Northern prairie wetlands occupy the expansive prairie pothole region (PPR) in central North America (figure 1). The PPR covers approximately 800,000 square kilometers (km²) and is delineated by two elements: (1) late Pleistocene (Wisconsin) glaciation that left millions of small depressions on the landscape and (2) a relatively dry and strongly seasonal climate supporting grassland vegetation (Tiner 2003).

The PPR and the larger Great Plains region extending southward have a notoriously extreme and variable climate (Woodhouse and Overpeck 1998). The climate is punctuated by severe droughts and deluges that influence both natural and human-dominated ecosystems. For example, drought in the 1930s produced major geographic shifts of grassland communities, killed millions of riparian trees, and caused massive economic losses to agriculture (Albertson and Weaver 1942). Conversely, deluges in the 1990s filled lakes and wetlands and flooded farms, towns, and roads (Winter and Rosenberry 1998, Johnson et al. 2004, Shapley et al. 2005).

These weather extremes are particularly important for the long-term productivity and biodiversity of semipermanent prairie wetlands that occupy deeper basins than associated seasonal and temporary wetland classes (van der Valk and Davis 1978). Low water and occasional drying of the wetland bottom during droughts (dry marsh phase) stimulate plant recruitment from a diverse seed bank and increase productivity by mobilizing nutrients. In contrast, high water during deluges (lake marsh phase) causes turnover in plant populations, and creates greater interspersion of emergent cover and open water, but lowers overall productivity. During a cover cycle that ranges from open water to complete vegetation cover, annual net primary productivity may vary 20-fold.

The PPR is the single most productive habitat for waterfowl in the world. In particular, demographic analyses for mid-continent populations of mallard (Anas platyrhynchos) show that approximately 90% of variation in population growth rate is associated with breeding activities that occur within the PPR (Austin 2002, Hoekman et al. 2002). Wetland availability and emergent cover conditions are the primary factors that determine the number and diversity of breeding waterfowl that will settle in the PPR (Weller and Spatcher 1965). Waterfowl are adapted to exploit periodic shifts in wetland conditions and are known to migrate past drought-stricken areas to settle in landscapes with an abundance of ponded wetlands.
(wetland basins with standing water). During times of widespread drought, waterfowl may only find favorable conditions near the wetter northern and eastern fringes of the PPR, or beyond in northern Canada, where wetlands are less productive but water levels are more stable.

North American duck numbers correspond well with the number of ponded wetlands in the PPR at the start of the breeding season (figure 2). The number of mallards has ranged from approximately seven million birds during wet periods to two million birds during droughts. Factors other than weather that also regulate continental waterfowl numbers include harvest, land use, and density-dependent controls (Viljugrein et al. 2005).

Climate is not uniform across the PPR. Strong north–south temperature and east–west precipitation gradients produce distinct regional climates, ranging from relatively wet and stable conditions in Iowa to the unstable, dry climates of Alberta and Saskatchewan. As a result, wetlands often exist in different stages of the cover cycle across the PPR at any single point in time. Moreover, the return time of the cover cycle (i.e., the time to complete one cycle) varies across the PPR according to climate variability. Central portions of the PPR with moderate precipitation and temperature have the fastest return times.

The well-established sensitivity of prairie wetlands to current climate variability portends a similarly sensitive response to climate change. Weather extremes and climatic fluctuations drive hydrology, which in turn drives key ecological processes in glaciated prairie wetlands. These include wetland hydroperiod, ratio of emergent plant cover to open water, species composition, water permanence class (i.e., temporary, seasonal, semipermanent), and primary and secondary productivity, among others (van der Valk 1989). Thus, additional climate variability of the magnitude suggested by global climate change models would profoundly affect wetland hydrology and many other linked processes and attributes.

The latest assessment from the Intergovernmental Panel on Climate Change, based on several different models, predicts increases in global average surface temperatures ranging from 1.4 degrees Celsius (ºC) to 5.8ºC by the year 2100 (Houghton et al. 2001). The temperatures increase most in the mid to high latitudes of the Northern Hemisphere. Precipitation is generally predicted to increase in the northern latitudes and decrease in the mid latitudes.

Increased drought conditions in the PPR are forecast to occur under nearly all global circulation model scenarios. Regional climate assessments (Ojima and Lackett 2002) suggest that the central and northern Great Plains of the United States may experience a 3.6°C to 6.1°C increase in mean air temperature over the next 100 years. Longer growing seasons, milder winters in the north, hotter summers in the south, and extreme drought are projected to be a more
common occurrence over the PPR. Trends in mean annual precipitation are more difficult to predict, and range from no change to an increase of 10% to 20% concentrated in the fall, winter, and spring, accompanied by decreased summer precipitation and a higher frequency of extreme spring and fall precipitation events.

In the past century, temperatures across parts of the northern and central Great Plains have risen more than 3°C, while annual precipitation over the last 100 years has decreased by 10% in eastern Montana and North Dakota (National Assessment Synthesis Team 2000). Winter (2000) assessed the vulnerability of wetlands in glacial landscapes, such as the PPR, where wetland hydrology is dependent on interactions with atmospheric moisture and groundwater. He predicted that in areas where groundwater movement through the glacial till is slow, wetlands will be highly vulnerable to climate change. Increased summer temperatures in these midcontinental regions also will result in higher summer evapotranspiration rates, putting increased demands on groundwater and resulting in earlier drying of wetlands. Our research indicates that trends in the Palmer Drought Severity Index (PDSI) for the PPR during the 20th century reflected increasing moisture availability for most weather stations; however, several stations in the western Canadian Prairies recorded effectively drier conditions.

Poiani and Johnson (1991) used a wetland simulation model (WETSIM) to show that a likely future climate (much warmer and slightly wetter) would produce poorer breeding conditions for waterfowl. Their simulations for a semipermanent wetland in east-central North Dakota showed a higher frequency of dry basins with too much emergent cover for optimal breeding. Larson (1995) and Sorenson and colleagues (1998) projected similar habitat degradation for breeding waterfowl in central North America under future climate warming scenarios, using statistical models based on historic relationships between PDSI and breeding waterfowl surveys. Sorenson and colleagues (1998) estimated that under a doubling of carbon dioxide by 2060, the north-central US duck population would be cut in half.

No geographically extensive analyses of the quantitative relationships between climate and prairie wetland structure and function have been conducted for the PPR. Most of the research progress in prairie wetland ecology has come from intensively studied but geographically restricted sites. The broader extrasite patterns have not been determined.

We devised an analytical approach to determine the long-term geographic patterns of wetland conditions across the PPR driven by historic and future climates. This was accomplished by making improvements to WETSIM (Poiani et al. 1996), recalibrating the model, and quantifying geographic variability in wetland condition by applying the model to 18 PPR weather stations with 95-year records. This methodology allowed us to compute various measures of wetland condition, such as hydroperiod, drought frequency, cover ratio, cover cycle return time, and water depth and variability across the climate space of the PPR under both historic and possible future conditions.

The main goals of our research were to use WETSIM to characterize the historic temporal and geographic variability of wetland conditions across the PPR, to identify in which ecoregions of the PPR wetlands are the most vulnerable to climate variability, and to determine how the most productive waterfowl breeding areas may shift geographically under different climates. It was assumed that wetlands across the PPR are not equally vulnerable to climate variability. The ecological and management implications of a geographic shift in the productivity of wetlands across the PPR in response to climate change would be considerable.

Simulating wetland dynamics

WETSIM is a process-oriented, deterministic model that simulates watershed and wetland surface processes, watershed groundwater, and wetland vegetation dynamics. The model uses daily precipitation and mean daily temperature to estimate wetland water balance, wetland stage, and wetland vegetation dynamics. Simulations were conducted using WETSIM 3.1, a next-generation wetland model, upgraded from WETSIM 1.0 and 2.0 (Poiani et al. 1996). The WETSIM 3.1 upgrade included (a) conversion of the multiple platform WETSIM 2.0 to a single platform using Mathematica software; (b) replacement of the Blaney-Criddle equation to calculate evapotranspiration by the Hargreaves (1994) equation and latitude adjustment using the maximum possible solar radiation equation (Williams et al. 1990); (c) replacement of estimates of groundwater discharge to the wetland from EPIC (Sharpley and Williams 1990, Williams et al. 1990) with those from a simplified groundwater submodel derived from MODFLOW-96 with boundary conditions obtained from piezometer data; (d) refinement of estimates of wetland evapotranspiration into three cover categories (open water, flooded emergent cover, and emergent cover in wet, unflooded soil); (e) development of an empirically based,
seasonally adjusted curve of leaf area index to estimate upland evapotranspiration to replace EPIC’s crop growth model; (f) programming of the bucket model for soil water content in the rooting zone and use of advanced numerical capabilities of Mathematica to iteratively solve the nonlinear soil moisture dynamics equation; and (g) increased wetland cell size from 9 square meters (m²) to 25 m² to better match the monthly resolution of the vegetation submodel.

WETSIM 3.1 was calibrated and tested using field data from semipermanent wetland P1 at the Cottonwood Lake study area in east-central North Dakota (figure 3), the same wetland used to parameterize and evaluate earlier versions of WETSIM. Model bathymetry was held constant during simulations. Wetland P1 has the longest and most detailed hydrological record of any wetland in the PPR (Winter 2003). Systematic measurements and monitoring began in 1979 and continue to the present. The testing of WETSIM 3.1 was more rigorous than for earlier model versions because the longer P1 data set included much greater climatic variability by capturing the record high water levels in the mid-1990s.

The revised model accurately simulated the spring rise, summer drawdown, and interannual variability typical of prairie wetlands and of P1 in particular (figure 4). The vegetation responded adequately to water-level dynamics, judging from historic photographs of P1.

Moving the model geographically to other weather stations required making adjustments. The depth at which water would begin to flow out of the P1 basin was reduced from 5.2 m (not reached in modern times) to 1.4 m to enable the model to potentially pass through most phases of the cover cycle in wetter PPR climates. Also, the Hargreaves evapotranspiration equation was adjusted by latitude to account for differences among stations in day length.

We tested the geographic mobility of WETSIM 3.1 by using data from another long-term prairie wetland monitoring site in South Dakota (Johnson et al. 2004) with a climate warmer and wetter than that of wetland P1 in North Dakota. The model closely captured the historic water level and vegetation dynamics of a semipermanent wetland at this site.

The P1 basin from the Missouri Coteau may not be representative of wetland basin structure in other parts of the PPR. Use of different basin structure for different ecoregions, if differences were found to exist, could accentuate or lessen the simulated differences among weather stations and ecoregions produced by the single-basin approach. Connections between groundwater and surface water are also known to differ even among adjacent wetlands; if there are systematic

Figure 3. The Cottonwood Lake study area in east-central North Dakota, managed by the US Fish and Wildlife Service. WETSIM, a wetland simulation model, was developed and tested using long-term monitoring data from wetland P1, located in the center of the scene (note white instrument barge). See Winter (2003) for site description. Photograph courtesy of George Swanson (retired), Northern Prairie Wildlife Research Center.
differences in groundwater fluxes among ecoregions, these could temper the WETSIM results.

**Ecoregions of the prairie pothole region**

We subdivided the PPR into six ecoregions by combining US and Canadian approaches (figure 1). The ecoregions were used as strata from which to select weather stations. We chose three widely separated weather stations from each ecoregion on the basis of their length and completeness of record. Most ecoregions were oriented north–south; thus, weather stations were selected from northern, central, and southern locations.

We compiled a 95-year data set comprising 104,097 records (daily precipitation, minimum daily temperature, and maximum daily temperature) for each of the 18 weather stations. Missing data were replaced by interpolating from three nearby stations where possible. We conducted accuracy assessments by estimating known data from nearby stations. Estimates of temperature were more strongly correlated to known values (86% moderate to strong correlations) than were estimates of precipitation (71% moderate to strong correlations). Error was higher for stations in less populated areas with fewer nearby stations.

**Historic water levels**

Simulated long-term water depths ranged widely among PPR stations during the historic period (figure 5). Mean water depth for the historic period was greatest, and nearest the outlet level, along the eastern and northern fringes of the PPR (Webster City and Algona, Iowa; Morris, Minnesota; Ranfurly, Alberta). Average water levels were lowest along the northwestern fringes of the PPR (0.32 m at Poplar, Montana). Mean water depths at most weather stations ranged from 0.8 to 1.1 m.

Drought conditions followed a similar pattern across the PPR. Droughts in the model wetland, defined as less than 0.1 m of standing water, were shortest (5 to 15 days) or absent along the eastern and northern fringes of the PPR (Webster City and Algona, Iowa; Morris, Minnesota; Ranfurly, Alberta). Average water levels were lowest along the northwestern fringes of the PPR (0.32 m at Poplar, Montana). Mean water depths at most weather stations ranged from 0.8 to 1.1 m.

Drought length was greatest (15 to 30 days) at northwesterly stations. Muenster, Saskatchewan, was an outlier (nearly 80-day average drought length) caused by two exceptionally long droughts. Overall, the length of the longest drought period correlated positively with mean length (except for Muenster), as did the percentage of time dry. The Medicine Hat, Alberta, and Poplar, Montana, stations were especially droughty, being dry 15% and 25% of the time, respectively (figure 6).

Geographic variability in wetland water budgets was evident when we compared outflow volume among the PPR weather stations. Outflow from the model wetland was indicative of the relative wetness of the PPR climates. The high-
est cumulative outflow of 2,099,366 m$^3$ occurred at Algona. Overflow at this station occurred in 87 of 95 years. Overflow was a rare event at Poplar and Medicine Hat; each had only one overflow event in 95 years, of about 4000 and 6000 m$^3$, respectively. Large overflow volumes in the southeastern PPR may have contributed to the development of an integrated drainage network. Smaller water surpluses in the central and northwestern PPR have maintained closed wetland basins with less integrated surface drainage.

### Historic vegetation response

Spatial and temporal variability in modeled water conditions across the PPR produced correspondingly variable and complex responses from vegetation. Temporal variability, including droughts and deluges, produced rapid changes in the ratios between cover and open water at a single station, while spatial variability in weather across the PPR produced widely differing cover ratios at a single point in time. At the station in Watertown, South Dakota, for example, wetland drawdown during drought in the 1930s stimulated rapid expansion of emergent cover and shrinkage of open water area during just eight consecutive growing-season months (figure 7). A deluge period in the 1940s at Minot, North Dakota, produced the opposite effect: large increases in open water area over a four-year period (figure 7).

---

**Figure 6.** Mean length and maximum length of dry periods estimated by WETSIM model for prairie pothole region weather stations from 1906 to 2000. Size of circle corresponds to percent time dry. Ranfurly (Alberta), Algona (Iowa), and Webster City (Iowa) had no dry periods. Ecoregion abbreviations: CAP, Canadian aspen forests and parklands; CTG, central tall grasslands; NMG, northern mixed grasslands; NSG, northern short grasslands; NTG, northern tall grasslands; PC, Prairie Coteau. State and province abbreviations: AB, Alberta; IA, Iowa; MB, Manitoba; MN, Minnesota; MT, Montana; ND, North Dakota; SD, South Dakota; SK, Saskatchewan.

**Figure 7.** Response of WETSIM to temporal and spatial weather extremes. Monthly water and cover conditions are included for three periods: drought (July 1933 to July 1934 for the Watertown, South Dakota, weather station), deluge (August 1942 to July 1945 for the Minot, North Dakota, weather station), and spatial variability (six ecoregion weather stations at a single point in time, May 1912). State and province abbreviations: AB, Alberta; IA, Iowa; MN, Minnesota; ND, North Dakota; SD, South Dakota; SK, Saskatchewan.
Spatial variability was as striking when comparing simulated cover ratios for six stations, one in each ecoregion, in May 1912 (figure 7). The model wetland indicated that at a single point in time, dry marsh conditions existed in the western Canadian prairies (Medicine Hat), balanced ratios of cover to open water in the aspen parklands of Canada (Muenster) and in the Dakotas (Minot and Watertown), and lake marsh conditions along the eastern PPR boundary (Crookston, Minnesota, and Algona).

Emergent cover averaged for each station during the 20th century ranged widely across the PPR, from only 11% at Webster City to 99% at Poplar (figure 8). The most cover occurred in the west-lying northern shortgrass ecoregion, while the least cover occurred along the northern and eastern fringe of ecoregions bordering forest ecosystems. Moderate cover percentages most favorable for waterfowl breeding formed a broad arc in the middle of the PPR.

The simulated number of completions of the wetland cover cycle (return times) during the 95-year historic period ranged from zero to three. Nearly half (48%) of the PPR remained stuck in one or two of the four cover stages and did not complete a single cycle (figure 9). Nearly as much of the PPR (40%) completed one cycle (95-year return time), while 10% and 2% of the PPR completed two (47.5-year return time) and three (31.7-year return time) cycles, respectively.

Simulations of hydrology and vegetation clearly identified a broad northwest–southeast running arc in the middle of the PPR as the most dynamic and, as a result, the most supportive for overall biodiversity in general and waterfowl breeding in particular. Areas farther west become productive only rarely, during especially wet periods, while wetlands farther north and east become so during dry periods. The eastern Dakotas and southeastern Saskatchewan stand out in this analysis as having been the heart of the PPR’s “duck factory” during the 20th century.

**Future climate and wetlands**

The historic patterns of wetland dynamics and favorability for waterfowl breeding across the PPR may shift in the future, depending on the extent and magnitude of climate change. We found that the PPR climate changed during the 20th century; nearly all major weather stations examined became warmer, but western stations became drier and eastern stations wetter. These results suggest that the historically strong west-to-east moisture gradient across the PPR has steepened. Since it cannot be known with certainty whether or not the trends of the past century will continue, we adopted the equilibrium scenario approach to examine the possible effects of climate change on PPR wetlands.

The effects of three combinations of temperature and moisture on wetland conditions were compared to the historical reference using WETSIM 3.1 for 6 of the 18 weather stations, one from nearest the center of each ecoregion. These three scenarios were (1) a 3°C temperature increase with no change in precipitation, (2) a 3°C temperature increase with a 20% increase in precipitation, and (3) a 3°C temperature increase with a 20% decrease in precipitation. The climate scenarios were applied uniformly across seasons to the historic weather data files.

**Figure 8.** Simulated historic pattern of wetland emergent cover (a) across the prairie pothole region and (b) by weather station. Cover percentages were scaled to a maximum potential open water area of 28,125 square meters (m²), with an outlet level of 1.4 m. Ecoregion abbreviations: CAP, Canadian aspen forests and parklands; CTG, central tall grasslands; NMG, northern mixed grasslands; NSG, northern short grasslands; NTG, northern tall grasslands; PC, Prairie Coteau.
The model was highly sensitive to alternative future climates. A temperature increase alone produced more emergent cover at the relatively wet stations in Iowa and South Dakota (figure 10). Cover ratios shifted strongly toward dense emergent cover under the warmer temperatures at the drier stations such as Medicine Hat and Minot. Most stations spent more time in the dry marsh phase under the warmer-only climate scenario.

Increasing both temperature and precipitation had a counterbalancing effect on water budgets, producing only a small change in cover compared with historic simulations at most stations. Warmer and wetter conditions at Algona, Watertown, and Medicine Hat produced cover ratios nearly identical to historic conditions, while hemimarsh conditions (i.e., conditions in which the mix of emergent cover and open water is roughly even) declined slightly at the other stations (figure 10). It is apparent from this simulation that a 20% increase in precipitation would generally compensate for a 3°C rise in temperature if applied uniformly. Altering seasonal patterns of temperature and precipitation in WETSIM would produce different results.

Increased temperature and decreased precipitation had the greatest effect on wetland conditions. The model wetland at five of the six stations became completely dominated by dry marsh conditions because of more frequent and longer drought (figure 10). Only Algona, the wettest station, formed hemimarsh conditions more often under this temperature and precipitation regime than under the two other climate scenarios. Cover dynamics at Algona under this driest condition were nearly identical to the historic reference at Crookston, located 250 km to the northwest.

The geographic pattern of return times shifted markedly with changes in temperature and precipitation. A change in temperature alone pushed the region of fastest return times eastward, where the generally wetter climate could accommodate the greater evaporative demand (figure 9c). The portion of the PPR with the fastest return times shifted geographically from the eastern Dakotas and southeastern Saskatchewan to western Minnesota and Iowa. Return times in this eastern fringe of the PPR increased two- to threefold. The warmer temperatures increased drawdown frequency and magnitude, thereby stimulating vegetation regeneration.

Increases in both temperature and precipitation produced the most spatially dynamic result (figure 9b). This scenario generated an area of four
return-time cycles in east-central South Dakota; four cycles did not appear in the other simulations (figure 9). These results suggest that a warmer future climate supplied with sufficient additional moisture may provide more favorable cover and water conditions for waterfowl breeding across the PPR than the climate during the 20th century. In particular, the high historic favorability of the central PPR for waterfowl production was strengthened under this scenario.

Reduced precipitation and warmer air temperatures, however, produced a nearly featureless map with no complete cover cycles except in a small area in north-central Iowa (figure 9d). The dry conditions failed to generate sufficient water depths across the PPR to produce and maintain sufficiently large areas of open water to qualify as hemimarsh. Overall, the three scenarios provide evidence that the cover cycle dynamics that are linked to the breeding opportunities for waterfowl provided by prairie wetlands are highly sensitive to climate.

Integrating return time and the occurrence of hemimarsh conditions produced a map of near optimal cover and water conditions for waterfowl breeding across the PPR (figure 11). As shown earlier, the central PPR produced the most favorable conditions during the historic period. Also, the largest proportion of the PPR under highly favorable conditions occurred during historic times.

Geographic shifts in the most favorable region for waterfowl breeding were marked under all three scenarios (figure 11). A temperature increase of 3°C and any decrease in precipitation shifted most favorable conditions to a much smaller area on the eastern fringe of the PPR. With an increasingly dry climate, this zone would shrink even further and move from western Minnesota south to Iowa. The main cause of the simulated reductions in highly favorable conditions for waterfowl breeding is the longer duration of low water levels, droughts, and choked marsh conditions developing in a warmer and drier future climate.

**Vulnerability to climate change**

The observed sensitivity of the model to climate variability suggests that wetlands in the drier portions of the PPR, such as the US and Canadian High Plains, would be especially vulnerable to climate warming, even if precipitation were to continue at historic levels. Only a substantial increase in precipitation would counterbalance the effects of a warmer climate. Additionally, the most productive wetlands, currently centrally located in the PPR, may become marginally productive in a warmer, drier future climate. Historically a mainstay for waterfowl, the region including the Dakotas and southeastern Saskatchewan would become a more episodic and less reliable region for waterfowl production, much as areas farther west have been during the past century.

Continental waterfowl populations are characterized by boom and bust cycles that are largely dictated by regional wetland conditions. Under historic conditions, population declines were commonplace during drought, because recruitment was limited to a few remaining regions with suitable wetland conditions. Populations would then rebound to previous levels when water returned to drier regions, because waterfowl quickly colonize favorable habitats. Under a warmer and drier climate, however, we estimate that populations would decline below historic levels, because wetlands in the central PPR that used to provide ample habitat would be too dry for most waterfowl in most years. We also estimate that populations would remain below historic levels, because favorable habitat conditions on which these birds depend would occur even less frequently in the driest regions of the PPR.

A logical question is whether the favorable water and cover conditions in the eastern PPR that we simulated can compensate for habitat losses in the western and central PPR. Historically, the eastern PPR and northern parklands served as a safe haven for waterfowl during periodic droughts. Today, however, options are limited, because more than 90% of eastern PPR wetlands have been drained for agricultural production (Tiner 2003). Although wetland restoration programs have been under way since the mid-1980s, less than 1% of basins drained in Minnesota and Iowa have been restored (Susan Galatowitsch, University of Minnesota, St. Paul, personal communication, 1 July 2005). Restoration
efforts in the east have developed slowly, largely because of the high cost of farmland easements.

The results of this research suggest that climate change may diminish the benefits of wetland conservation in the central and western PPR. Simulations further indicate that restoration of wetlands along wetter fringes of the PPR may be necessary to ameliorate potential impacts of climate change on waterfowl populations. While this research provides grist for discussion of the restoration and management of PPR wetlands under climate change, as urged by Anderson and Sorenson (2001), we also see ways that wetland modeling could be improved to make its output more meaningful to decision-makers. Namely, we have developed and are testing a new wetland landscape simulator (WETLANDSCAPE) that calculates the effect of climate variability simultaneously on multiple wetlands of each water regime (i.e., temporary, seasonal, and semipermanent types) in a landscape. This next-generation model also will be developed to reflect regional differences that may exist in wetland bathymetry across the PPR. Finally, we plan to use WETLANDSCAPE to evaluate the possibility that farming practices (crops and cropping systems) can lessen the impacts of climate change by producing more favorable water budgets for prairie wetlands.

Acknowledgments
This research was supported by grants from the US Environmental Protection Agency (Habitat and Biological Diversity Research Program) and the US Geological Survey (USGS; Biological Resources Division, Global Change Research Program). Rosemary Carroll and John Tracy of the Desert Research Institute in Reno, Nevada, provided groundwater equations for wetland P1. Tom Winter of USGS generously provided water-level and topographic data for wetland P1. We acknowledge the pioneering work of Karen Poiani of The Nature Conservancy in prairie wetland modeling, and George Swanson of the Northern Prairie Wildlife Research Center and Tom Winter for their vision in establishing a long-term monitoring program at Cottonwood Lake.

References cited