	1.0	2.0	2.0[a]	V	IV
Drier	1.0	3.0	2.5[a]	V	IV

[a] Minimum water depth >0 (m)

Table 7 Mean water depths and ranges of water levels for 15 potholes at the Cottonwood Lake study site during the 1988–2001 and 2002–2012 wet–dry cycles and the wetland class of each during both these cycles

Wetland[a]	Wet–dry cycle				Wetland class	
	1988–2001		2002–2012			
	Mean (m)	Range (m)	Mean (m)	Range (m)	1992–2001	2002–2012
P7	2.33	4.18	3.37	1.33	IV	V
P11	2.12	3.63	2.97	1.73	IV	V
P2	1.83	3.46	2.26	1.41	IV	V
P4	1.79	3.46	2.26	1.41	IV	V
P6	1.75	3.04	2.01	1.39	IV	V
P1	1.71	2.79	1.86	1.29	IV	V
T9	0.74	1.47	0.42	1.23	IV	IV
T3	0.55	1.18	0.29	0.79	IV	IV
P3	0.54	0.89	0.54	0.88	IV	IV
T8	0.41	0.98	0.28	1.09	IV	III
T2	0.41	0.68	0.44	0.66	IV	IV
T7	0.24	0.66	0.18	0.65	III	III
T6	0.24	0.48	0.19	0.41	IV	III
T5	0.17	0.66	0.12	0.66	III	III
T4	0.15	0.48	0.13	0.54	III	III

The vegetation class is based on the vegetation type (see Table 1) found in the deepest part of the wetland during each cycle. Wetlands have been ordered by mean depth during 1988–2001

[a] Original classification P = semipermanent (Class IV); T = seasonal (Class III) (Winter 2003)

separate wetland (Euliss et al. 2014) and our findings support this argument.

The potholes classified as Class V at Cottonwood Lake during the 2002–2012 wet–dry cycle had interannual water-level fluctuations of about 1.3–1.7 m with the exception of P3 (Table 7). During the previous cycle, they ranged from 2.8 to 4.2 m, again with the exception of P3. The Class III wetlands, on the other hand, during the 2002–2012 wet–dry cycle had water-level fluctuations ranging from 0.4 to 1.3 m and during the 1988–2001 cycle from 0.5 to 2.2 m. These are comparable, but often with larger interannual water-level fluctuations than those reported for similar potholes in Saskatchewan by Price (1993).

By examining the vegetation types recorded in each wetland during the two wet–dry cycles, it was possible to determine from their vegetation cycles to which Stewart and Kantrud class each wetland belonged (Table 7). The results suggest that these wetlands are very dynamic and can change class from one wet–dry cycle to another. Most of the wetlands that were classified as Class IV during the 1988–2001 wet–dry cycle (P1, P2, P4, P6, P7, and P11) were classified as Class V during the 2002–2012 cycle. Wetland P3 was classified as Class IV in both cycles. Three other potholes were also classified as Class IV in the 1988–2001 and 2002–2012 cycles (T2, T3, and T9); two (T6 and T8) as Class IV in the first and Class III in the second cycle; and three (T4, T5, and T7) remained Class III during both cycles.

Discussion

Prairie potholes vary continuously in their hydrology (mean water depth, interannual water-level fluctuations). Each wetland has a unique landscape setting (basin morphometry, catchment characteristics, connection to groundwater, connectivity with other potholes, etc.) and local climate (rainfall, temperatures, snow accumulation, etc.). Nevertheless, the four Stewart and Kantrud (1971) classes we studied represent four broad slices along this environmental continuum that differ in significant ways in their hydrology and vegetation, and hence potential utilization by waterfowl, amphibians, fish, and other animals. This makes these classes useful for evaluating the potential effects of climate change.

Based on observations of various wetlands around the world, including prairie potholes, van der Valk et al. (2015) proposed that a permanent increase or decrease of 0.25–0.30 m in the range of water-level fluctuations over a wet–dry cycle would result in an increase or decrease of one vegetation zone in a wetland, as long as the new range is less than hypervariable. Data from the prairie pothole region indicate, however, that each of the vegetation types in prairie potholes has unique optimal depths and interannual water-level fluctuations that are not linearly related (Table 2). Consequently, the change in interannual water depths and ranges of water-level fluctuations that will result in the addition or loss of a vegetation type varies among pothole classes. Much smaller changes (ca. 0.1–0.2 m for both means and ranges; Table 2) will affect Class II and Class III wetlands than Class IV and Class V wetlands (0.5–0.7 m means; 0.5 to 1+ m ranges). In deeper and typically larger Class IV and Class V wetlands, mean water depths overlap and can vary by meters over wet–dry cycles (Table 2). For these classes, it is the range of water-level fluctuations over a wet–dry cycle that is their most important hydrological characteristic. If this range is large enough for the wetland to go dry, it is Class IV; if it is not, it is Class V.

Because they are so shallowly flooded, Class II and Class III wetlands might be thought to be the most susceptible to climate change (Johnson et al. 2004), regardless if it gets wetter or drier in the future. (Most potholes in the Dakotas (ca. 90 %) are either Class II or Class III wetlands (Niemuth et al. 2010).) This, however, proved to be only partially true. The harmonic models suggest that Class II wetlands are predicted to be the least likely to be transformed into another wetland class. The most likely to be transformed, as noted above, are Class IV wetlands into Class V wetlands/lakes. The results of the harmonic modeling suggest that Class IV wetlands can be transformed into Class V wetlands/lakes with only modest changes in mean water depths and/or range of interannual water-level fluctuations.

Data from the Cottonwood Lake site (Table 7) demonstrate that the kinds of transformations from one class of wetland to another that the models suggest can happen actually do occur from one wet–dry cycle to another. During the wetter, 2002–2012 cycle with an increase in mean water depth, all Class IV wetlands whose range of water-level fluctuations decreased were transformed into Class V because they no longer went dry. Most of the shallower, Class II potholes, however, did not change their class, which is consistent with the models. Results from the Orchid Meadow study in South Dakota (Johnson et al. 2004) also are consistent with our modeling results. At this site, during the drought, Class IV wetlands behaved in the short-term as Class III, and Class III as Class II (Johnson et al. 2004). Likewise during the unusually wet years: “In the short-term, temporary wetlands behave as seasonals, seasonals as semi-permanent, and semi-permanent as shallow lakes”.

The Cottonwood Lake data, the Orchid Meadow data, and our harmonic models indicate that the Stewart and Kantrud (1971) class of a wetland is not fixed. A shift of one permanence class can occur fairly quickly from one wet-dry cycle to another. Wetlands can shift from one class to another due to changes in climate (primarily precipitation), even in the short term; i.e., due to factors other than global climate change. These shifts may be constrained by the nature of the wetland basin, closed (no outlet) or overflow (with an outlet), and the role of groundwater (discharge, flow-through, recharge) in its water budget, which can change depending on relative wetland stage (Winter and Rosenberry (1998). Wetlands with closed basins are more likely to shift to a more permanently ponded class than a comparable wetland in a basin with an outflow. As previously demonstrated by Johnson et al. (2005, 2010) prairie pothole wetlands will potentially be affected by climate change. Our results suggest that the vegetation cycles in these wetlands can be altered by prolonging the length of some stage in the cycle as previously demonstrated by Johnson et al., but also their class can change because their mean water depths increase or decrease and/or because of an increase or decrease in the range of interannual water levels.

The vegetation and vegetation cycles of prairie pothole wetlands can respond rapidly to changes in their hydrology (Millar 1973; Kantrud et al. 1989; van der Valk 2000, 2007; Johnson et al. 2004), and this has enabled them to cope with the large changes in annual water levels that occur normally during wet–dry cycles. The mechanisms such as seed banks (van der Valk and Davis (1978), rapid short and long distance seed dispersal by birds (Mueller and van der Valk 2002), acclimation to different water depths (Squires and van der Valk 1992), clonal growth, etc. that characterize the wetland plant species of the prairie pothole region should also enable these species to cope with climate change. While the percentage of different classes of potholes in the region or its subregions may change, prairie potholes wetlands will endure.

Unfortunately, data on mean water depths and interannual ranges of water-level fluctuations are still very rare for prairie pothole wetlands, especially data for multiple wet–dry cycles. We concur with Conly and van der Kamp (2001) that monitoring the hydrology (and we would add vegetation) of potholes across the entire pothole region is essential in order to detect long-term changes due to climate change and other factors such as changes in land use. Such data are also needed to improve and refine our understanding of the hydrological characteristics of the different classes of prairie potholes. Each class in the Stewart and Kantrud (1971) classification has two or more subclasses depending on basin characteristics and groundwater interactions. More attention needs to be placed on understanding the hydrology and vegetation of these subclasses.

Acknowledgments Data from Cottonwood Lake area wetlands are available through the Missouri Coteau Wetland Ecosystem Observatory (https://www.sciencebase.gov/catalog/item/52f0ffd9e4b0f941aa181fc6) and maintained through funding received from the U.S. Geological Survey’s Climate and Land Use Change—Research and Development Program. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. Support for this project was provided to the senior author by the Department of Ecology, Evolution and Organismal Biology, Iowa State University.

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