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ORIGINAL RESEARCH

Hydrology of Prairie Wetlands: Understanding the Integrated Surface-Water and Groundwater Processes

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Abstract Wetland managers and policy makers need to make decisions based on a sound scientific understanding of hydrological and ecological functions of wetlands. This article presents an overview of the hydrology of prairie wetlands intended for managers, policy makers, and researchers new to this field (e.g., graduate students), and a quantitative conceptual framework for understanding the hydrological functions of prairie wetlands and their responses to changes in climate and land use. The existence of prairie wetlands in the semi-arid environment of the Prairie-Pothole Region (PPR) depends on the lateral inputs of runoff water from their catchments because mean annual potential evaporation exceeds precipitation in the PPR. Therefore, it is critically important to consider wetlands and catchments as highly integrated hydrological units. The water balance of individual wetlands is strongly influenced by runoff from the catchment and the exchange of groundwater between the central pond and its moist margin. Land-use practices in the catchment have a sensitive effect on runoff and hence the water balance. Surface and subsurface storage and connectivity among individual wetlands controls the diversity of pond permanence within a wetland complex, resulting in a variety of eco-hydrological functionalities necessary for maintaining the integrity of prairie-wetland ecosystems.

Keywords Prairie pothole · Slough · Water balance · Wetland complex · Land use · Climate change

Introduction

The Prairie-Pothole Region (PPR) or the Northern Prairie Region (Fig. 1) extends across more than 750,000 km^2 of the Northern Great Plains of North America (Eisenlohr et al. 1972) and exists at the intersection of unique climatic and geologic conditions as explained below. Depressional wetlands in this region are commonly called prairie potholes in the U.S.A and prairie sloughs in Canada. Ecological processes in these wetlands (hereafter prairie wetlands) are strongly influenced by hydrological processes, which control the dynamics of surface water and groundwater, as well as inputs and outputs of dissolved matter and sediments. Therefore, management and policy decisions concerning prairie wetlands require a sound understanding of hydrological processes.

The PPR has a dry climate, where mean annual precipitation is exceeded by potential evaporation (Winter 1989). It also has a cold winter, which allows snow to accumulate on the ground, and soils to freeze to considerable depths affecting a host of hydrological and ecological processes (Hayashi 2013). The region is covered by a thick (up to 180 m) blanket of glacial deposits left by the Pleistocene continental ice sheets (Winter 1989). Most of these are glacial tills containing a considerable amount (up to 20 % by weight) of clay, resulting in a low hydraulic conductivity that transmits groundwater very slowly.

The glaciated landscape of the PPR is generally flat on a regional scale but locally has a hummocky or undulating topography with numerous small depressions. These depressions lack an integrated drainage network due to insufficient amounts of runoff, unless they are artificially drained. Owing

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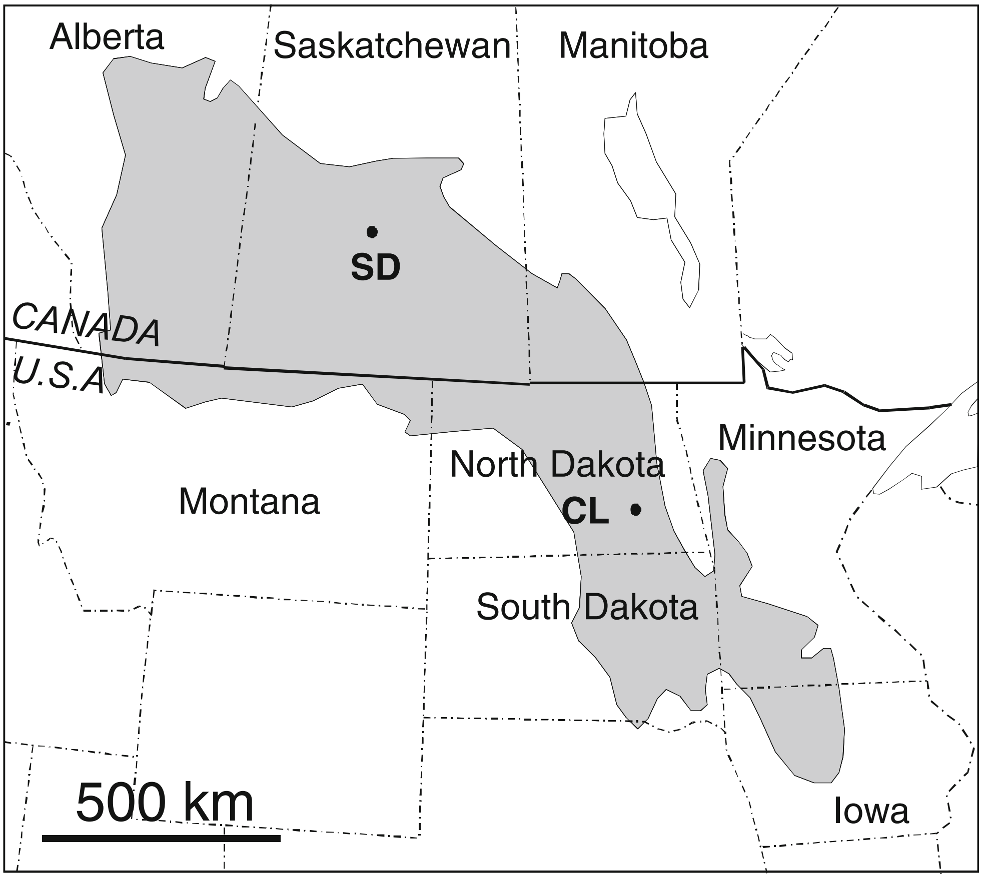

Fig. 1 Map showing the extent of Prairie Pothole Region and location of the St. Denis National Wildlife Area (SD) and the Cottonwood Lake study area (CL).Modified from van der Kamp and Hayashi (2009), with permission

to the low hydraulic conductivity of the glacial deposits, water is retained in the depressions for a long time. Since the vertical input of water to wetlands by precipitation is smaller than the output by evapotranspiration, existence of these wetlands depends on lateral water inputs from the surrounding uplands via blowing snow, snowmelt runoff over frozen ground, and occasional summer runoff due to heavy rains. Decisions regarding the conservation or restoration of prairie wetlands need to consider how these climatic and geologic conditions affect the hydrological functions of wetlands and their interactions with the surrounding landscape.

Winter (1989) synthesized the body of hydrological knowledge and suggested a number of future study topics including effects of wetland drainage on downstream floods, integrated study of surface water-groundwater interaction, long-term studies to understand the effects of a large variability of climatic conditions, and accurate characterization of evapotranspiration. Winter's suggestions motivated hydrological studies in the ensuing years. LaBaugh et al. (1998) summarized the progress made over the next decade and suggested further need for studies in expanding detailed hydrological investigations to a wider range of geological settings, examining sediment records in wetlands to see if instrumentally recorded hydrological extremes and the frequency of wet and dry periods are similar to those of the recent millennia, and understanding hydrological processes at the edge of wetlands and their relations with soil and vegetation dynamics.

Much progress has been made in the past quarter century, which has enhanced the conceptual frameworks laid out by Winter (1989) and LaBaugh et al. (1998). Some questions posed by these authors have been partially answered, while others continue to challenge us. The objective of this article is to present the current hydrological understanding of prairie wetlands and provide a quantitative water-balance framework for understanding their basic hydrological functions and responses to natural and anthropogenic stresses such as meteorological forcing (e.g., drought and deluge), land-use practices in surrounding areas, and drainage of wetlands. The water-balance framework provides the scientific basis for management practices and policy decisions concerning prairie wetlands as well as the essential building block of numerical models (e.g., Liu and Schwartz 2011; Johnson and Poiani 2016) that can be used to assess the sensitivity of the wetlands to climate change (LaBaugh et al. 1996; Johnson et al. 2005).

The article starts with an introduction to the water balance of an individual wetland and brief descriptions of input, output, and storage processes. The water-balance concept is then expanded to a complex of multiple wetlands, followed by discussion of how the hydrological functions of wetlands are affected by natural and anthropogenic changes in input and output processes. The key point of this overview article is that the hydrological and ecological functions of prairie wetlands need to be understood in the context of both surface-water and groundwater processes that govern the storage of moisture and the connectivity between individual wetlands and their respective catchments, and among the wetlands within a wetland complex.

Water Balance of a Prairie Wetland

Overview

The amount of water stored in a wetland changes in response to the balance between input and output of water. Wetlands in humid environments typically have sufficient inputs to sustain continuous outflow throughout the year, thereby maintaining relatively steady water levels. In contrast, due to small and highly variable inputs, water levels in prairie wetlands have a strong seasonal pattern characterized by a sharp increase in spring with snowmelt inputs from the surrounding uplands, and a gradual decline during summer and fall. Central ponds in wetlands often become dry, especially in the wetlands with small catchments providing lateral inputs. However, the wetland hydrological processes continue through the dry period, drawing on subsurface (i.e., soil water and groundwater) storage beneath the dry pond area and beneath the rest of the wetland. The subsurface moisture condition has a strong influence on the pond reappearance during the subsequent wet period.

The limited outflow from the wetlands means that nutrients derived from the surrounding glaciated landscape largely remain sequestered in the wetlands, thus leading to the high biological productivity that supports the most important waterfowl-production habitat in North America (Smith et al. 1964; Batt et al. 1989). The high variability of the pond water levels within the wetlands means that nutrients are recycled within the wetlands through repeated drying and wetting episodes (e.g., LaBaugh et al. 1987). The presence of wetlands having highly variable water levels within a landscape allows waterfowl to use them at different stages during the nesting and breeding season (Swanson and Duebbert 1989).

The hydrology of a prairie wetland must be considered together with the hydrology of the surrounding uplands because the wetland existence depends on water contributions from the uplands in addition to direct precipitation (P). Runoff (R) is supplied from the uplands in the form of snow drift, snowmelt runoff, and occasional summer runoff during heavy rains (Fig. 2). The primary output is evapotranspiration (E) from the entire wetland area, including a pond (if one is present) and the surrounding non-inundated wetland area. Groundwater flow (G) may add water to the wetland ($G > 0$) from the uplands or an underlying aquifer (if present), or remove water from the wetland ($G < 0$). Note that input ($G > 0$) to the wetland is considered a "discharge" and output ($G < 0$) is a "recharge" in the groundwater nomenclature. Depending on its position within a complex of wetlands, the wetland may receive or contribute occasional overflow (O) from or to other wetlands during very wet periods (Eisenlohr et al. 1972; Leibowitz and Vining 2003; Shaw et al. 2012).

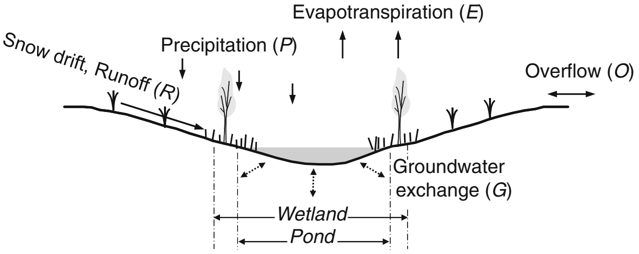

Fig. 2 Schematic diagram of the water balance components of a prairie wetland. *Dashed lines* indicate the exchange of groundwater with surface water. The pond is an inundated area within the wetland (modified from van der Kamp and Hayashi 2009, with permission)

The water balance of a wetland is expressed as:

$$\frac{\Delta S}{\Delta t} = \text{input}-\text{output} = A_w(P-E) + (A_c-A_w)R + G + O \quad (1)$$

where A_w is the area of the wetland and A_c is the area of the catchment defined by surface drainage divides (see Fig. 3). ΔS is the change of water storage in the wetland during a small time step Δt, for example one day, and includes surface storage in the central pond and subsurface storage in the form of soil moisture and groundwater. Note that the catchment area includes the wetland area. The basic unit of G, O, and $\Delta S/\Delta t$ is volume per time ($m^3\ s^{-1}$) and of P, R, and E is volume per unit area per time ($m^{-3}\ m^{-2}\ s^{-1}$ or $m\ s^{-1}$), which is typically expressed in more practical units (e.g., mm d^{-1}).

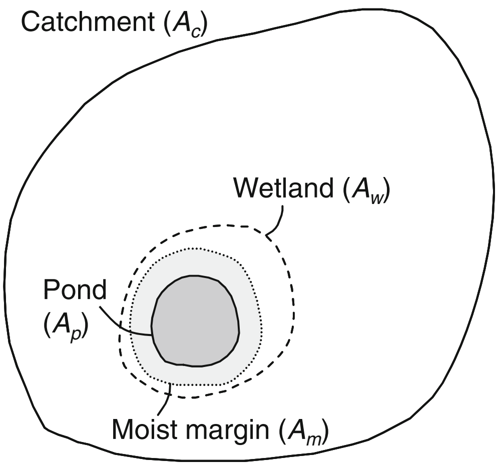

Fig. 3 Schematic diagram showing a wetland and its catchment. The pond and moist margin expand and contract depending on the water balance, whereas the wetland has a fixed area typically defined by the presence of wetland soil

The essence of wetland hydrology is in understanding the processes controlling individual terms in the water-balance equation and feedbacks among them, and their responses to climatic variability and land-management practices (Rosenberry and Hayashi 2013). Most critical is the understanding of processes that influence the lateral input term R, which maintains the wetland despite the atmospheric moisture deficit (i.e., $P - E < 0$). A relatively small increase of annual precipitation may result in a much larger increase of water input to a wetland by both P and R.

Seasonality and Pond Permanence

Seasonal patterns of water levels in wetland ponds are demonstrated by examples (Fig. 4) from Wetland 109 in the St. Denis National Wildlife Area (hereafter St. Denis) in Saskatchewan and Wetland P1 in the Cottonwood Lake study site (hereafter Cottonwood Lake) in North Dakota (see Fig. 1 for locations). The strong seasonality is a defining feature of prairie wetlands and is used to characterize the wetlands as having ephemeral, seasonal, semi-permanent or permanent ponds (Stewart and Kantrud 1971). Fluctuating water levels cause central ponds to expand or contract, even to the point of dryness, because wetland basins are generally shallow (< 2 m) with a bowl-shaped bottom of gentle curvature (Hayashi and van der Kamp 2000).

Fluctuations of water level and pond size have strong effects on the composition of emergent vegetation (van der Valk 2005). The duration and frequency of ponding is an important ecological variable for aquatic species dependent on surface water (Snodgrass et al. 2000; Euliss and Mushet 2004). "Hydroperiod" has often been used to indicate the duration and frequency of ponded water (e.g., Euliss et al. 2004; van der Kamp and Hayashi 2009). However, hydroperiod has a much broader meaning encompassing the dynamics of both surface and subsurface water (Mitsch and Gosselink 2007, p.111). The use of hydroperiod to indicate the duration of inundation is misleading, as it minimizes the importance of subsurface water dynamics such as water-table fluctuations and their effects on aquatic species and soil biochemical processes. Therefore, we suggest using "pond permanence" instead of hydroperiod both as a qualitative descriptor (e.g., ephemeral vs. seasonal, Stewart and Kantrud 1971) and as a quantitative variable representing the actual duration of the pond and its statistics (e.g., mean and standard deviation). In this context, Wetland 109 (Fig. 4a) had a seasonal pond during 1968–2001 with $\mu = 4.5$ and $\sigma = 3.4$, where μ and σ are the mean and standard deviation, respectively, of the duration of ponded water each year in months. It had a semi-permanent pond during 2005–2015 ($\mu = 11.5$, $\sigma = 1.0$). Wetland P1 (Fig. 4b) had a semi-permanent pond during 1979–1993 ($\mu = 10.0$, $\sigma = 2.8$), which became more permanent and never dried during 1994–2015. The decadal shift in the pond permanence and its implication will be discussed later in the section on the wetland continuum.

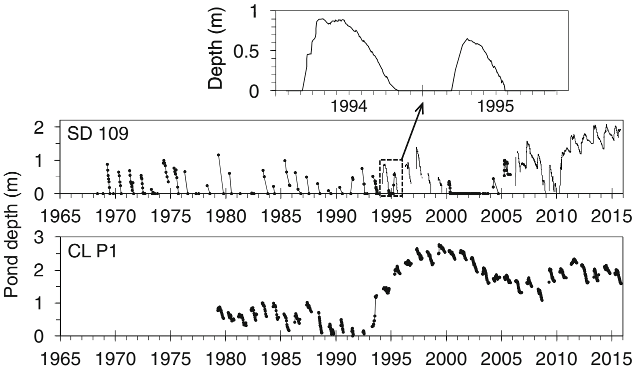

Fig. 4 Pond water depth in representative wetlands, Wetland 109 at St. Denis (SD) National Wildlife Area and Wetland P1 at the Cottonwood Lake (CL) wetland study area. *Solid circles* indicate manual measurements and *continuous lines* indicate instrumental measurements. The expanded chart is an example illustrating a sharp increase in pond depth with snowmelt runoff, followed by a relatively flat period sustained by summer precipitation, and a gradual decline until the pond dries

Having defined the water-balance equation for a wetland (Eq. 1) and briefly discussed its implications regarding the seasonality and permanence of wetland ponds (Fig. 4), the specifics of individual terms in the water balance equations are described below along with their significance and relevance.

Precipitation and Evapotranspiration

Precipitation is the main driver of hydrological processes as it provides direct input of water (P in Fig. 2) to the wetland and generates runoff (R) on the uplands. Its seasonal, inter-annual, and longer-scale variability is the cause of highly variable pond water levels. The PPR is subject to decadal-scale fluctuations of precipitation amounts (Shabbar et al. 2011). The past two decades have been particularly wet, resulting in high pond water levels in the PPR (Fig. 4). Note that the decadal-scale fluctuation is a change in *meteorological condition*, and should not be confused with a variability of *climate*, which is defined as an average meteorological condition over a long period (e.g., 30 years) (Arguez and Vose 2011). Observation and reporting of precipitation at a local scale is reasonably straightforward for rain but is complex for snow as measurements are strongly influenced by wind-induced undercatch (Rosenberry and Hayashi 2013, p.106). Variation in instrument types and correction procedures (or lack thereof) may generate artificial trends of precipitation data (Mekis and Vincent 2011), which should not be mistaken as a climate-change signal.

Evaporation is the transfer of water vapor from the earth surface (including land and water) to the atmosphere. While meteorologists consider all forms of vapor fluxes evaporation, we use "evapotranspiration" to indicate explicitly the combination of abiotic (evaporation) and biotic (transpiration) processes. The driver of evapotranspiration is energy inputs. Most energy comes from net radiation, which is the sum of shortwave radiation emitted by the sun (+) and reflected by the earth surface (−) and longwave radiation emitted by the atmosphere (+) and the earth surface (−). Note that heat transfer from a warmer air to a colder surface, called sensible heat flux, is a minor component of energy input (e.g., Oke 1987, p.24). Put simply, air temperature is not a driver of evapotranspiration, even though it often is used as a surrogate indicator of radiation. For this reason, temperature-based climatic indices (e.g., Thornthwaite 1948) do not provide reliable estimates of evapotranspiration (Rosenberry and Hayashi 2013, p.117) and tend to exaggerate the effects of temperature increase when used in numerical simulations of climate-change impacts. In contrast, energy-balance methods using radiation data (e.g., Priestley and Taylor 1972) provide more accurate and reliable estimates of evapotranspiration when they are used in relatively shallow water bodies and non-inundated portions of wetlands where evapotranspiration is usually not limited by moisture availability (Rosenberry et al. 2004). Evapotranspiration from the moist margin (see Fig. 3) can have a major influence on the water balance of prairie wetlands (LaBaugh et al. 1998), which is discussed below in relation to groundwater exchange.

Snowdrift and Snowmelt Runoff

Water input from the surrounding catchment (see Fig. 2) is critical to the existence of wetlands in the PPR where mean potential evaporation exceeds precipitation, as discussed above. Much of the precipitation falling on the catchment is consumed by plants during the growing season, meaning that the lateral input is largely driven by processes related to snow. Wind can move a substantial amount of snow within and across catchments. Snow accumulates preferentially in a dense vegetation ring around a wetland or on the lee side of a wetland depression if a vegetation ring is absent (Hayashi et al. 1998a; Fang and Pomeroy 2009). This input of snowdrift to the wetland water balance is included as runoff from the catchment in Eq. 1. Ungrazed perennial grass or tall stubble on uplands traps snow and reduces drifting, whereas fields that have undergone fall cultivation have little ability to trap snow (van der Kamp et al. 2003). Therefore, land management practice can strongly influence snow accumulation, and farmers often alter their cultivation strategy to retain snow on uplands (Steppuhn 1981), which provides soil moisture.

The relatively thin (< 0.3 m) snowpack common in the PPR provides little insulation from cold winter weather, resulting in a deep soil frost (Hayashi et al. 2003). Ice crystals forming in wet clay-rich soils dramatically reduce their infiltration capacity (Granger et al. 1984), and a substantial portion of snowmelt water runs off from uplands and accumulates in wetlands, causing a sharp water-level rise during the spring snowmelt period. Land-use practices influence the hydraulic property of near-surface soils that control the partitioning of snowmelt water into infiltration and runoff (van der Kamp et al. 2003; Renton et al. 2015), which can have a dramatic effect on a wetland water balance. Additional effects of land use on wetland hydrological processes are discussed later.

Groundwater Exchange

A wetland may receive water from or lose water to underlying groundwater depending on the hydrogeological setting. For the vast majority of prairie wetlands that are underlain by clay-rich glacial tills, hydraulic conductivity (K) decreases sharply with depth (van der Kamp and Hayashi 2009). This is critically important to the groundwater exchange between a central pond and its moist margin (Fig. 2). Glacial tills typically have relatively high K values (> 1 m y^{-1}) in the intensely fractured near-surface zone, normally within 4–5 m of the surface, and much lower K values (10^{-3} to 10^{-2} m y^{-1}) in the zone below (Winter 2003). As a result, the lateral exchange of groundwater between a pond and its margin through the high-K zone is a major component of the pond water balance (Winter and Rosenberry 1995; Hayashi et al. 1998a). In contrast, deeper groundwater flow through the low-K zone to underlying aquifers is commonly too slow to have a significant influence on the water balance of the wetland as a whole (van der Kamp and Hayashi 2009).

Water Storage in Wetlands

The area (A_p) and volume (V_p) of the surface water stored in a wetland pond can generally be represented as a function of water depth (h) by:

$$A_p = s(h/h_0)^{2/p} \tag{2}$$

$$V_p = sh(h/h_0)^{2/p}/(1+2/p) \tag{3}$$

where s (m^2) is a scale parameter, h_0 (= 1 m) is a unit length, and p is a basin profile parameter. The latter takes a value of 1 for an inverted cone-shaped basin, 2 for a parabolic basin, and a very large value for a bathtub-shaped basin with a flat bottom and steep slopes (Hayashi and van der Kamp 2000). Eqs. 2 and 3 reasonably well represent the bathymetry of depressional ponds in many locations (e.g., Brooks and Hayashi 2002; Minke et al. 2010). Entering the overflow depth (h_{max}) in Eq. 3 gives the surface storage capacity of a wetland basin. Dividing Eq. 3 by Eq. 2, surface storage capacity per unit area of a wetland basin is given by $h_{max}/(1+2/p)$. Most prairie wetlands have p values ranging between 1.5 and 6 (Hayashi and van der Kamp 2000), meaning that surface storage capacity per unit area ranges between $0.4h_{max}$ and $0.8h_{max}$. This translates to 0.4 m to 1.6 m of water per unit area for a common h_{max} range of 1 to 2 m (Eisenlohr et al. 1972; Hayashi and van der Kamp 2000).

Much attention has been given to surface storage in the context of wetland drainage and its potential effects on flood retention capacity (Todhunter and Rundquist 2004; McCauley et al. 2015). In contrast, little attention has been given to subsurface storage, perhaps because it appears insignificant when a pond occupies a large fraction of a wetland. However, when the pond dries out, soil moisture and groundwater dominate wetland hydrological processes. The water table declines rapidly under a dried-up wetland as plants continue to transpire and draw water upward to the root zone. The rate of decline slows after the growing season but the decline continues due to the combination of recharge to the deeper zone and frost-induced removal of water from the water table (Ireson et al. 2013). This was particularly evident during 1981–1982 and 2000–2002 (Fig. 5) under Wetland 109 in St. Denis (Miller et al. 1985; Hayashi et al. 1998a; Parsons et al. 2004). Similar observations were made at Cottonwood Lake (Winter and Rosenberry 1998) and the Orchid Meadow study site (Johnson et al. 2010).

The clay-rich till underlying most of the PPR has a high water-holding capacity and is nearly saturated 1 m or so above the water table, leaving little air-filled void space for storing infiltrating water in this nearly saturated zone (Fig. 6a) referred to as the capillary fringe. As the water table declines over time, plant roots extract water from deeper zones and a large volume of air-filled void space becomes available between the ground surface and the water table, which can accommodate a significant amount of infiltrating water. The actual distribution of air-filled void space is more complex due to depth-variation of soil properties such as porosity. The air-filled porosity at the center of Wetland 109 in January 2002 after a very dry year (Fig. 6c) had a total storage capacity of roughly 500 mm.

To demonstrate relative magnitudes of surface and subsurface storage capacity in a wetland, Fig. 6b shows pond water volume (i.e. surface storage) as a function of water level (Eq. 3) for a hypothetical wetland having $p = 2$ and $s = 2000$ m^2, which is similar to Wetland 109. It also shows subsurface storage capacity as a function of the water-table depth for the till shown in Fig. 6a. Relatively little subsurface storage capacity develops as the water table drops to −2 m, but subsurface storage capacity increases as the water table continues to drop (Fig. 6b). The subsurface storage capacity for a 5-m deep water table is comparable to the surface storage for a pond depth of 1.5 m, which is close to a typical overflow depth of small prairie wetlands (see above). Depending on the timing and condition of soil freeze-thaw and snowmelt runoff, a wetland having a deep water table and dry soil over winter can absorb a large amount of snowmelt runoff before a surface pond forms, as illustrated by the water-table dynamics of Wetland 109 in the spring of 2001 and 2003 (Fig. 5). However, if runoff water refreezes in the wetland during a cold event, it impedes the infiltration of additional runoff water during subsequent warm events, thereby allowing a surface pond to form above the thick unsaturated soil zone. The complex interaction among soil freeze-thaw, snowmelt, and subsurface water dynamics in wetlands having a deep water table is not well understood. It will require further research to understand the effects of the large subsurface storage capacity and its implication for wetland drainage effects on regional flood retention capacity (discussed later).

Pond Water Balance and Permanence

Groundwater uptake by dense vegetation in the moist margin, directly from the water table or indirectly through the vadose zone, drives outward flow of groundwater and induces infiltration of pond water to the wetland margins through the high-K zone (Meyboom 1966; Rosenberry and Winter 1997; Hayashi et al. 1998a). Re-analysis of water-level recession data in 106 wetlands at three different regions in Saskatchewan collected by Millar (1971) show that

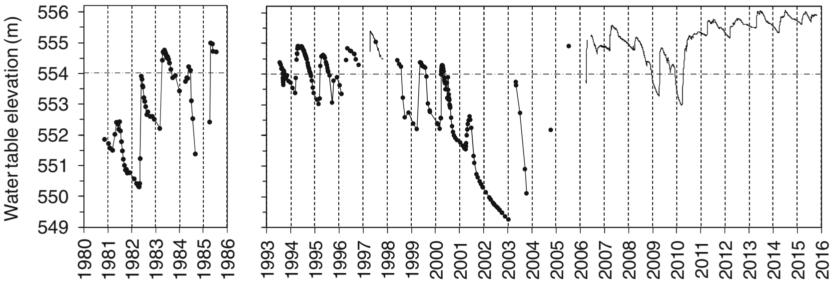

Fig. 5 Elevation of the water table under Wetland 109 in St. Denis. The *horizontal dashed line* indicates the lowest elevation of the wetland basin. The water table above this line indicates pond water level. In the winters of 2008–2009 and 2009–2010, the pond froze completely to the bottom, and the groundwater table kept declining under the frozen pond. Note a data gap between 1986 and 1993

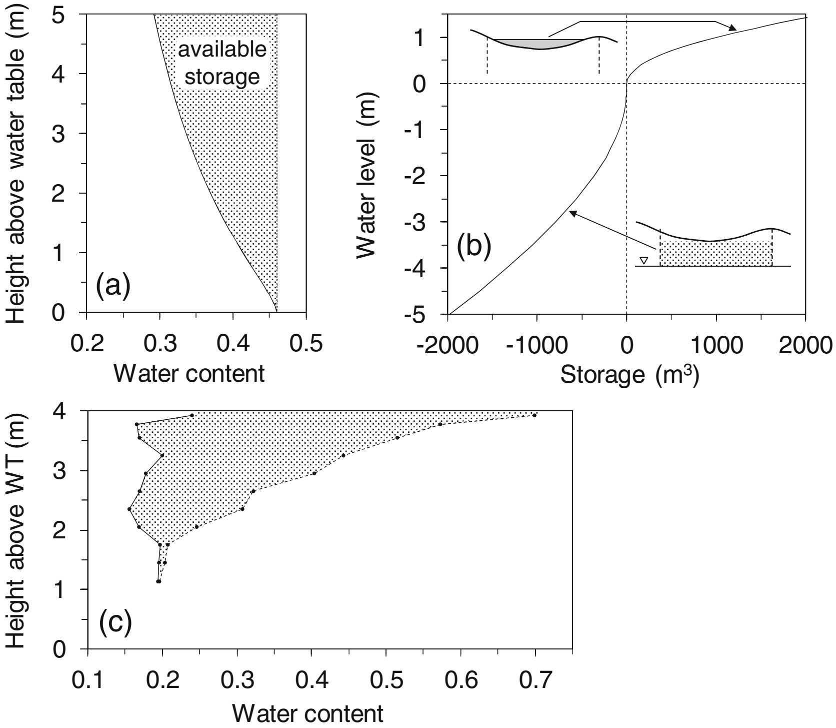

Fig. 6 **a** Theoretical distribution of volumetric water content as a function of distance above the water table for a typical glacial till (Hayashi et al. 1997, Fig. 9). The difference between porosity and water content is air-filled void space available for storing water. **b** Theoretical relation between pond water level and surface storage volume (positive values), and between the water-table depth and the available capacity to store subsurface water (negative values). (c) Actual distribution of volumetric water content (*solid line*) and porosity (*dashed line*) measured under Wetland 109 in St. Denis in January 10, 2002 as part of the soil sampling program by Jokic et al. (2003)

pond recession rates during periods of no precipitation and no runoff are explained by the water balance.

Based on Eq. 1, the water balance of the central pond is written as:

$$\frac{\Delta V_p}{\Delta \mathrm{t}} = A_p\left(P - E_p\right) + \left(A_c - A_p\right)R_p + G_p + O_p \tag{4}$$

where V_p (m^3) and A_p (m^2) are variable volume and area of the pond, respectively, and other symbols are the same as in Eq. 1 except that the subscript "p" indicates water inputs and outputs in the pond area, instead of the larger wetland area. For a period of no rain ($P = 0$), no runoff ($R_p = 0$), and no overflow ($O_p = 0$), Eq. 4 simplifies to

$$A_p \frac{\Delta \mathrm{h}}{\Delta \mathrm{t}} = -A_p E_p + G_p \tag{5}$$

where the volume change (ΔV_p) over a short time period (Δt) is approximated by the pond area multiplied by the change in water level (Δh). As mentioned earlier, most exchange between groundwater and the ponded wetland is primarily lateral through the high-*K* zone. Diurnal fluctuations of pond recession rates associated with diurnal fluctuations of the water table under the moist margin indicate that the majority of groundwater outflow is induced by water uptake by plants during the daytime (e.g., Sloan 1972; Hayashi et al. 1998a). Replacing the groundwater component (G_p) in Eq. 5 with evapotranspiration in the moist margin around the pond (E_m) having an area of A_m (Fig. 3), the pond water balance can be written as:

$$\frac{\Delta \mathrm{h}}{\Delta \mathrm{t}} = -E_p - \frac{A_m E_m}{A_p} \tag{6}$$

Assuming a ring-shaped moist margin (Fig. 3), A_m can be approximated by the product of the pond perimeter length (l) and the width of the moist margin (w). Evapotranspiration rates in the moist margin are expected to be roughly comparable to that in the pond (Shjeflo 1968) because both are not moisture limited (i.e. $E_p \cong E_m$), although this may not be strictly valid for small ponds surrounded by a dense tree ring shading direct sunlight and blocking wind flow over the pond (Hayashi et al. 1998b). Therefore, the recession rate c ($= -\Delta h/\Delta t$) is approximated by:

$$c = E_p + \left(wl/A_p\right)E_p = (1 + wn)E_p \tag{7}$$

where n (m^{-1}) is the ratio of pond perimeter to area ($= l/A_p$) (van der Kamp and Hayashi 2009). All data sets of Millar (1971) were consistent with Eq. 7 with w ranging between 5 and 15 m. This range of w estimated on the basis of Eq. 7 corresponds remarkably well to the typical widths of the "willow ring" or 'wet prairie zone", indicating that the water balance equations (Eqs. 4–6) provide a useful description of the internal dynamics of the wetland pond.

To demonstrate the fundamental importance of moist-margin evapotranspiration, a simple calculation assuming a

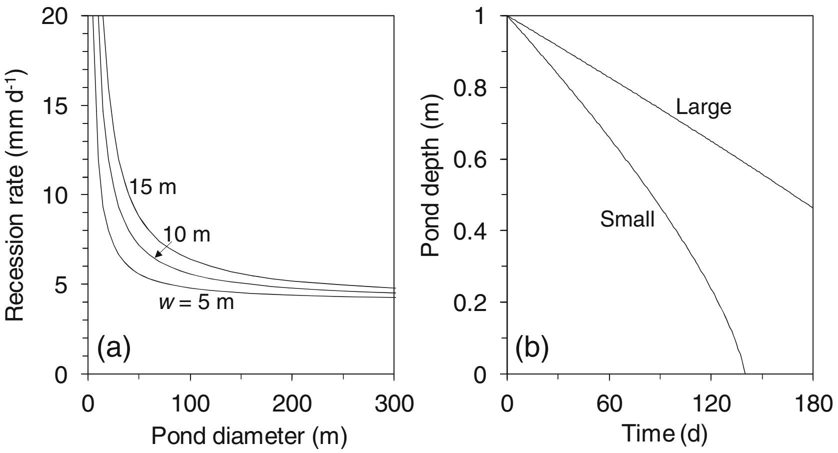

Fig. 7 **a** Recession rates of pond water level as a function of pond diameter and the width (w) of moist margin for a case of $E = 4$ mm d^{-1}. **b** Theoretical graph showing changes in pond water depth with time for ponds with large (200 m) and small (50 m) initial diameters

circle-shaped pond is useful. The l/A_p of a circle is equal to $4/d$, where d is the diameter. For a hypothetical case with $E_p = 4$ mm d^{-1}, the recession rate is roughly equal to E_p for large ponds and increases dramatically as pond size decreases (Fig. 7a). The relationship in Fig. 7a with $w = 10$ m is used for a hypothetical simulation of pond depth for an initial depth of 1 m in the beginning of a plant growing season (e.g., May 1). Figure 7b shows hypothetical pond-depth recessions for two wetland basins having parabolic slopes ($p = 2$ in Eq. 2) assuming a constant $E_p - P$ of 2 mm d^{-1} applied to the pond and moist margin throughout the entire growing season. The large basin has $s = 32{,}000$ m^2 and the small basin has $s = 2000$ m^2. The recession rate is higher from the start in the smaller pond than in the larger pond and increases non-linearly as the pond becomes smaller. The smaller pond disappears after three months, while the larger pond persists until the end of the growing season.

While this exercise is very simple, it demonstrates clearly that the variation of pond permanence in a given region is related to the size of the pond, whereby smaller ponds have shorter permanence because: 1) they have smaller lateral water inputs by runoff and by fill-spill overflow, and 2) they have larger outflow of shallow groundwater per area. The size of a wetland and its pond is determined by the size of its catchment that supplies runoff, as discussed below in the section on wetland and catchment areas, meaning that the holistic understanding of hydrological interactions between uplands and wetlands is key to understanding pond permanence and its effects on ecological processes.

Hydrological Understanding of Wetland Complexes

Landscape Position and Hydrological Connectivity of Wetlands

Prairie wetlands have a wide range of pond permanence depending on the amount of lateral inputs of water and evapotranspiration-related loss to pond margin vegetation (Fig. 2). Pond permanence also varies among wetlands depending on relative position within a landscape (spatial variability) and from year to year and decade to decade due to the variability in precipitation inputs and antecedent moisture conditions (temporal variability). Having a variety of pond permanence contributes to biological species diversity. Since each wetland has different hydrological and ecological functions (Stewart and Kantrud 1971), ecological integrity of the prairie landscape needs to be understood in the context of a wetland complex, rather than individual wetlands (Winter 1989; Euliss et al. 2004).

When hydrological studies of prairie wetlands started a half a century ago, researchers noted that those wetlands located in lower positions in the landscape tended to have more permanent ponds and higher salinity suggestive of groundwater inputs (Sloan 1972). Applying the emerging concept at the time of topography-driven groundwater flow system (Toth 1963) to prairie wetland settings, Lissey (1971) put forward a conceptual model in which topographically high wetlands that lose water to groundwater beneath them are called (groundwater) *recharge* wetlands. Wetlands in topographically low positions that receive groundwater are called *discharge* wetlands, and those in intermediate positions are called *flow-through* wetlands. This concept has been applied for explaining observed patterns of pond permanence and salinity in relation to topographic positions in numerous locations (Miller et al. 1985; LaBaugh et al. 1987), although Swanson et al. (1988) found no regional correlation between pond salinity and elevation. This concept also promoted a widespread notion by wetland conservationists and land-use managers that more permanent ponds in larger wetlands are maintained by groundwater discharge.

However, numerous studies of groundwater processes in the PPR since the 1960's have shown that the fundamental assumption made by Toth (1963) and Lissey (1971) regarding uniform hydraulic conductivity is not applicable to most of the

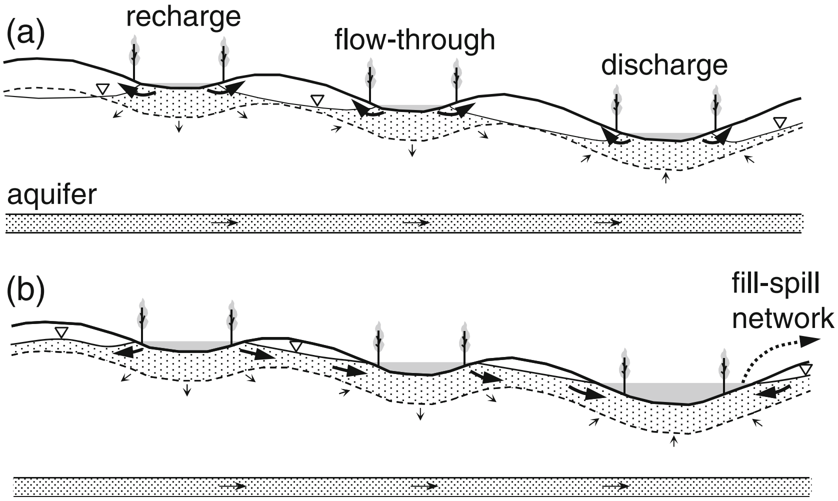

Fig. 8 Schematic diagram showing groundwater flow under wetlands. *Dashed lines* indicate the boundary between sediments with high and low hydraulic conductivity, *solid lines with triangles* indicate the water table, stippled area indicate the effective zone of groundwater flow, and the size of arrows indicate relative magnitude of flow. The wetland complex is underlain by an inter-till sand aquifer. **a** Normal condition. **b** Extremely wet condition. Adapted from van der Kamp and Hayashi (2009), with permission

PPR, where hydraulic conductivity in glacial tills sharply decreases (by several orders of magnitude) below the near-surface zone of 4–5 m (Winter 2003; van der Kamp and Hayashi 2009). For the majority of prairie wetland complexes underlain by glacial tills, active groundwater flow through the effective transmission zone (dotted region in Fig. 8) is largely limited to local areas around individual wetlands and between closely adjacent wetlands (Fig. 8a). Flow through the deeper zone is insignificant compared to other water-balance components (Eq. 1), even though adjacent wetlands may be hydraulically connected. Only during a period of extreme and persistent wet conditions (e.g., 1995–2000 in Cottonwood Lake or 2011–2015 in St. Denis, see Fig. 4), is the water table likely to remain close to the ground surface and provide effective shallow groundwater flow paths connecting multiple wetlands (Fig. 8b) or connecting wetlands to streams as documented by Brannen et al. (2015).

Hydrological connectivity among prairie wetlands is commonly provided by surface-water processes involving filling and spilling of wetlands (see *O* in Fig. 2) from higher to lower topographic (i.e., landscape) positions (Fig. 9) (Leibowitz and Vining 2003; Shaw et al. 2012) or merging of adjacent wetlands (Leibowitz et al. 2016). Fill-spill connections between neighboring wetlands have been observed in the earlier literature (e.g., Eisenlohr et al. 1972). However, such connections have become much more apparent during the recent wet period as compared to relatively dry conditions that prevailed during the earlier period (Fig. 4), and the recent availability of high-resolution satellite imageries and digital elevation models has revealed complicated fill-spill networks of numerous wetlands over a large spatial scale. This surface flow can also transport large amounts of dissolved salts and nutrients to lower-elevation wetlands.

Hydrological Positions and the Wetland Continuum

Euliss et al. (2004) proposed the wetland continuum to provide a useful framework for understanding the diverse ecological functions of prairie wetlands in the context of landscape position (spatial variability) and meteorological fluctuations between persistent dry and wet conditions (temporal variability). The spatial axis of the original wetland continuum was named "hydrologic relations to groundwater" (Euliss et al. 2004; Fig. 1), which may have been misinterpreted to overemphasize the role of long-range, deep groundwater flow on pond permanence. However, it is clear that pond permanence is controlled by a combination of surface-water processes through runoff inputs from uplands (*R* in Fig. 2) and fill-spill connections (Fig. 9), and groundwater exchange with the pond margin (Fig. 8a) and occasional connection with neighboring wetlands during extremely wet periods (Fig. 8b). Therefore, re-labeling the spatial axis of the wetland continuum as "hydrological position" will better serve the community of prairie wetland scientists by providing a more accurate representation of hydrological processes, without changing the usefulness of the original wetland-continuum concept. Figure 10 shows the wetland continuum using a revised spatial axis. Note that the original wetland continuum (Euliss et al. 2004) has a far broader scope than Fig. 10 as it links the hydrological variability to the variability of ecological processes.

Wetlands located in higher positions within a wetland complex tend to be smaller and have a less permanent pond with fresher water due to the strong influence of evapotranspiration in the moist margin (Fig. 7b). Wetlands located in lower positions tend to be larger and have a more permanent pond with higher salinity due to large amounts of water inputs by fill-

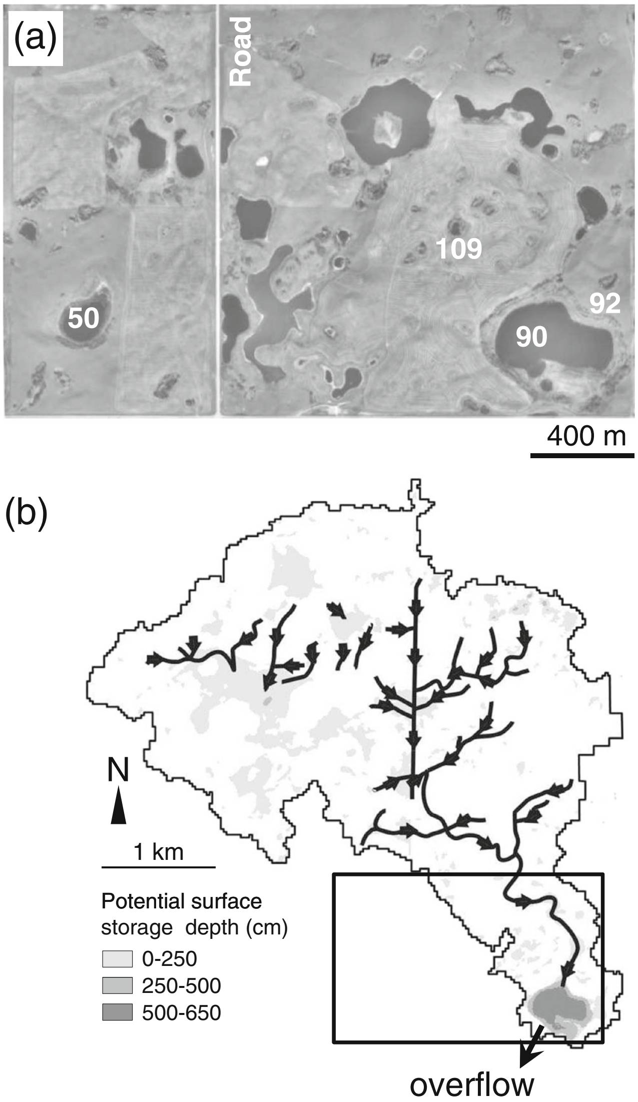

Fig. 9 **a** Surface connectivity among wetlands in the St. Denis study area, showing locations of Wetlands 50, 90, 92, and 109. **b** Contribution of fill-spill flow from a larger watershed outside of the study area. The terminal wetland started to overflow in 2008 (Modified after Shaw et al. 2012, with permission)

spill processes and the upward gradient of deep groundwater that prevents downward transport of solutes, even though the flow rate of deep groundwater is too small to be of any significance to pond permanence. During a dry condition, wetlands in higher positions function as independent hydrological systems, and those in lower positions have a limited connection to the fill-spill network (DRY row in Fig. 10). During a persistently wet condition, the entire fill-spill network becomes connected, and the subsurface connectivity is also established due to the high water table (WET row in Fig. 10). The spatial and temporal diversity of pond permanence and salinity, which can be called *hydro-diversity*, within a wetland complex is vital to the diversity of ecological processes in the wetland complex and beyond (Euliss et al. 2004).

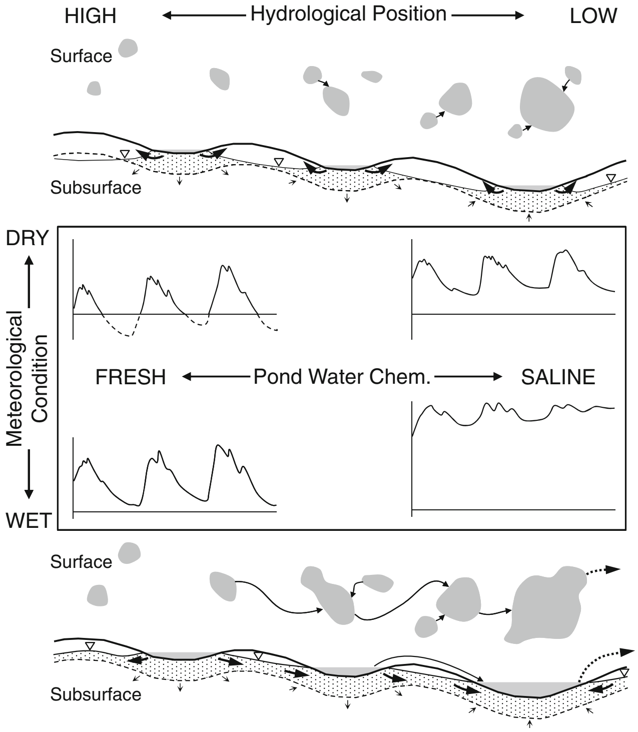

Fig. 10 The revised wetland continuum (Euliss et al. 2004). The horizontal axis represents hydrological positions in relation to surface and subsurface water. The vertical axis represents meteorological conditions depicting persistently dry and wet periods. In the middle panel, horizontal lines in graphs indicate the bottom elevation of wetland basin, solid curves indicate surface water level, and dashed curves indicate the groundwater table. In general, wetland ponds in higher positions tend to have fresher water compared to those in lower positions

Proportion of Wetland Area to Catchment Area

For the long-term (several decades or longer) average water balance of a hydrologically isolated wetland, or wetland complex within a closed drainage basin, the changes of water storage in the wetland are negligible in comparison to other terms ($\Delta S/\Delta t \cong 0$ in Eq. 1) and outflow from the basin (O) is zero. The net groundwater outflow from the wetlands to the catchment is generally very small owing to the low hydraulic conductivity of the glacial till, as is the case for groundwater flow to or from underlying regional aquifers. Thus G is usually much smaller than the other terms. Equation 1 can then be simplified to represent the steady-state condition of wetlands within a closed drainage basin:

$$(A_c - A_w)\,R \cong A_w\,(E - P) \tag{8}$$

Since A_w is much smaller than A_c, the ratio of wetland area compared to the catchment (A_w/A_c) is approximated from Eq. 8 by

$$A_w/A_c \cong A_w/(A_c - A_w) \cong @R/(E - P) \tag{9}$$

This provides a hydrological basis for the possible range of A_w/A_c in closed basins of the PPR, showing how wetland area depends on climate and water input from uplands. Long-term average values of R from uplands in the PPR have been reported in several studies. Ehsanzadeh et al. (2012) reported 24 mm y^{-1} based on 40 years of runoff records for a 4.9-ha cultivated experimental plot near Swift Current, Saskatchewan. Shook et al. (2015) reported 17 mm y^{-1} for the 43-year average spring-time runoff to a large wetland with a 55-ha cultivated watershed in St Denis. For both sites, the average annual precipitation is about 420 mm. Tiessen et al. (2010) reported average annual runoff of 70 mm from cultivated fields with clay-loam soils in the South Tobacco Creek watershed in southern Manitoba where the average precipitation was 516 mm. Hayashi and Farrow (2014) reported that 11-year average spring runoff in eleven catchments (0.4–2.4 ha) near Calgary, Alberta, ranged from 6 mm y^{-1} for unmanaged grassland to 20 mm y^{-1} in crop fields, where the average annual precipitation was 482 mm. In general, the annual runoff from cultivated prairie uplands is likely in the range of 20 to 70 mm with higher values for the regions with wetter climate or heavier-texture soils.

Shjeflo (1968) estimated an average value of $E - P$ for a number of wetlands in North Dakota of 270 mm y^{-1} (0.9 ft) which is similar to the value estimated by Su et al. (2000) from the water-balance analysis of a wetland in St. Denis. The range of $E - P$ in the PPR is expected to be on the order of 400 to 200 mm y^{-1} for the dry to the wet areas, respectively (Winter 1989). Together with the R values reported above, Eq. 9 gives values of A_w/A_c in a range from 5 to 35 %.

These estimates of A_w/A_c reflect the water balance at the wetland complex scale and can be compared with the reported data of wetland areas in the PPR. Hayashi et al. (1998b) compiled data for 12 wetlands from previous studies and reported an average A_w/A_c of 11 %. Haan and Johnson (1967) analyzed aerial photographs of four 1300-km^2 areas in Iowa and reported an average A_w/A_c of 9 %. Watmough and Schmoll (2007) reported an average A_w/A_c of 8 % over the 5.7×10^5 km^2 Canadian portion of the PPR in 2001, with a range of 5 to 10 % from the driest to the wettest regions. Analysis of 13 wetlands at Cottonwood Lake during the current high-stage period indicates an average A_w/A_c of 18 %. Dumanski et al. (2015) reported that wetland ponds occupied 24 % of the Smith Creek watershed in eastern Saskatchewan (near the wet eastern boundary of the PPR) in 1958, which had been reduced to10% in 2009 by drainage. In these wettest parts of the PPR many wetlands are likely to fill and spill during wet periods, thus leading to a reduction in the A_w/A_c ratio compared to what would be based on $R / (E - P)$. Allowing for the effects of fill and spill, wetland area lost to drainage, and for areas of lakes, all published studies indicate that A_w/A_c is in a range 5–25 % for prairie wetlands in internally drained watersheds.

The consistency between the range of A_w/A_c based on the long-term water balance (Eq. 9) and the range based on field observations indicates the strong controls of water balance on wetland areas in the PPR. It is likely that the landscape of the PPR has evolved over thousands of years to achieve the dynamic equilibrium maintained by various feedbacks among hydrological and ecological processes. Changes in $E - P$ associated with climate change or R associated with land-use change may shift the equilibrium and affect wetland areas.

Long-Term Fluctuations of Pond Water Level and Extent

Water Balance and Memory Effects

Long-term observations of water levels at well-maintained study sites provide critical insights into the hydrological responses of prairie wetland systems to meteorological variability (Winter and Rosenberry 1998; Johnson et al. 2010). Large-scale mapping of the historic extents of wetland ponds using aerial photographs (Zhang et al. 2009; Niemuth et al. 2010) or satellite images (Rover et al. 2011) complement detailed, but localized ground-based observations. There are general correlations between pond water levels (or area extents) and meteorological indices such as the standardized precipitation index (SPI) (WMO 2012), whereby a prolonged drought (e.g., 1989–1992, 2001–2003) draws water levels down (Fig. 4). However, individual wetlands have complex responses to meteorological "signals" depending on their water balance (Fig. 2), storage capacity (Fig. 6), and fill-spill connection with other wetlands (Fig. 9).

Figure 11 compares the SPI in Saskatoon, Saskatchewan, computed for 24-month time windows (WMO 2012) and pond water depth in several wetlands in St. Denis, located 40 km east of Saskatoon. Wetland 50 is located in a low landscape position and receives a small amount of groundwater discharge from the underlying aquifer (Heagle et al. 2013), but has a limited fill-spill network consisting of small wetlands. Due to its relatively large area (31,000 m^2), the summer pond level recession is not strongly affected by evapotranspiration from the moist margin (see large pond in Fig. 7b), and it retains water all year except during major droughts (Fig. 11b). In comparison, Wetland 109 is a small wetland (2400 m^2) located in a high landscape position (see HIGH in Fig. 10) and provides a small amount of recharge to deep groundwater in the underlying aquifer, estimated at 2 mm y^{-1} averaged over the area of its catchment (Hayashi et al. 1998b). It has a much faster summer recession than Wetland 50 due to evapotranspiration from the moist margin (small pond in Fig. 7b), and it usually dries out before winter (Fig. 11d). Due primarily to the difference in sizes of wetlands and their catchments, Wetland 109 responds more sensitively to changes in the SPI than

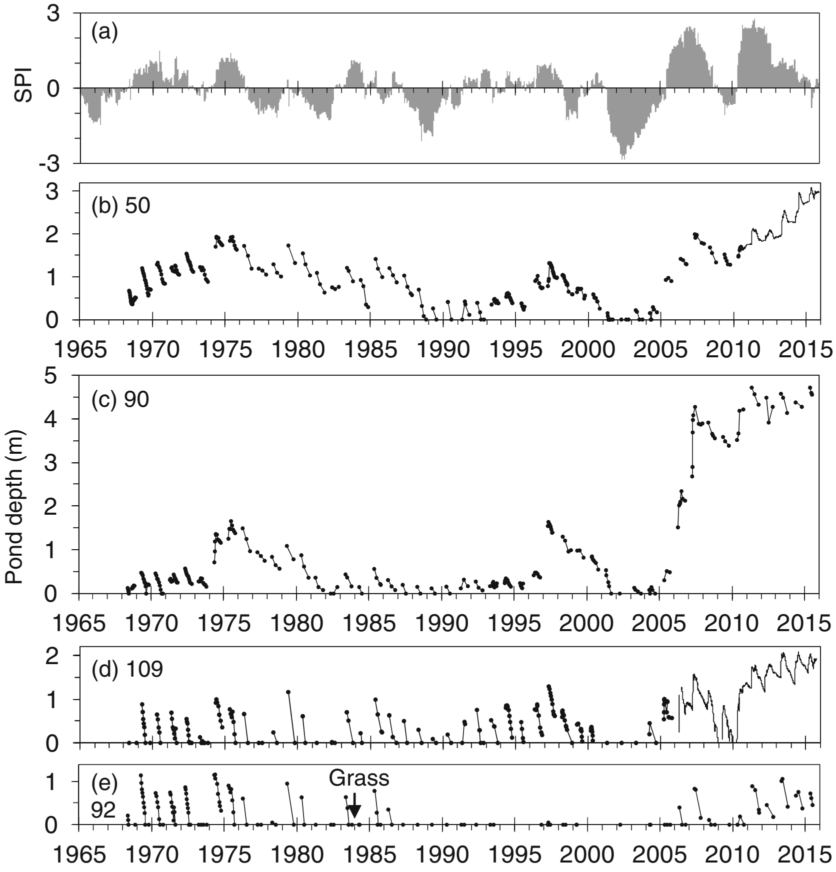

Fig. 11 Comparison of the standardized precipitation index (SPI) and pond water depths measured in wetlands in St. Denis (see Fig. 9a for locations). **a** 24-month SPI at Saskatoon. **b** Wetland 50 located in an independent basin in low landscape (i.e. discharge) setting. **c** Wetland 90 located in a near-terminal position of fill-spill network. **d** Wetland 109 in an independent basin in a high landscape (i.e. recharge) setting. **e** Wetland 92 in an independent basin in a high landscape setting. The land cover of 92 was changed from standard cropland to unmanaged grassland in 1983

Wetland 50, which has an ability to buffer inter-annual variability in meteorological conditions to some extent. In other words, wetlands like Wetland 50 have a longer-term "memory" of past meteorological conditions (Shook et al. 2015).

Wetland 90 is located at the end of a series of wetlands (Fig. 9a), and also near the end of a large fill-spill system (Fig. 9b) (see LOW in Fig. 10). The integrated drainage network of the fill-spill system was largely inactive until 2005. The system started to become fully connected in 2006–2007, and the pond water level in Wetland 90 rose by a disproportionately large magnitude compared to other wetlands in the area (Fig. 11b-e). The water level in Wetland 90 kept rising, and eventually it started to spill to the terminal basin located southwest (Fig. 9b). Due to continually wet conditions after 2007 (Fig. 11a), Wetland 90 continued to spill during most of the subsequent years, including the summer of 2013 when it received and spilled about 400,000 m^3 of water or the equivalent of 40 mm distributed over its 10 km^2 fill-spill catchment (Brannen et al. 2015).

Effects of Hydrological Processes on Solute Transport and Accumulation

Wetlands in low landscape positions often are in areas of upward groundwater flow (discharge setting in Fig. 8) and lack efficient mechanisms to export solutes, such as by recharging groundwater. Oxidized glacial tills in the PPR contain abundant sulphates (Van Stempvoort et al. 1994; Goldhaber et al. 2014), which are transported by surface and subsurface processes and accumulate in these discharge wetland basins over thousands of years (Nachshon et al. 2013). In some cases surface crusts of sulphates in a dried-up wetland may be transported by wind and deposited in the surrounding area (LaBaugh et al. 1996), but they are transported back to the wetland by runoff (Hayashi et al. 1998b). Since sharp increases in pond water level are primarily caused by inputs of fresh snowmelt water, pond water salinity temporarily drops after large flooding events (e.g., 2005–2007 in Fig. 11b and c). However, a large mass of subsurface salts beneath the pond gradually enters the pond water and re-establishes high-salinity conditions within several years (Heagle et al. 2013). Long-term reversals of the shallow groundwater flow towards the central pond may also transport salts back into the pond (Nachshon et al. 2014). Therefore, pond salinity should be observed over a long time period for reliable biogeochemical characterization of wetlands. This topic is discussed further by LaBaugh et al. (2016).

Soils within and around prairie wetlands reflect the long-term dissolution, precipitation, and transport of minerals associated with groundwater flow processes. The presence of hydric soil is the essential criterion defining a wetland (Gilbert et al. 2006; van der Kamp et al. 2016). Many prairie wetlands have a zone of salt accumulation called a "saline ring" reflecting the outward flow of groundwater towards the wetland margin (Mills and Zwarich 1986; Arndt and Richardson 1989; Hayashi et al. 1998b). Pennock et al. (2014) documented a consistent relationship between the occurrence of wetland soils and long-term water-level regimes of prairie wetlands with seasonal ponds. On the basis of detailed soil characterizations and 45 years of water-level records they found that hydric (or gleyed) soils are roughly limited to the area below the average maximum elevation of pond water. Additionally, they found that the hydric soil area was surrounded by an adjacent area of calcareous soils identified by the presence of secondary carbonates in the soil A-horizon that had accumulated due to the capillary rise and evapotranspiration in the moist margins of the wetland.

These accumulations of carbonate and sulfate salts at the outer margins of wetlands attest to the net long-term outflow of water from the center of the wetlands to the margins (*G*) in Eq. 1. However, these flows can be reversed during wet periods (Rosenberry and Winter 1997), and persistent reverse flows during prolonged wet periods (see LOW position wetlands in Fig. 10) can bring the accumulated sulfate salts back into the wetland leading to increases of pond water salinity (Nachshon et al. 2014; LaBaugh et al. 2016). The dynamics of pond water salinity associated with water-level fluctuations have a strong influence on the species compositions of wetland vegetation (Kantrud et al. 1989), invertebrates (McLean et al. 2016), amphibians, and avifauna (Euliss et al. 2004).

Effects of Land Use and Management

As shown above, runoff from the catchment is critical to the existence of prairie wetlands. Thus, the effects of upland land use and management on runoff have important implications for the long-term water balance of the wetlands. The main land covers in the PPR are dryland crops and perennial grasses. These contrasting land covers together with various management practices affect water supply to wetlands through various hydrological processes. Renton et al. (2015) reviewed the effects on runoff of different grassland management practices such as haying, grazing, burning, and leaving the grass undisturbed. Heavy grazing tends to lead to more rain runoff, likely due to soil compaction and removal of organic debris on the soil. However, the effects of various grass-management practices on snow water input to wetlands are less clear because of opposing effects: removal of vegetation leads to more snow transport to wetlands but also results in greater sublimation losses of snow (Fang and Pomeroy 2009) and reduced snowpack on the uplands. On the whole, reduction of grass cover and compaction of soil is expected to increase water supply to wetlands.

This was demonstrated at St Denis (van der Kamp et al. 2003), where conversion from croplands to unmanaged grasslands led to drying out of small wetland ponds within the grassed area. Wetlands 92 (Fig. 11e) and 109 (Fig. 11d) are similar in size and had similar patterns of water-level fluctuations prior to 1983, when the catchment of Wetland 92 was converted to grassland and that of Wetland 109 was kept as cropland. The pond in Wetland 92 dried out a few years after the conversion to grass, and has shown noticeably less recovery during the recent wet period commencing in 2004. The dramatic change is primarily attributed to the greatly increased infiltration capacity of the soils in the grass area due to the development of networks of large pores associated with decaying roots and animal burrows (Bodhinayake and Si 2004).

Cultivation and cropping practices in the PPR have undergone large changes in the past two or three decades, mostly involving a change-over to minimal tillage, continuous cropping, and leaving tall stubble on the fields (Awada et al. 2014). Cultivated summer fallow fields, common into the 1990's, are now a rarity. These changes, aimed in part at conserving moisture on upland crop areas, could possibly reduce the water supply to wetlands. However, long-term and well-planned field studies of the hydrological effects of different upland management practices within the PPR are surprisingly scarce, with few exceptions such as the aforementioned St. Denis study and a long-term observation by Tiessen et al. (2010) comparing runoff from conventionally tilled and lightly tilled (conservation tillage) fields in southern Manitoba. The latter found indications of somewhat reduced runoff in conservation-tillage fields but the difference was not statistically significant. The scarcity of well-designed studies of land-use effects is perhaps due to the logistical difficulty of carrying out long-term measurements in cropped and cultivated fields.

Hydrological Functions and Perceived Values of Wetlands

Functions of Wetlands and their Alteration

Prairie wetlands have obvious ecological functions providing essential habitat to flora and fauna. Much of the societal values of wetlands are based on these ecological functions. In addition, they have important hydrological functions including storing snowmelt and storm runoff water (Liu and Schwartz 2012; Shaw et al. 2012), recharging groundwater (van der Kamp and Hayashi 1998), and providing atmospheric moisture by evapotranspiration and enhancing summer precipitation by the recycled moisture (Parkhurst et al. 1998;

Mekonnen et al. 2014). Despite these important ecological and hydrological functions, a substantial percentage of prairie wetlands have been altered by anthropogenic activities including drainage and filling associated with agricultural production, removal of vegetation and cultivation during dry periods, excavating wetland basins, and industrial activities such as hydrocarbon extraction, road construction, and expansion of urban areas (Dahl 2014; McCauley et al. 2015). It is difficult to regulate the alteration of wetland habitats by farming practices, but many jurisdictions have implemented policies regarding the conservation and restoration of wetlands lost by industrial activities and urban development (e.g., Alberta Government 2013).

Flood Retention

The surface-water storage properties of prairie wetland depressions are visually obvious in the form of the numerous ponds that dot the prairie landscape in wet years. Several studies have evaluated average surface-water storage capacity in depressions over large areas within the PPR using aerial images and statistical analysis, for example, ca. 30 mm in the hummocky-moraine landscape of South Dakota (Hubbard and Linder 1986), ca. 90 mm in a 527-km^2 watershed in Minnesota (Gleason et al. 2007), and ca. 400 mm in a 196-km^2 area in North Dakota (Huang et al. 2011). Most of these numbers represent the "maximum" storage capacity for filling empty depressions to overflow depths, and may not actually represent the flood retention capacity, which is dependent on the antecedent water levels that vary substantially depending on meteorological conditions and memory effects (see Fig. 11).

In consequence of the water retention in depressions, a large fraction of the PPR is considered "internally drained" or "non-contributing" areas that are rarely or never connected to the continental rivers. Instead much of runoff is retained in individual depressions or drained to a terminal wetland or lake located in a deep basin through the large-scale fill-spill systems (Fig. 9). The high storage capacity (400 mm) reported by Huang et al. (2011) likely represents the effects of fill-spill storage, which would only be exceeded after a succession of very wet years. The dynamic connection and disconnection of fill-spill systems in response to variation of precipitation can have a major influence on the expansion and contraction of effective (i.e. contributing) drainage area and surface storage capacity (Shook and Pomeroy 2011).

The effects of artificial wetland drainage on downstream flooding have generated much interest in the hydrological literature. Drainage of wetlands in the PPR through ditches and subsurface tile systems is extensive: Ehsanzadeh et al. (2016) estimate that 30 % of wetland area has been drained in the Canadian portion of the PPR, and drainage is even more extensive in the American portion (Huang et al. 2011). Recent studies all agree that drainage will increase downstream flooding in some watersheds, but the magnitude of the effects remains uncertain. Ehsanzadeh et al. (2016) found that the outflow of most small watersheds has not been significantly affected by wetland drainage, except for one intensely drained basin, Smith Creek, in a topographically flat area in Saskatchewan. Dumanski et al. (2015) found that flows from the Smith Creek watershed have increased sharply in recent years, but concluded that the relative effects of wetland drainage, land-use changes, and changes in the amount and nature of precipitation need further investigation. McCauley et al. (2015) found that wetland drainage in North Dakota tended to lead to an increase in the ponded water areas of end-basin depressions and this can be considered a flooding impact although not on out-flowing streams. This suggests that increased runoff from drained wetlands may have little effect on flows in regional rivers unless the terminal wetlands and lakes are effectively drained to the rivers.

From the perspective of a long-term water balance (i.e. $\Delta S/\Delta t = 0$ in Eq. 1), a major increase in outflow (O) from a drained wetland or wetland complex requires a major reduction in evapotranspiration from the drained wetland area, if precipitation and runoff to the wetland area remain unchanged. After the initial adjustment in the water-balance equilibrium after drainage, a decline in the water table will increase subsurface storage capacity in the wetland area (Fig. 6b), compensating for the loss of surface storage capacity, while transpiration by crops and other vegetation will still remove water from the moist soil, perhaps at a rate that may be only slightly smaller than wetland evaporation. The aforementioned studies and many others indicate that the drainage effects on regional river systems still have a large degree of uncertainty, and reducing the uncertainty will require rigorous field-based long-term studies of surface and subsurface hydrological processes in wetland complexes.

Groundwater Recharge

Due to the semi-arid climate of the PPR, evapotranspiration during the plant-growing season consumes essentially all precipitation inputs on the uplands and leaves very little, if any, for groundwater recharge (Hayashi et al. 1998a). The transfer of runoff (R in Eq. 1) from uplands to depressions generates a sufficient amount of water input in excess of evapotranspiration demand, resulting in depression-focused groundwater recharge. The magnitude of recharge flux to underlying aquifers is relatively small (5–40 mm y^{-1}) (van der Kamp and Hayashi 1998) due to the low hydraulic conductivity of glacial tills below the effective transmission zone (see Fig. 8). Individual depressions occupy small areas, but numerous depressions distributed over a large area provide the critical recharge of regional groundwater for the PPR.

It is important to recognize that depression-focused recharge of aquifers occurs primarily under those wetlands in a recharge position (Fig. 8) as well as smaller depressions on uplands that may not be registered as wetlands in wetland inventories based on aerial-image analysis. Larger wetlands with more permanent ponds located in a discharge position may recharge shallow groundwater in the moist margin surrounding the wetland (Fig. 8a), but not contribute recharge to regional aquifers. Artificial drainage of small wetlands and upland depressions may divert the source of recharge (i.e. snowmelt water) to larger wetlands and, hence, reduce the amount of regional groundwater recharge.

Flood retention and groundwater recharge are commonly cited as the important "values" of wetlands, yet these perceived values are dependent on complex surface and subsurface hydrological processes. Different wetlands have different hydrological functions and values within a wetland complex. Policies regarding wetland conservation, restoration, and compensation need to consider an integrated value of the diversity of wetlands. It may not be appropriate to replace a groundwater recharge function (or value) of many small wetlands with a flood retention function of a large wetland.

Concluding Remarks and Recommendations

The water-balance approach provides a foundational understanding of hydrological functions of prairie wetlands. Recent studies summarized in this article have shown that it is critically important to consider wetlands and catchments as highly integrated hydrological units because the existence of prairie wetlands depends on lateral inputs of runoff water from their catchments in addition to direct precipitation. Our analysis of long-term water balances indicates that prairie wetlands require catchments that are roughly 3 to 20 times larger than the areas of those wetlands, depending on the climatic and geologic conditions within different parts of the PPR. This area proportion serves as a useful guide in considerations of how land management may affect particular wetlands. Because a wetland water balance is highly sensitive to the amount of runoff from catchments, land management (e.g., cultivation, grazing) designed to maintain or increase runoff can both conserve wetland habitat and reduce the uncertainty of wetland response to climate-change impacts. However, the effects of various cultivation practices on runoff are still poorly understood and little studied in spite of the fact that the great proportion of PPR uplands are cultivated and subject to ongoing changes of farming practices.

Artificial drainage of wetlands is consistently highlighted as a major concern with regard to flooding, stream-water quality, and groundwater recharge, yet there do not appear to have been any long-term field studies examining the effects of wetland drainage on both surface and subsurface storage. This article clearly demonstrates the importance of soil water and groundwater storage (Fig. 6), which have been largely neglected in the discussion of drainage effects. Previous studies have shown that hydrological responses of prairie wetlands to decadal-scale meteorological variability are complex, and sometimes unexpected. Carefully planned, long-term field experiments examining the effects of drainage and various land-use practices will be highly beneficial for filling the critical knowledge gaps.

The permanence of wetland ponds is largely determined by the amount of runoff inputs, which in turn depends on the size of the catchment and the conditions controlling runoff, such as precipitation and land use. It also depends on the hydrological position within a landscape (Fig. 10). The shallow groundwater exchange between a pond and its moist margin is a major component of the pond water balance, but recharge or discharge of deeper groundwater is usually a negligible component of the pond water balance. However, a small amount of groundwater discharge or recharge has strong effects on the salinity of wetland as it determines whether or not the wetland accumulates solutes over a long time.

The spatial and temporal diversity of pond permanence and salinity, or hydro-diversity within a wetland complex is vital to the diversity of ecological processes both within the wetland complex and the broader PPR landscape, as represented in the wetland continuum concept (Euliss et al. 2004). This article provides a refinement to the wetland continuum by clarifying the inter-connected roles of the surface-water connectivity via fill-spill networks and groundwater connectivity via active flow zones where hydraulic conductivity is enhanced by fractures and macropores. Policies regarding wetland conservation, restoration, and compensation need to consider an integrated value of the diversity of wetlands.

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