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THE WETLAND CONTINUUM: A CONCEPTUAL FRAMEWORK FOR INTERPRETING BIOLOGICAL STUDIES

Ned H. Euliss, Jr.[1], James W. LaBaugh[2], Leigh H. Fredrickson[3], David M. Mushet[1], Murray K. Laubhan[1], George A. Swanson[4], Thomas C. Winter[5], Donald O. Rosenberry[5], and Richard D. Nelson[6]

[1] *U.S. Geological Survey*
Northern Prairie Wildlife Research Center
8711 37th Street SE
Jamestown, North Dakota, USA 58401-7317

[2] *U.S. Geological Survey*
Mail Stop 411 National Center
12201 Sunrise Valley Drive
Reston, Virginia, USA 20192

[3] *Gaylord Memorial Laboratory*
University of Missouri
Route 1, Box 185
Puxico, Missouri, USA 63960

[4] *122 18th Avenue NE*
Jamestown, North Dakota, USA 58401

[5] *U.S. Geological Survey*
Mailstop 413 Denver Federal Center
Lakewood, Colorado, USA 80225

[6] *U.S. Bureau of Reclamation*
Dakotas Area Office
P.O. Box 1017
Bismarck, North Dakota, USA 58502

Abstract: We describe a conceptual model, the wetland continuum, which allows wetland managers, scientists, and ecologists to consider simultaneously the influence of climate and hydrologic setting on wetland biological communities. Although multidimensional, the wetland continuum is most easily represented as a two-dimensional gradient, with ground water and atmospheric water constituting the horizontal and vertical axes, respectively. By locating the position of a wetland on both axes of the continuum, the potential biological expression of the wetland can be predicted at any point in time. The model provides a framework useful in the organization and interpretation of biological data from wetlands by incorporating the dynamic changes these systems undergo as a result of normal climatic variation rather than placing them into static categories common to many wetland classification systems. While we developed this model from the literature available for depressional wetlands in the prairie pothole region of North America, we believe the concept has application to wetlands in many other geographic locations.

Key Words: amphibians, aquatic invertebrates, birds, climate, hydrology, hydrophytes, geochemistry, prairie potholes, wetlands, wildlife

INTRODUCTION

Traditional wetland classification systems (e.g., Stewart and Kantrud 1971, Cowardin et al. 1979) are useful for many purposes, including quantifying changes in wetland area and status of individual wetland types. However, these systems do not consider variability in short- and long-term climatic cycles that cause concomitant shifts in abiotic components integral to wetland processes and, ultimately, the biotic community that inhabits wetlands. For example, changes in precipitation patterns can influence wetland hydrology by altering the timing and amount of atmospheric and ground-water inputs, which alters important abiotic features (e.g., water depth, solute concentration, temperature, drying rate of exposed substrates) that influence the composition of wetland plant, invertebrate, and vertebrate communities.

Another shortcoming of many traditional systems is the failure to consider geomorphic setting in classifying wetlands explicitly. Inclusion of geomorphic setting is extremely important as evidenced by wetlands in close proximity to one another supporting remarkably different biological communities. This phenomenon was recognized by early scientists as reflected by the following statement: ''It sometimes happens that, in comparing two adjacent prairie ponds of closely similar general appearance, one is found to teem with animal life while the other is practically barren'' (Jewell 1927). Although Jewell was discussing prairie ponds in an unglaciated region within the middle of North America, similar observations of variability in plant and animal life have been made in the prairie pothole region (PPR) with respect to aquatic vegetation (Stewart and Kantrud 1972, Kantrud et al. 1989a, Robinson et al. 1997) and aquatic invertebrates (Kantrud et al. 1989b, Euliss et al. 1999). Although the Hydrogeomorphic Method developed by Brinson (1993) uses geomorphic setting, water source, and hydrodynamics as the primary factors to classify wetlands, the temporal component is not considered. Thus, there currently is no classification system that adequately captures these two important concepts that are known to determine wetland functions and values.

We believe that wetlands should be thought of as being within a spatial and temporal continuum that regulates critical wetland processes. Changes in these processes can result in a given wetland being classified differently through time. Ignoring such shifts tends to focus our ecological thinking about wetland processes into static rather than dynamic categories that hinders advancement of wetland science and management. Therefore, we have created a conceptual model that examines how the interplay between hydrologic input and climate determine the biological communities in wetlands. Our model is based on an extension of observations by earlier scientists (Shunk 1917, Jewell 1927), existing classification systems that relate vegetation to water permanence (Stewart and Kantrud 1971, Millar 1976, Cowardin et al. 1979), plant-salinity relationships of Stewart and Kantrud (1972), and the vegetation model of van der Valk and Davis (1978). The intent is to provide a method that can be used to complement existing classification systems by placing dynamic shifts in wetland class and function within an ecological context to improve interpretation among biological studies conducted in different locales and times. We use PPR wetlands as an example because previous research has expanded our understanding beyond individual wetland components of vegetation (Harris and Marshall 1963, van der Valk and Davis 1978), invertebrates (Euliss et al. 1999, Murkin and Ross 2000, Euliss et al. 2001), and waterfowl (Swanson and Duebbert 1989), to include long-term studies of water levels (van der Kamp and Hayashi 1998, Winter and Rosenberry 1998) and integration of ground-water relationships with studies of closed-basin depressional wetlands (G. A. Swanson et al. 1988, Winter and Rosenberry 1998, Brooks 2000, Brooks and Hayashi 2002). While we use the PPR because of the availability of existing research, these wetlands have similarities to many wetlands in other geographic locations (Tiner 2003). We term the relation of wetlands to atmospheric and ground-water inputs, and their combined influences on the abiotic and biotic features of wetlands, the wetland continuum concept.

THE WETLAND CONTINUUM CONCEPT

Although multidimensional, the wetland continuum is most easily represented as a two-dimensional gradient, with ground water and atmospheric water constituting the horizontal and vertical axis, respectively (Figure 1). The beginning and end points on the ground-water axis represent wetlands that function hydrologically to recharge ground water (hereafter referred to as recharge wetlands) and those that receive ground-water discharge (hereafter referred to as discharge wetlands), respectively. Wetlands that both recharge ground water and receive ground-water discharge are termed flow-through wetlands and occupy a spatial position between the endpoints on this axis (Figure 1). The proportion of ground-water discharge versus water lost to recharge strongly influences the hydrogeochemistry of flow-through wetlands. Although the physical location of a specific wetland does not change, its relationship to ground water does change on a seasonal or interannual basis. For example, in wet years or seasons, some wetlands might receive ground-water discharge and not lose water to recharge, whereas in dry years or seasons, the reverse could be true (Winter and Rosenberry 1995, LaBaugh et al. 1996, Rosenberry and Winter 1997, Conley and van der Kamp 2001). However, when interpreting ecological data, the spatial positions of individual wetlands along the ground-water axis of the wetland continuum are fixed since natural seasonal and interannual shifts in hydrologic function of specific wetlands are accounted for by the atmospheric water axis.

The vertical axis of the wetland continuum (Figure

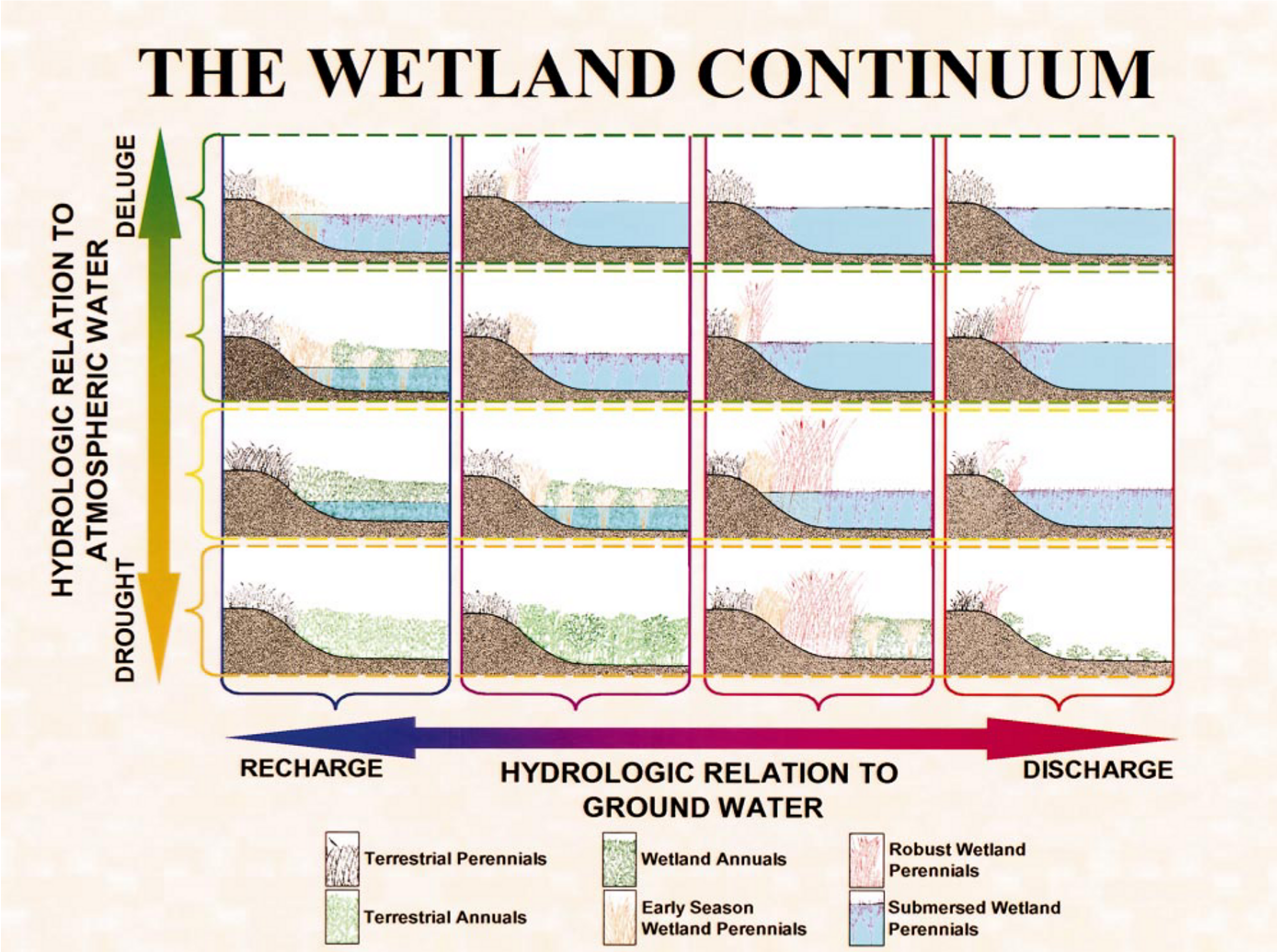

Figure 1. Here we provide a visual depiction of the Wetland Continuum. Wetlands located at the recharge end of the ''hydrologic relation to ground water'' axis recharge ground water but do not receive ground-water discharge. Wetlands at the discharge end of the same axis receive ground-water discharge but do not recharge ground water. Wetlands located between the two extremes are located along the axis based on their relative ratio of ground-water recharge to ground-water discharge. Potential plant communities in wetlands at four discrete points along this axis are depicted. The ''climate condition'' axis extends from drought to deluge. Again, the plant communities of the same four wetlands are depicted at different points in the drought-deluge cycle to show how community response to climatic change is largely dictated by the hydrologic relation to ground water.

1) represents the dynamics of atmospheric water caused by natural climatic (e.g., precipitation and temperature) variability that determines the ratio between atmospheric precipitation and evaporation. In the closed-basin wetlands of the PPR, this axis represents the largest annual input and loss of water (Winter and Rosenberry 1998). The end points of this axis range from drought (i.e., extremely dry) to deluge (i.e., extremely wet). At any given time, the relative location of a wetland on this axis determines the potential expression of the biological community. However, the position of a wetland on the atmospheric axis is constrained, or limited, by the position along the ground-water axis. Hence, both axes of the wetland continuum must be considered simultaneously to interpret observed biological phenomena correctly. Our hypothesis is that by locating the position of a wetland on both axes of the continuum, the potential biological expression of the wetland can be predicted at any point in time. Further, we argue that the biological expression will change temporally in response to short- and long-term changes in atmospheric conditions that influence the abiotic environment. Although interactions within the biotic community may determine the actual biological community, changes in the abiotic environment constrain such interactions.

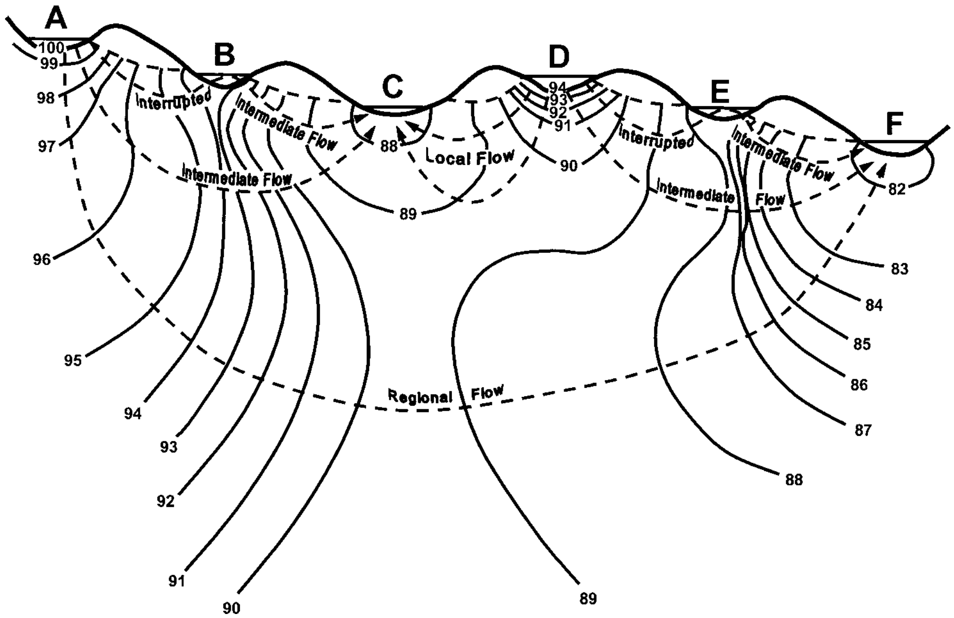

Figure 2. Schematic diagram of ground-water continuum. Solid lines are lines of equal hydraulic head; dashed lines indicate ground-water flow paths. A and D are recharge wetlands, B and E are flow-through wetlands, C is a discharge wetland for local and intermediate flow systems, and F is a discharge wetland for local, intermediate, and regional flow systems. (Modified from Lissey 1971)

DYNAMICS OF THE CONCEPT

Wetland processes respond to changes in abiotic and biotic components that are unique at various spatial scales. For example, wetlands in glaciated areas differ from wetlands in unglaciated areas with respect to numerous factors, including soils and hydrology. Similarly, individual wetlands within a geographic area differ depending on differences in the physical attributes of the wetland basin and catchment area. Thus, within specific geographic locations, only certain combinations and ranges of abiotic features (e.g., precipitation, evaporation, soil types, solute composition, mudflat drying rates) are possible for specific wetlands. Within these constraints, however, there remains great variability with respect to interactions among factors and, therefore, the biotic community supported in individual basins. It is within this spatial context that the wetland continuum concept provides insights to understanding how these abiotic factors interact and influence biotic composition.

The importance of land-surface form or ''landscape'' (Kratz et al. 1991) in affecting hydrogeochemical characteristics and processes has been outlined by Winter (2001). F. J. Swanson et al. (1988) defined ''landscape'' as ''the form of the land surface and associated ecosystems at scales of hectares to many square kilometers.'' According to Winter (2001), the fundamental hydrologic landscape unit is an upland separated from a lowland by an intervening steeper slope. Landscape position (i.e., elevation) on a regional scale often explains many chemical and biological properties of wetlands. The landscape of the glaciated prairie of North America is characterized by hummocky moraines and relatively flat outwash plains that contain many depressional wetlands (Winter 1989). Thus, the PPR contains numerous small hydrologic landscape units superimposed on a background matrix of prairie. One result of this configuration is that ground-water flow systems are complex (Figure 2) and cannot be inferred from topographic position alone (Lissey 1971, G.A. Swanson et al. 1988, Winter and Rosenberry 1995). However, temporary wetlands (Stewart and Kantrud 1971), also known as ephemeral and intermittent wetlands (Woo et al. 1993), generally are recharge wetlands, and seasonal wetlands (Stewart and Kantrud 1971) may be recharge or flow-through wetlands. Hence, temporary and seasonal wetlands lose water to evapotranspiration and to ground-water recharge. In contrast, semipermanent and permanent wetlands (Stewart and Kantrud 1971) usually function as flow-through or discharge wetlands and lose water to evapotranspiration. However, only flow-through semipermanent and permanent wetlands lose water to ground water.

Although atmospheric water is the largest water source for all PPR wetlands (Winter 1989), complex ground-water flow paths connecting prairie wetlands exert considerable influence on wetland chemistry because ground water is responsible for transporting the majority of solutes and other dissolved substances into and out of wetlands. Solute concentrations may be quite diluted during deluge or highly concentrated during drought, especially in wetlands that receive ground-water discharge. In discharge wetlands, solutes transported into basins accumulate when evapotranspiration removes surface water. Thus, wetlands that receive primarily ground-water discharge have greater salt concentrations than recharge or flow-through wetlands. The solute concentration of ground water discharging into flow-through or discharge wetlands varies in relation to flow-path length; ground water delivered to wetlands via shorter local flow systems is generally fresh in comparison to ground water discharging into wetlands from longer intermediate or regional flow systems (G. A. Swanson et al. 1988). Therefore, biotic components of wetlands are influenced not only by simple hydrologic conditions (i.e., water depth, hydroperiod) but also by abiotic characteristics associated with specific hydrologic conditions. Further, abiotic characteristics change in relation to interannual climate variation, which alters the relative importance of ground water and atmospheric water in wetlands (Figure 1). In the PPR, a highly variable and dynamic climate, in combination with poorly drained mineral soils, results in a wide array of dissolved salt concentration within and among wetlands. Salt concentrations in wetland waters can vary from fresh (Petri and Larson 1973) to nearly ten times the salinity of the world's oceans (Hammer 1978).

At any given point in time, the ground-water axis of the wetland continuum (Figure 1) reflects the potential concentration of dissolved salts in prairie wetlands (Sloan 1972, G. A. Swanson et al. 1988, LaBaugh et al. 1987, van der Kamp 1988, Arndt and Richardson 1989). Dissolved salt concentrations in these wetlands are a function of the chemistry of watershed soils, water depth and permanence, and the relative contribution of ground-water input that transports chemicals from the surrounding upland soils into wetlands. Wetlands receiving ground water tend to be more saline than those that do not receive ground water; however, as the relative quantity of atmospheric water increases, the solutes delivered to wetlands via ground-water flow paths are increasingly diluted. Hence, wetlands occupying a specific position on the ground-water axis, regardless of the total solute load within specific basins, will be fresher during wetter than drier periods.

Vegetation dynamics provide a good example of how biotic components of wetlands are influenced by abiotic characteristics associated with specific hydrologic conditions. These relationships are captured by both axes of the wetland continuum. In general, the atmospheric water axis emulates the vegetation cycle of wetlands described by Harris and Marshall (1963) and van der Valk and Davis (1978). In the PPR, alternating deluge and drought conditions caused by variable climate patterns are responsible for the cyclic nature of wetland productivity and plant community composition (Kantrud et al. 1989a). Prolonged inundation during deluge results in decreased availability of plant nutrients, whereas drought facilitates aerobic decomposition of accumulated macrophyte litter (Bärlocher et al. 1978) and other oxidative processes that enhance nutrient availability. When reflooded, these nutrients foster the development of new aquatic plant communities that contribute to the nutrient and detritus pool (Kadlec et al. 2000, van der Valk et al. 2000) and enhance overall wetland productivity, at least for a short time (Harris and Marshall 1963). The sharp increase in wetland productivity when wetlands reflood after dry periods is the reason wetland managers manipulate water levels to enhance waterfowl habitat (Cook and Powers 1958, Kadlec and Smith 1992), and it is the basis for the modern practice of moist-soil management (Fredrickson and Taylor 1982).

Harris and Marshall (1963) and van der Valk and Davis (1978) noted that a key to understanding differences in prairie wetlands was the magnitude and timing of water-level changes and whether or not they resulted from deliberate management decisions or natural climate cycles. Wetland sediments contain seed banks composed primarily of species produced during previous climate cycles. The seed bank is a vital component of van der Valk and Davis' (1978) conceptual model of plant dynamics in these prairie wetlands and is captured in the wetland continuum concept. As water levels decrease during drought, part or all of the wetland bottom is exposed, and seeds from terrestrial, mud-flat annuals, and emergent plants germinate (Harris and Marshall 1963). When such wetlands reflood, mud-flat annuals and terrestrial plants are replaced by emergent and submersed vegetation adapted to more aquatic conditions. Typically, this results in rather distinct vegetative zones that are related primarily to water-depth gradients. Although we rely on literature from the PPR in this manuscript, climate clearly exerts similar influences on the abiotic characteristics of all wetlands.

In contrast, the ground-water axis influences vegetation by moderating the residence time of surface water (i.e., hydroperiod), which influences the time and rate of natural drawdowns (Harris and Marshall 1963), solute concentrations (Stewart and Kantrud 1972), seed and egg bank composition (van der Valk and Davis 1978, Euliss and Mushet 1999, Gleason et al. 2003), and soil characteristics such as oxygen concentration and temperature (Harris and Marshall 1963). For example, a survey of the vegetation in nearly 200 wetlands of differing salinities enabled Stewart and

Kantrud (1972) to identify specific salinity tolerances for individual species of wetland plants in prairie potholes. Stewart and Kantrud (1971, 1972) also demonstrated that the salinity regimes in wetlands are related to the residence time of surface water in the basin: the shorter the residence time, the fresher the water was likely to be. In addition to seed banks, prairie wetlands also contain repositories of invertebrate eggs and organisms in resting stages that reflect past limnological conditions (Euliss et al. 1999, Murkin and Ross 2000, Euliss et al. 2001). ''Egg banks'' of aquatic invertebrates seem to retain their viability even during prolonged drought phases and are not easily destroyed by mechanical means such as freezing and thawing (Euliss et al. 1999, 2001, 2002). While flight is the most common dispersal and recolonization method for many insects, other wetland invertebrates survive unfavorable periods by means of eggs and cysts resistant to drying and freezing, diapause, aestivation, waterproof epiphragms (snails), burrowing, and inter-wetland transport (see review by Euliss et al. 1999). Increased water permanence is associated with increased diversity of invertebrates (Driver 1977, Euliss et al. 1999, Murkin and Ross 2000). Thus, changes in the hydrologic condition (i.e., drought to deluge) of a wetland (Kantrud et al. 1989b) not only affects wetland vegetation but also invertebrate community composition.

Just as the rise and fall of water levels in the prairie potholes affects aquatic vegetation and invertebrates, these changes also influence wetland use by vertebrates, especially waterfowl (Batt et al. 1989, Swanson and Duebbert 1989). Based on data collected in Canada and the United States between 1955 and 1985, waterfowl abundance and reproductive success were greater when more wetlands contained water in May than in years when fewer wetlands were flooded. Abundance of different species of waterfowl depended on the availability of their individual habitat requirements and their food preferences related to wetland productivity (Swanson and Duebbert 1989). The length of time any single wetland retained surface water in any one year and the salinity of the wetland were the major factors determining wetland use by different waterfowl species (Dreiwen and Springer 1969, Stewart and Kantrud 1973).

Amphibian communities are also strongly influenced by specific hydrologic conditions associated with both axes of the wetland continuum (Pechmann et al. 1989, Semlitsch et al. 1996). For instance, tiger salamanders (*Ambystoma tigrinum* (Green, 1825)) can produce metamorphs only in wetlands that retain water for at least 3 to 4 months (Semlitsch 1983). By contrast, the larval period of spadefoot toads (*Scaphiopus* spp.) can be as short as 21 days (Semlitsch 2000). Both adult and larval tiger salamanders are carnivorous and frequently occur at high densities exerting considerable predation pressure on other amphibian species (Morin 1981). Spadefoot toad tadpoles are extremely vulnerable to predation and are dependent on wetlands with hydroperiods too short to support predatory populations (Pechmann et al. 1989). In North Dakota, Euliss and Mushet (2004) documented a complete absence of plains spadefoot toad tadpoles (*Spea bombifrons* (Cope, 1863)) in wetlands with hydroperiods sufficiently long to allow the establishment of tiger salamander populations. They also found that populations of other anuran species were influenced greatly by predation pressures exerted by salamanders and predatory insects associated with longer wetland hydroperiods. Working in a Carolina bay wetland, Semlitsch et al. (1996) also concluded that pond hydroperiod was a primary source of variation in community structure for amphibians.

IMPLICATIONS OF THE CONCEPT

Historically, changes in wetland plant communities have been attributed to natural climatic variability or specific management actions (e.g., magnitude and timing of drying and reflooding), whereas little attention has been given to specific conditions at the site (Weller and Spatcher 1965, van der Valk and Davis 1978, Fredrickson and Taylor 1982). Many biologists describe, critique, and manipulate plant communities based on visible above-ground characteristics relative to some predetermined end point and largely ignore the importance of hydrogeochemical processes in determining site potential. Failure to consider site potential often results in implementing actions that have a low probability of success and may actually do greater harm than good relative to long-term wetland productivity. Therefore, thinking of a given wetland, or group of wetlands, in the context of a continuum is important because it provides a framework to conceptualize, describe, and understand the variability in biological communities.

To illustrate the potential utility of the wetland continuum for organizing biological data into ecological frameworks, we prepared additional figures to depict general patterns of biological variation that could be expected to occur in wetlands in the PPR. Information used to construct the figures was derived from published studies (Drewein and Springer 1969, Stewart and Kantrud 1972, Millar 1973, Stewart and Kantrud 1973, Weller and Fredrickson 1974, Millar 1976, Fredrickson and Reid 1986, McCrady et al. 1986, Wrubleski 1987, Batt et al. 1989, Kantrud et al. 1989a, Kantrud et al. 1989b, Swanson and Duebbert 1989, Poiani et al. 1996, Robinson et al. 1997, Euliss et al. 1999,

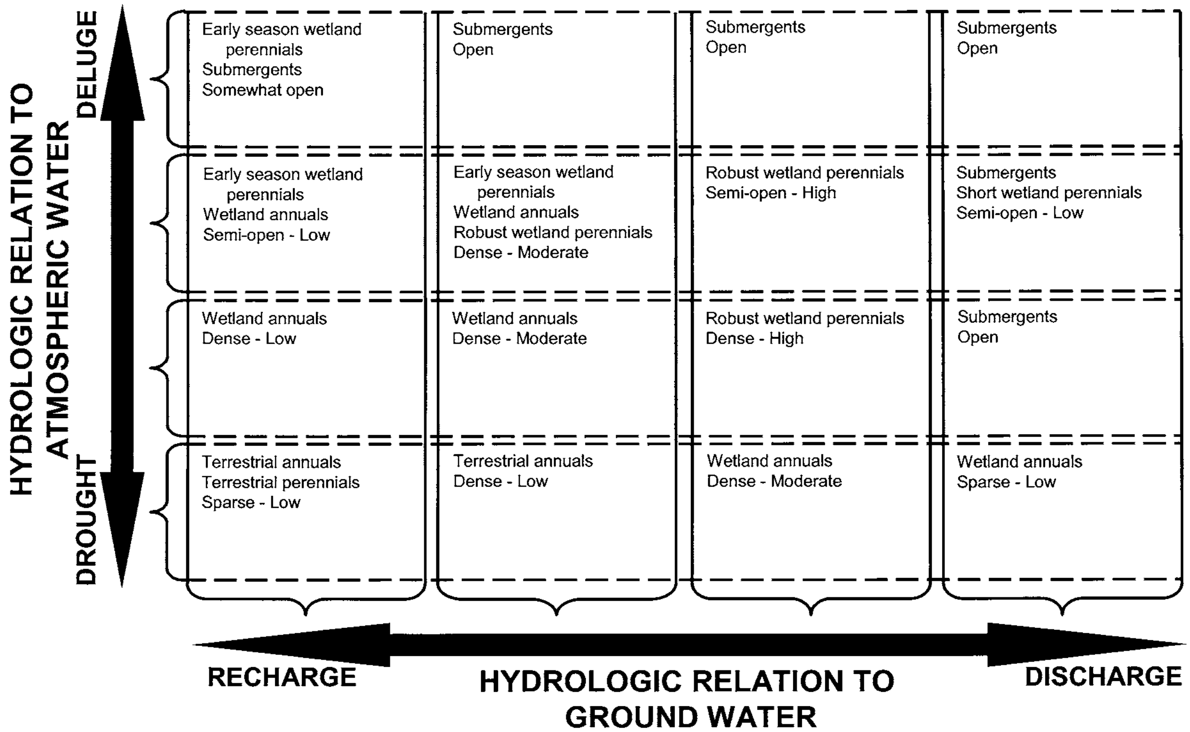

Figure 3. General pattern of plant community variation in wetlands along the spatial and temporal gradients of the wetland continuum.

Murkin and Ross 2000, Euliss et al. 2002, Isselstein et al. 2002). We purposely did not identify specific indicator species because taxonomic composition will vary considerably within the range of the hydrogeochemical conditions as a result of complex biotic interactions and varying tolerance ranges of individuals to environmental factors. Further, the continuum concept is not meant to drive management toward a predetermined end point; rather, it is intended to help scientists and managers understand the potential response of wetlands to direct and indirect perturbations.

Figures 1 and 3 illustrate that the seasonality, form, height, and density of vegetation in any particular wetland is a combined function of atmospheric water characteristics, ground-water characteristics, seed-bank composition, and solute composition and concentration. In the PPR, vegetation patterns in recharge wetlands varies from dry basins dominated by low-growing terrestrial plants during drought to somewhat open, freshwater wetlands dominated by early season perennial and submersed plants during deluge. In contrast, discharge wetlands located at the other end of the ground-water axis support low-growing, salt-tolerant wetland annuals during drought and submersed plants typical of more brackish conditions during deluge. Plant community composition in flow-through wetlands can vary greatly depending on wetland position relative to the recharge and discharge endpoints. Flow-through wetlands closest to the recharge endpoint have shorter hydroperiods and tend to contain reduced solute loads compared to flow-through wetlands situated closer to the discharge endpoint. However, the magnitude of the difference between these extremes is dependent on the position along the atmospheric water axis. In general, hydroperiod and solute concentrations, and therefore plant communities, among flow-through wetlands at different ends of the ground-water axis will vary most during drought and be most similar during deluge (Figure 3).

The composition of aquatic invertebrate communities in wetlands also varies within the hydrogeochemical boundaries defined by the wetland continuum (Figure 4). In the PPR, recharge wetlands support populations of terrestrial invertebrates during drought and aquatic invertebrates with mostly r-selected traits that are adapted for passive dispersal during deluge periods. During extended deluge periods, however, the invertebrate communities become more diverse and include active dispersers and species with k-selected traits (Euliss et al. 1999). During drought periods, the invertebrate communities of short hydroperiod, flow-through wetlands are similar to recharge wetlands because they typically support common terrestrial insects. However, these species are replaced by crustaceans when basins reflood and finally develop diverse assemblages of aquatic prey and predatory inverte-

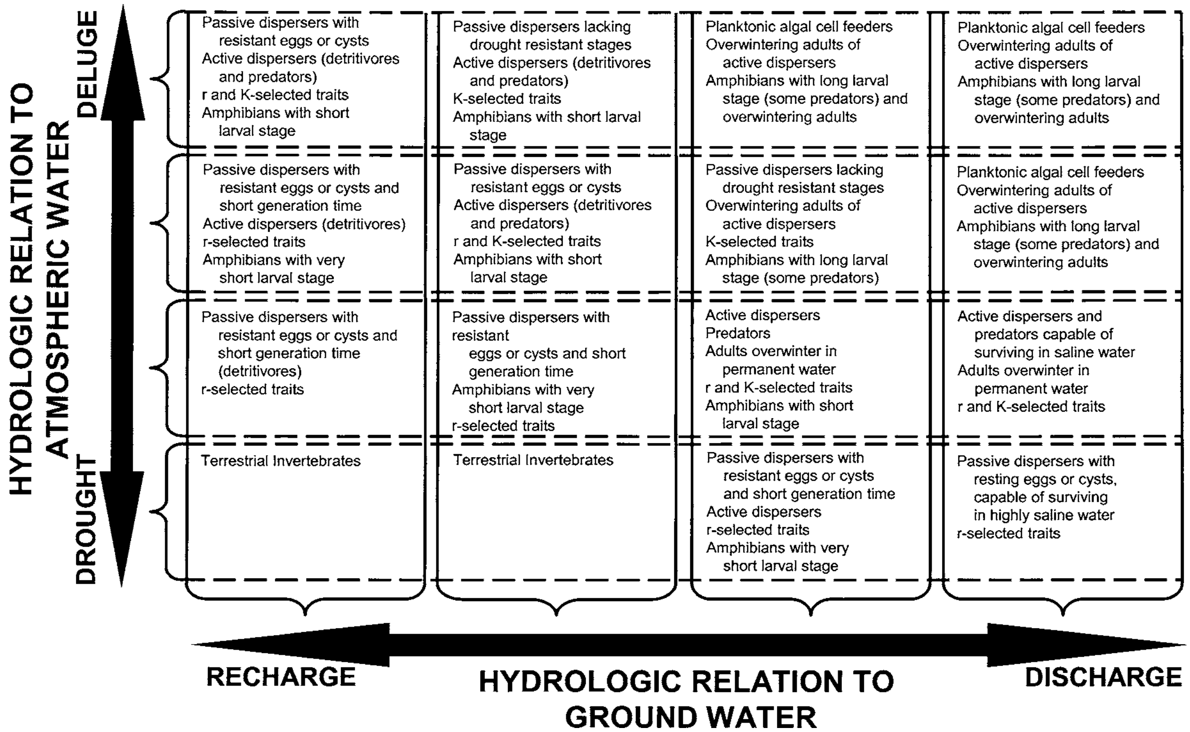

Figure 4. General pattern of invertebrate and amphibian community variation in wetlands along the spatial and temporal gradients of the wetland continuum.

brates adapted to fresher water during deluge periods (Figure 4). In contrast, discharge wetlands dry up infrequently and tend to pond water even during very dry periods. During extreme drought, these wetlands support mostly passive dispersers with r-selected traits, whereas, during deluge periods, viable populations of zooplankton and active dispersers develop. During extended deluge periods in the PPR, the solute concentration of water is diluted and salt-tolerant species such as brine shrimp (*Artemia salina* (Linnaeus, 1751)) are replaced by less salt-tolerant species.

Aquatic plants and invertebrates form the base of food webs for vertebrates; thus, it is not surprising that plant and invertebrate composition correlate well with the use of wetlands by amphibians and avifauna (Figures 4 and 5). The response of amphibians and birds to the processes driving the wetland continuum is indirect since the animals are mainly responding to habitat and food resources provided by vegetation and invertebrates. The mobility of wetland-dependent avifauna allows them to exploit diverse wetland landscapes over large geographic areas as necessary for completion of necessary life-cycle events. This is most likely in regions with great variation in wetland size, type, and function, where the resulting biodiversity provided by variable water depth, substrate conditions, and plant and invertebrate communities provides the proper ecological and habitat niches for a varied avifauna to exploit (Fredrickson and Reid 1986, Weller 1999). Some avifauna can successfully exploit a wide range of conditions (e.g., mallard [*Anas platyrhynchos* Linnaeus, 1758]), but others are restricted to specific habitat niches (e.g., American avocet [*Recurvirostrata americana* J. F. Gmelin, 1789]). The same general paradigm may apply to amphibians, although they are less mobile and respond to diverse wetland landscapes at smaller spatial scales.

Uplands are a dominant part of the prairie wetland landscape, and the relationships between wetlands and the surrounding uplands can have a major effect on the use of wetlands by biota (Naugle et al. 1999). Land-use practices clearly affect water levels through draining, ditching, and increased watershed erosion (Leitch 1989, Euliss and Mushet 1996). Agricultural land also has altered the biotic communities of wetlands by influencing water quality in wetlands, especially sediments that have a negative influence on seed and egg banks (Gleason et al. 2003). Although we have focused on the fundamental elements affecting wetlands in undisturbed landscapes in this paper, the wetland continuum concept can be applied to disturbed landscapes. In many respects, this may be one of the most appropriate uses of the continuum concept because understanding changes in processes is a critical foundation of scientific investigations, evaluating site

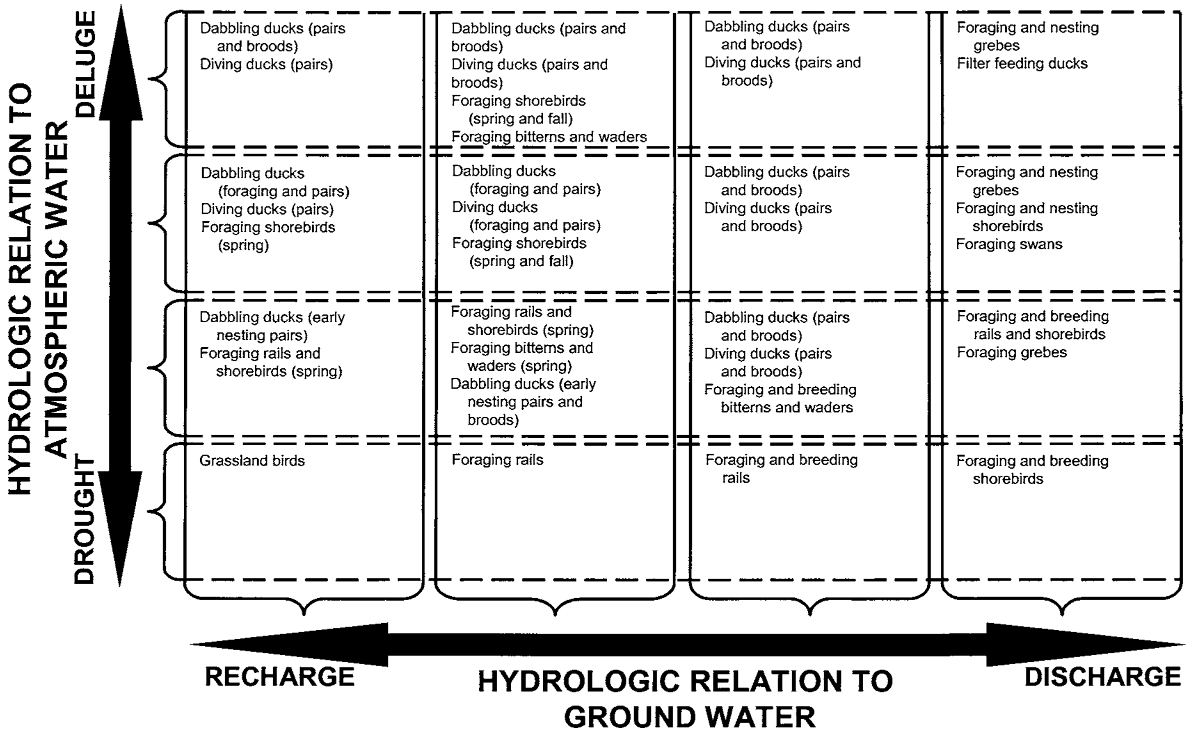

Figure 5. General pattern of bird community variation in wetlands along the spatial and temporal gradients of the wetland continuum.

potential, and developing sound wetland management plans.

SUMMARY

The interplay of climate conditions and ground water in relation to wetland processes can be used to integrate predictable and observable biological features of prairie wetlands in a manner similar to that provided by Vannote et al. (1980) for integrating predictable and observable features of lotic systems with the river continuum concept. There is a need to merge hydrologic and ecologic classifications as a means to improve organization of our knowledge about biological shifts in response to climate-driven changes in the hydrogeochemical characteristics of prairie wetlands. Further, a conceptual framework that places ecological studies into the proper hydrologic and climatic framework enhances our knowledge of wetland ecology by facilitating valid comparisons among studies, ensuring that research data are properly evaluated, and reducing misinterpretations of data. We propose that the wetland continuum concept described herein provides such a useful framework.

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LITERATURE CITED

Arndt., J. L. and J. L. Richardson. 1989. Geochemistry of hydric soil salinity in a recharge-throughflow-discharge prairie-pothole wetland system. Soil Science Society of America Journal 53:848–855.

Bärlocher, F., R. J. Mackay, and G. B. Wiggins. 1978. Detritus processing in a temporary vernal pool in southern Ontario. Archiv für Hydrobiologie 81:269–295.

Batt, B. D. J., M. G. Anderson, C. D. Anderson, and F. D. Caswell. 1989. The use of prairie potholes by North American ducks. p. 2–14. *In* A. G. van der Valk (ed.) Northern Prairie Wetlands. Iowa State University Press, Ames, IA, USA.

Brinson, M. M. 1993. A hydrogeomorphic classification for wetlands. U. S. Army Corps of Engineers Waterways Experiment Station, Vicksburg, MS, USA. Wetlands Research Program Technical Report WRP-DE-4.

Brooks, R. T. 2000. Annual and seasonal variation and the effects of hydroperiod on benthic macroinvertebrates of seasonal forest (''vernal'') ponds in central Massachusetts, USA. Wetlands 20: 707–715.

Brooks, R. T. and M. Hayashi. 2002. Depth-area-volume and hydroperiod relationships of ephermeral (vernal) pools in southern New England. Wetlands 22:247–255.

Conley, F. M. and G. van der Kamp. 2001. Monitoring the hydrology of Canadian prairie wetlands to detect the effects of climate change and land use changes. Environmental Monitoring and Assessment 67:195–215.

Cook, H. H. and C. F. Powers. 1958. Early biochemical changes in the soils and waters of artificially created marshes in New York. New York Fish and Game Journal 5:9–65.

Cowardin, L. M., V. Carter, F. C. Golet, and E. T. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United

States. U. S. Fish and Wildlife Service, Washington, DC, USA. FWS/OBS-79/31.

Drewein, R. C. and P. F. Springer. 1969. Ecological relationships of breeding blue-winged teal to prairie potholes. Transactions of the Saskatoon Wetlands Seminar. Canadian Wildlife Service Report Series 6:102–115.

Driver, E. A. 1977. Chironomid communities in small prairie ponds: some characteristics and controls. Freshwater Biology 7:121–133.

Euliss, N. H., Jr. and D. M. Mushet. 1996. Water-level fluctuation in wetlands as a function of landscape condition in the prairie pothole region. Wetlands 16:587–593.

Euliss, N. H., Jr. and D. M. Mushet. 1999. Influence of agriculture on aquatic invertebrate communities of temporary wetlands in the prairie pothole region of North Dakota, USA. Wetlands 19:578–583.

Euliss, N. H., Jr. and D. M. Mushet. 2004. Impacts of water development on aquatic macroinvertebrates, amphibians, and plants in wetlands of a semi-arid landscape. Aquatic Ecosystem Health and Management 7:1–12.

Euliss, N. H., Jr., D. M. Mushet, and D. H. Johnson. 2001. Use of macroinvertebrates to identify cultivated wetlands in the prairie pothole region. Wetlands 21:223–231.

Euliss, N. H., Jr., D. M. Mushet, and D. H. Johnson. 2002. Use of aquatic invertebrates to delineate seasonal and temporary wetlands in the prairie pothole region of North America. Wetlands 22:256–262.

Euliss, N. H., Jr., D. A. Wrubleski, and D. M. Mushet. 1999. Invertebrates in Wetlands of the Prairie Pothole Region—Species Composition, Ecology, and Management. p. 471–514. *In* D. Batzer, R. B. Rader, and S. A. Wissinger (eds.) Invertebrates in Freshwater Wetlands of North America—Ecology and Management. John Wiley and Sons, Inc., New York, NY, USA.

Fredrickson, L. H. and F. A. Reid. 1986. Wetland and riparian habitats: a nongame management overview. p. 59–96. *In* J. B. Hale, L. B. Best, and R. L. Clawson (eds.) Management of Nongame Wildlife in the Midwest: a Developing Art. BookCrafters, Chelsea, MI, USA.

Fredrickson, L. H. and T. S. Taylor. 1982. Management of seasonally flooded impoundments for wildlife. U. S. Fish and Wildlife Service, Resource Publication 148.

Gleason, R. A., N. H. Euliss, Jr., D. E. Hubbard, and W. G. Duffy. 2003. Effects of sediment load on emergence of aquatic invertebrates and plants from wetland soil egg and seed banks. Wetlands 23:26–34.

Hammer, U. T. 1978. The Saline Lakes of Saskatchewan, III. Chemical characterization. International Revue der Gesamten Hydrobiologie 63:311–335.

Harris, S. W. and W. H. Marshall. 1963. Ecology of water-level manipulations on a northern marsh. Ecology 44:331–343.

Isselstein, J., J. R. B. Tallowin, and R. E. N. Smith. 2002. Factors affecting seed germination and seedling establishment of fen-meadow species. Restoration Ecology 10:173–184.

Jewell, M. E. 1927. Aquatic biology of the prairie. Ecology 8:289–298.

Kadlec, J. A., H. A. Murkin, and A. G. van der Valk. 2000. The baseline and deep-flooding years. p. 55–74. *In* H. A. Murkin, A. G. van der Valk, and W. R. Clark (eds.) Prairie Wetland Ecology: The Contribution of the Marsh Ecology Research Program. Iowa State University Press, Ames, IA, USA.

Kadlec, J. A. and L. M. Smith. 1992. Habitat management for breeding areas. p. 590–610. *In* B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu (eds.) Ecology and Management of Breeding Waterfowl. University of Minnesota Press, Minneapolis, MN, USA.

Kantrud, H. A., J. B. Millar, and A. G. van der Valk. 1989a. Vegetation of wetlands of the prairie pothole region. p.132–187. *In* A. G. van der Valk (ed.) Northern Prairie Wetlands. Iowa State University Press, Ames, IA, USA.

Kantrud, H. A., G. L. Krapu, and G. A. Swanson. 1989b. Prairie basin wetlands of the Dakotas: a community profile. U. S. Fish and Wildlife Service, Washington, DC, USA. Biological Report 85.

Kratz, T. K., B. J. Benson, E. R. Blood, G. L. Cunningham, and R. A. Dahlgren. 1991. The influence of landscape position on temporal variability in four North American ecosystems. American Naturalist 138:355–378.

LaBaugh, J. W., T. C. Winter, V. A. Adomaitis, and G. A. Swanson. 1987. Hydrology and chemistry of selected prairie wetlands in the Cottonwood Lake area, Stutsman County, North Dakota, 1979–82. U. S. Geological Survey Professional Paper 1431.

LaBaugh, J. W., T. C. Winter, G. A. Swanson, D. O. Rosenberry, R. D. Nelson, and N. H. Euliss, Jr. 1996. Changes in atmospheric patterns affect midcontinent wetlands sensitive to climate. Limnology and Oceanography 41:864–870.

Leitch, J. A. 1989. Politicoeconomic overview of prairie-potholes. p. 2–14. *In* A. G. van der Valk (ed.) Northern Prairie Wetlands. Iowa State University Press, Ames, IA, USA.

Lissey, A. 1971. Depression-focused transient groundwater flow patterns in Manitoba. Geological Association of Canada Special Paper No. 9:333–341.

McCrady, J. W., W. A. Wentz, and R. L. Linder. 1986. Plants and invertebrates in a prairie wetland during duck brood-rearing. Prairie Naturalist 18:23–32.

Millar, J. B. 1973. Vegetation changes in shallow marsh wetlands under improving moisture regime. Canadian Journal of Botany 51: 1443–1457.

Millar, J. B. 1976. Wetland classification in western Canada: a guide to marshes and shallow open water wetlands in the grasslands and parklands of the prairie provinces. Canadian Wildlife Service, Ottawa, ON, Canada. Report Series No. 37.

Morin, P. J. 1981. Predatory salamanders reverse the outcome of competition among three species of anuran tadpoles. Science 212: 1284–1286.

Murkin, H. R. and L. C. M. Ross. 2000. Invertebrates in prairie wetlands. p. 201–247. *In* H. R. Murkin, A. G. van der Valk, and W. R. Clark (eds.) Prairie Wetland Ecology: the Contribution of the Marsh Ecology Research Program. Iowa State University Press, Ames, IA, USA.

Naugle, D. E., K. F. Higgins, S. M. Nusser, and W. C. Johnson. 1999. Scale-dependent habitat use in three species of prairie wetland birds. Landscape Ecology 14:267–276.

Pechmann, J. H. K., D. E. Scott, J. W. Gibbons, and R. D. Semlitsch. 1989. Influence of wetland hydroperiod on diversity and abundance of metamorphosing juvenile amphibians. Wetlands Ecology and Management 1:3–11.

Petri, L. R. and L. R. Larson. 1973. Quality of water in selected lakes of eastern South Dakota. South Dakota Water Resources Commission Report No. 1.

Poiani, K. A., W. C. Johnson, G. A. Swanson, and T. C. Winter. 1996. Climate change and northern prairie wetlands: simulations of long-term dynamics. Limnology and Oceanography 41:871–881.

Robinson, G. G. C., S. E. Gurney, and L. G. Goldsborough. 1997. Response of benthic and plankton algal biomass to experimental water-level manipulation in a prairie lakeshore wetland. Wetlands 17:167–181.

Rosenberry, D. O. and T. C. Winter. 1997. Dynamics of water-table fluctuations in an upland between two prairie-pothole wetlands in North Dakota. Journal of Hydrology 191:266–289.

Semlitsch, R. D. 1983. Structure and dynamics of two breeding populations of the eastern tiger salamander, *Ambystoma tigrinum*. Copeia 1983:608–616.

Semlitsch, R. D. 2000. Principles for management of aquatic breeding amphibians. Journal of Wildlife Management 64:615–631.

Semlitsch, R. D., D. E. Scott, J. H. K. Pechmann, and J. W. Gibbons. 1996. Structure and dynamics of an amphibian community: evidence from a 16-year study of a natural pond. p. 217–248. *In* M. L. Cody and J. A. Smallwood (eds.) Long-term Studies of Vertebrate Communities. Academic Press, San Diego, CA, USA.

Shunk, R. A. 1917. Plant associations of Shenford and Owego Townships, Ransom County, North Dakota, MS Thesis. University of North Dakota, Grand Forks, ND, USA.

Sloan, C. E. 1972. Ground-water hydrology of prairie potholes in North Dakota. U. S. Geological Survey Professional Paper 585, (C): C1–C28.

Stewart, R. E. and H. A. Kantrud. 1971. Classification of natural

ponds and lakes in the glaciated prairie region. Bureau of Sport Fisheries and Wildlife, Washington, DC, USA. Resource Publication 92.
Stewart, R. E. and H. A. Kantrud. 1972. Vegetation of prairie potholes, North Dakota, in relation to quality of water and other environmental factors. U.S. Geological Survey Professional Paper 585-D.
Stewart, R. E. and H. A. Kantrud. 1973. Ecological distribution of breeding waterfowl populations in North Dakota. Journal of Wildlife Management 37:39–50.
Swanson, G. A., T. C. Winter, V. A. Adomaitis, and J. W. LaBaugh. 1988. Chemical characteristics of prairie lakes in south-central North Dakota—their potential for impacting fish and wildlife. U. S. Fish and Wildlife Service, Washington, DC, USA. Technical Report 18.
Swanson, G. A. and H. F. Duebbert. 1989. Wetland habitats of waterfowl in the Prairie Pothole Region. p. 228–267. *In* A. G. van der Valk (ed.) Northern Prairie Wetlands. Iowa State University Press, Ames, IA, USA.
Swanson, F. J., T. K. Kratz, N. Caine, and R. G. Woodmansee. 1988. Landform effects on ecosystem patterns and processes. Bioscience 38:92–98.
Tiner, R. W. 2003. Geographically isolated wetlands of the United States. Wetlands 23:494–516.
van der Kamp, G. 1988. The water and salt balance of prairie wetlands in relation to groundwater flow. p. 115–127 *In* Proceedings of the symposium on water management affecting the wet-to-dry transition: Planning on the margins. Water Studies Institute, Regina, Saskatchewan, Canada.
van der Kamp, G. and M. Hayashi. 1998. The groundwater recharge function of small wetlands in the semi-arid northern prairies. Great Plains Research 8:39–56.
van der Valk, A. G. and C. B. Davis. 1978. The role of seed banks in the vegetation dynamics of prairie glacial marshes. Ecology 59: 322–335.
van der Valk, A. G., H. A. Murkin, and J. A. Kadlec. 2000. The drawdown and reflooding years. p. 55–74. *In* H. A. Murkin, A. G. van der Valk, and W. R. Clark (eds.) Prairie Wetland Ecology: The Contribution of the Marsh Ecology Research Program. Iowa State University Press, Ames, IA, USA.
Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The River Continuum Concept. Canadian Journal of Fisheries and Aquatic Science 37:130–137.
Weller, M. W. 1999. Wetland Birds. Cambridge University Press, Cambridge, UK.
Weller, M. W. and L. H. Fredrickson. 1974. Avian ecology of a managed glacial marsh. The Living Bird 12:269–281.
Weller, M. W. and C. S. Spatcher. 1965. Role of habitat in the distribution and abundance of marsh birds. Iowa Agriculture and Home Economics Experimental Station, Ames, IA, USA. Special Report 43.
Winter, T. C. 1989. Hydrologic studies of wetlands in the Northern Prairie. p. 16–54. *In* A. G. van der Valk (ed.) Northern Prairie Wetlands. Iowa State University Press, Ames, IA, USA.
Winter, T. C. 2001. The concept of hydrologic landscapes. Journal of the American Water Resources Association 37:335–349.
Winter, T. C. and D. O. Rosenberry. 1995. The interaction of ground water with prairie pothole wetlands in the Cottonwood Lake Area, east-central North Dakota, 1979–1990. Wetlands 15:193–211.
Winter, T. C. and D. O. Rosenberry. 1998. Hydrology of prairie pothole wetlands during drought and deluge: a 17-year study of the Cottonwood Lake wetland complex in the perspective of longer term and proxy hydrological records. Climatic Change 40: 189–209.
Woo, M. K., R. D. Roswell, and R. G. Clark. 1993. Hydrological classification of Canadian prairie wetlands and prediction of wetland inundation in response to climatic variability. Canadian Wildlife Service Occasional Paper No. 79.
Wrubleski, D. A. 1987. Chironomidae (Diptera) of peatlands and marshes in Canada. Memoirs of the Entomological Society of Canada 140:141–161.

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