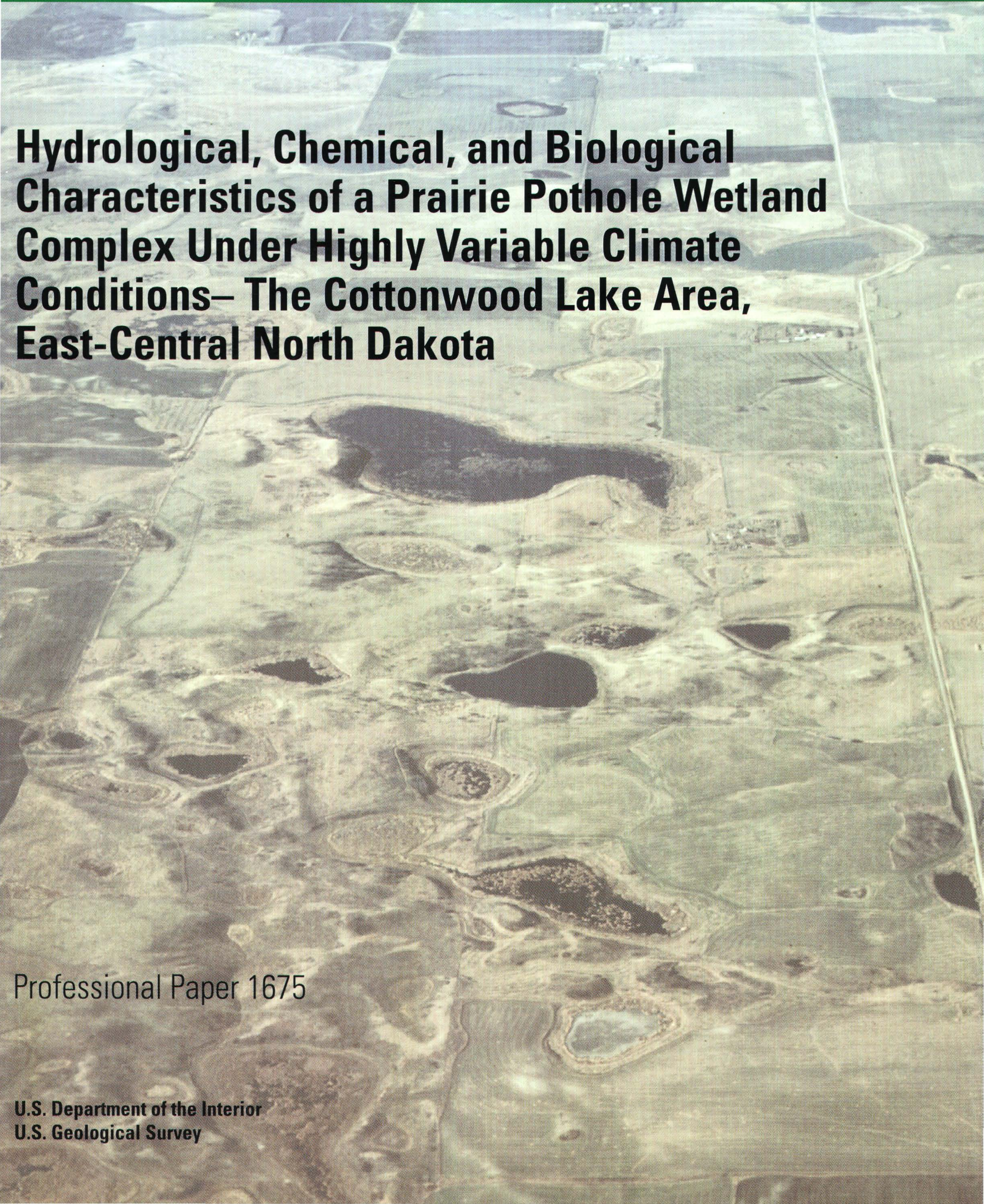
USGS
science for a changing world



Hydrological, Chemical, and Biological Characteristics of a Prairie Pothole Wetland Complex Under Highly Variable Climate Conditions– The Cottonwood Lake Area, East-Central North Dakota

Professional Paper 1675

U.S. Department of the Interior
U.S. Geological Survey

Hydrological, Chemical, and Biological Characteristics of a Prairie Pothole Wetland Complex Under Highly Variable Climate Conditions – The Cottonwood Lake Area, East-Central North Dakota

Edited by Thomas C. Winter

U.S. GEOLOGICAL SURVEY PROFESSIONAL PAPER 1675

U.S. DEPARTMENT OF THE INTERIOR
GALE A. NORTON, Secretary

U.S. GEOLOGICAL SURVEY
Charles G. Groat, Director

Library of Congress Cataloging in Publications Data:

ISBN 0-607-89431-8

For sale by U.S. Geological Survey, Information Services
Box 25286, Federal Center
Denver, CO 80225

FOREWORD

The Cottonwood Lake area is a prairie pothole wetland complex on the Missouri Coteau in east-central North Dakota. Studies to investigate the relation between waterfowl and prairie wetlands in the area were initiated in 1967 and continue to the present (2003). The studies complemented concurrent investigations of the feeding ecology and renesting characteristics of breeding waterfowl. The studies were expanded in 1979 to include investigations of the hydrology of the wetland complex and the effects of hydrology on wetland water chemistry and on plant and animal communities. Studies of the soils in part of the area were done from 1991 to 1993. Further expansion of the biological work in 1992 involved detailed monitoring of macroinvertebrates, macrophytes, herptiles, and birds.

This report presents selected results of the research conducted from 1967 to 1998 at the Cottonwood Lake area. Information on the area is supplemented in Chapters 4 and 5 by information from Eisenlohr and others (1972) that dates back to 1961. The timing of the studies was fortuitous because during the last 2 decades of the 20th century, the area experienced a major climate cycle that included the second worst drought of the 20th century and the greatest amount of precipitation in more than a century. At the outset of the studies in 1967, most of the semipermanent wetlands in the area were open-water lakes. At present, those wetlands are again open-water lakes. However, in the intervening years, all of the wetlands dried up at least once, and some dried up more than once.

The dynamic climate conditions in the Cottonwood Lake area caused equally dynamic hydrological, chemical, and biological responses from plant and animal communities. The effects of the climate and hydrological conditions on plants and animals, and the implications for wetland management, which was the primary impetus for this report, are presented in Chapter 4. Background information on the geology and hydrology of the area is presented in Chapter l, information on the climate is presented in Chapter 2, and information on the water chemistry and biology is presented in Chapter 3. Results of mathematical models of the vegetation changes in response to water-level changes for the present as well as for a condition of climate change are presented in Chapter 5.

CONTENTS

Chapter 1 1
Geohydrologic Setting of The Cottonwood Lake Area 1
Abstract 1
Introduction 1
Geologic Origin and Physiographic Features 1
Characteristics of Geologic Deposits 2
  Distribution and Physical Characteristics of Geologic Deposits 3
  Mineralogy of Glacial Deposits 7
Hydrologic Characteristics of Wetlands 7
  Interaction of Wetlands And Atmospheric Water 7
  Wetland Water Levels 10
  Interaction of Wetlands and Ground Water 11
References 24

Chapter 2 25
Climate of the Cottonwood Lake Area 25
Abstract 25
Introduction 25
Methods 26
Regional Climate of Central North Dakota 26
Local Climate of the Cottonwood Lake Area 27
  Comparison of Evaporation and Precipitation at the Cottonwood Lake Area 31
Acknowledgments 34
References 34

Chapter 3 35
Spatial and Temporal Variabilityin Specific Conductance and Chemical Characteristics of Wetland Water and in Water Column Biota in the Wetlands in the Cottonwood Lake Area 35
Abstract 35
Introduction 35
Methods 36
Specific Conductance And Chemical Characteristics Of Wetland Water 37
Biological Characteristics Of Wetlands 44
Discussion 49
References 52

Chapter 4 55
Dynamics of a Prairie Pothole Wetland Complex: Implications for Wetland Management 55
Abstract 55
Introduction 55
Methods 57
Response of Wetlands in and Near the Cottonwood Lake Area to Climate Variability fom 1961 to 1998 57
Key Wetlands 63
  Wetland T8 63

Wetland T3 63
Wetland P1 67
Wetland P8 74
Wetland P11 76
Hydrological, Chemical, and Biological Interactions in a Wetland Complex and the Broader Prairie Pothole Region 78
Spatial Relations 78
Temporal Relations -- Response To Climate Extremes 79
Implications for Wetland Management 82
Biodiversity and Productivity 82
Wetland Preservation and Restoration 83
Waterfowl 84
Conclusions 86
Acknowledgments 86
References 86

Chapter 5 95
Simulation of Hydrology and Vegetation Dynamics of Prairie Wetlands in the Cottonwood Lake Area 95
Abstract 95
Introduction 95
Spatial Simulation Model 96
Structure And Development 96
Validation And Testing 98
Hydrologic Submodel 99
Vegetation Submodel 99
Overall Model 99
Climate Change Studies 99
Goddard Institute For Space Studies (GISS) Simulation 100
Sensitivity Simulations 101
Seasonal Simulations 101
Management and Restoration Applications 103
Future Needs And Directions 107
Acknowledgments 107
References 107

FIGURES

1. Map showing Physiographic regions of North Dakota, location of the Cottonwood Lake area, locations of National Weather Service stations, and location of geohydrologic section shown in figure 2. 2
2. Hydrogeologic section showing the Cottonwood Lake area with respect to regional geology and numerical simulation of intermediate and regional ground-water flow systems. Line of section shown in figure 1. (Modified from Winter and Carr, 1980). 3
3. Map showing locations of wetlands and locations of test holes and ground-water wells in the Cottonwood Lake area. 4
4. Hypsometric map of the Cottonwood Lake area and the regional topographic low occupied by Wetland P11 and Eric Lake. 5
5 Map showing distribution of buried sand deposits in the Cottonwood Lake area and locations of geologic sections shown in figure 6. 6
6. Geological sections of the Cottonwood Lake area. Lines of sections shown in figure 5. 8
7. Graphs showing wetland water levels, 1979-98. Wetlands P1 and T3 (A), Wetlands P1, P6, and P7 (B), Wetlands P2 and P4 (C), Wetland P11 (D), Wetlands P3, P8, and T2 (E), Wetland T6 (F), WetlandsT8 and T9 (G), Wetlands T5 and T7 (H). 12
8. Map showing extent of open water in wetlands in the Cottonwood Lake area in the fall of 1996 following 4 years of unusually wet climate conditions. All wetlands are larger than shown in figure 3, and a number of wetlands merged to form single water bodies. (From Winter and Rosenberry, 1998) 13
9. Hydrologic section through the Cottonwood Lake area showing the relation of wetlands to the water-table profile. (Modified from Winter and Carr, 1980) 14
10. Graph showing water level of Wetland P1 and water levels in selected ground-water wells in the uplands, 1979-98. 15
11. Graph showing water level of Wetland P1 and water levels in selected ground-water wells in the lowlands near the wetland, 1979-98. 16
12. Map showing configuration of the water table in the Cottonwood Lake area, May 31, 1987, indicating that ground water was discharging to Wetland P1 around its entire perimeter. (From Winter and Rosenberry, 1995) 17
13. Map showing configuration of the water table in the Cottonwood Lake area, August 31, 1989, showing the cones of depression caused by transpiration directly from ground water around much of the perimeter of Wetland P1. (From Winter and Rosenberry, 1995) 18
14. Sketches showing direction of flow between Wetland P1 and nearby ground-water wells for the periods of high and low water levels of each year from 1981 to 1990. (From Winter and Rosenberry, 1995) 19
15. Hydrologic sections showing water-table profiles between Wetlands T3 and P1 indicating the formation of water-table mounds in response to early-summer rainfall (A-E) and in response to late-summer rainfall (F-J). (From Rosenberry and Winter, 1997) 21
16. Map showing configuration of the water table in the Cottonwood Lake area, May 25, 1990, indicating one of the few times during the study when a ground-water divide was not present between Wetlands P1 and P8. 22
17. Sketch showing numerical simulation of ground-water flow in the vicinity of a highly conductive aquifer of limited extent within a porous media having lower hydraulic conductivity. (Modified from Winter, 1976) 23
18. Hydrologic section showing intermediate ground-water flow systems passing at depth beneath local ground-water flow systems associated with selected wetlands. Note the local and intermediate flow systems discharging into Wetland P11. The intermediate flow system is also shown in figure 2 where ground water moves from the Cottonwood Lake area to Eric Lake. Wetland names are shown along top of figure. U indicates unnamed. Line of section shown in figure 4 23
19. Map showing generalized distribution of soils in the Cottonwood Lake area. (Map courtesy of Dr. James Arndt, then of North Dakota State University) 24
20. Graph showing normal (1961-90) monthly precipitation and temperature for the Cottonwood Lake area based on data from three nearby National Weather Service stations. 27
21. Graph showing summer monthly average air temperatures measured at the Cottonwood Lake area and monthly average air temperatures calculated as weighted means of data from the Carrington, Jamestown airport, and Pettibone National Weather Service stations, 1982-85. 28

22. Graph showing monthly mean hours of occurrence for daily maximum and minimum air temperatures, and one standard deviation from the monthly mean, for the Cottonwood Lake area, 1982-85. 28
23. Graph showing measured daily total incident shortwave solar radiation at the Cottonwood Lake area from 1982 to 1987 and clear-sky shortwave solar radiation at 47 degrees north latitude. 29
24. Graph showing monthly average percent of clear-sky shortwave solar radiation for the Cottonwood Lake area, 1982-87. 30
25. Graph showing monthly average windspeed, and one standard deviation from the monthly average, for the Cottonwood Lake area, 1982-91. 30
26. Graph showing monthly average temperatures of air, surface water, bottom water, and sediment at 0.5 meter and 1.0 meter below the sediment-water interface at the center of Wetland P1, 1982-85. 31
27. Graph showing cumulative departure from normal monthly average temperature and cumulative departure from normal monthly total precipitation for the Cottonwood Lake area, 1978-98. 32
28. Graph showing cumulative departure from normal monthly total precipitation and water level of Wetland P1, 1978-98. 33
29. Graph showing Palmer Drought Severity Index (PDSI) for climate region 5, North Dakota, 1900-98. 33
30. Graph showing monthly total evaporation and precipitation for Wetland P1 during the open-water season, 1982-85, and 1987. 34
31. Graph showing monthly average evaporation from Wetland P1 (1982-87) and normal (1961-90) monthly precipitation for May-October. 34
32. Graph showing summary of specific-conductance data for five wetlands for 1984 to 1987. 37
33. Graph showing specific conductance of water in Wetland P1 for the months when the wetland was ice free during 1984 to 1987. Gaps between lines are periods when the wetlands were ice covered. Lines connect median values. Points represent data from each of the three transects from which water samples were collected for chemical analysis. Many points overlie one another for individual dates. 38
34. Graphs showing specific conductance of water in semipermanent Wetlands P1 (A), P8 (B), and P11 (C), for the months when the wetlands were ice free during 1979 to 1998. Gaps between lines are periods when the wetlands were ice covered. 38
35. Graph showing summary of pH data for five wetlands for 1984 to 1987. 40
36. Graph showing pH of water in Wetland P11 for the months when the wetland was ice free during 1984 to 1987. Gaps between lines are periods when the wetlands were ice covered. Lines connect median values. Points represent data from each of the three transects from which water samples were collected for chemical analysis. Some points overlie one another for individual dates. 40
37. Graphs showing modified Schoeller diagram of the abundance of major ions in water within five wetlands (A) and selected ground-water wells (B). 42
38. Graph showing summary of total phosphorus data for five wetlands for 1984 to 1987. 42
39. Graph showing summary of orthophosphate phosphorus data for five wetlands for 1984 to 1987. 43
40. Graph showing summary of total nitrogen data for five wetlands for 1984 to 1987. 43
41. Graph showing summary of chlorophyll *a* data for five wetlands for 1984 to 1987. 44
42. Graph showing chlorophyll *a* concentrations for Wetland P11 for the months when the wetland was ice free during 1984 to 1987. Gaps between lines are periods when the wetlands were ice covered. Lines connect median values. Points represent data from each of the three transects from which water samples were collected for chemical analysis. Some points overlie one another for individual dates. 44
43. Graphs showing summary, based on biovolume data from 1985 to 1987, of the relative abundance of taxa in the algal communities of Wetland P1 (A), Wetland P8 (B), Wetland P11 (C), Wetland T8 (D) and Wetland T3 (E). 48
44. Graphs showing seasonal changes in the relative abundance of taxa in the algal community of the open-water zone of Wetland P1 during 1986. 49
45. Graph showing summary of the abundance of microinvertebrates for five wetlands during 1984 to 1987. 51
46. Graph showing seasonal changes in the abundance of microinvertebrates in Wetland T8 during the ice-free period of 1987. 51
47. Graphs showing seasonal changes in the relative abundance of the microinvertebrate community of Wetland P1 during the ice-free period of 1986. 52

48. Photograph showing aerial view of the Cottonwood Lake area looking west on July 1, 1981. The tip of the cultivated right triangle in the lower left side of the photograph intersects the south end of Wetland P7. The east-west road bends around the north side of Wetland P11 located in the background. 56
49. Map showing upland vegetation in the Cottonwood Lake area, 1989 58
50. Photographs showing Wetland P6 on October 1, 1983, dominated by deep-marsh vegetation established during the drought of 1976-77 (A); Wetland P6 on October 28, 1997, dominated by open water following the deluge of 1993-98 (B); Wetland P7 on October 5, 1996, dominated by open water that flooded a 33-year old aspen stand located on the east side of the wetland (C). 60
51. Photographs showing aerial view during May, 1970, of Wetland P11 (A), wetlands in the Cottonwood Lake area (B) and wetlands studied by Eisenlohr and others (1972) (C). 61
52. Photographs showing Wetland P4 on July 1, 1973, during a period of drawdown. A circular stand of hybrid cattail that survived flooding during 1962-66 is shown in the center (A); Wetland P4 on July 10, 1974, during a second year of drawdown (B); aerial view of Wetland P4 on October 30, 1975, showing three circular stands of hybrid cattail that survived flooding during 1962-66 and persisted as distinct units for 10 years (C). 64
53. Photographs showing Wetland P4 on October 30, 1975, dominated by recently germinated cattail. (The persistent clump of hybrid cattail located in the center dominates the mixed-species stand of recently germinated cattail) (A); Wetland P4 on July 20, 1979, dominated by a monotypic stand of cattail that persisted for 18 years (B); Wetland P4 on October 28, 1997, during the deluge of 1993-98 that integrated Wetlands P2, P4, and P5 (C) 65
54. Photographs showing Wetland T8 on May 5, 1975, following flooding (A); Wetland T8 on August 1, 1975, dominated by smartweed and sloughsedge following drawdown (B); Wetland T8 on July 23, 1991, dominated by Canada thistle (*Cirsium arvense*) during the drought of 1988-92 (C). 66
55. Photographs showing Wetland T3 on July 23, 1991, dominated by Canada thistle during the drought of 1988-92 (A); Wetland T3 on July 27, 1994, showing a small stand of cattail (B); Wetland T3 integrated with Wetland P1 on October 28, 1997, during the deluge of 1993-98 (C). 68
56. Photographs showing Wetland P1 on June 1, 1967, following a rise in water levels during 1962-1966 (A); Wetland P1 on October 29, 1992, dominated by deep-marsh vegetation following the drought of 1988-92 (B); Wetland P1 on September 25, 1999, dominated by open water following a rise in water level initiated by the deluge of 1993-98 (C). 70
57. Photographs showing Wetland P1 on September 12, 1977, following drawdown (A); Wetland P1 on September 9, 1978, dominated by shallow-marsh vegetation that germinated on the mudflat inside the deep-marsh zone (B); Wetland P1 on July 1, 1984, following flooding that eliminated shallow-marsh vegetation in the center of the wetland (C). Shallow-marsh vegetation persisted in the seasonally flooded zone shown in the background. 71
58. Photographs showing aerial view looking south toward the Cottonwood Lake area on July 19, 1989, showing Wetlands P4 (lower left), P2 (lower right), and open water in the central zones of Wetlands P1 (center) and P8 (right edge) during the early stage of the drought of 1988-92 (A); Wetland T1 on October 28, 1997, looking east toward Wetland P1 into Wetland T3 located in the background (B); aerial view of the Cottonwood Lake area on October 1, 1976, showing the persistence of open water in Wetland P8 located in the lower left corner (C). 73
59. Photographs showing Wetland P8 on July 1, 1981, dominated by an open-water zone surrounded by a mat of floating cattail (A); Wetland P8 on October 29, 1992, dominated by deep-marsh vegetation following drawdown (B); Wetland P8 on October 28, 1997, dominated by deep-marsh vegetation persisting in the central zone following the deluge of 1993-98 (C). 75
60. Photographs showing Wetland P11 on October 11, 1985, visited by tundra swan that feed on sago pondweed tubers (A); Wetland P11 on October 1, 1990, during drawdown that exposed salt crystals (B); Wetland P11 on June 10, 1991, during drawdown (C). Windrows of salt crystals that were blown from the basin and deposited in the upland southeast of the basin are shown. 77
61. Graph showing observed water volume in Wetland P1 compared to calculated water volume obtained using WETSIM 2.0 model, 1961-92. 99
62. Graph showing model output of water-level changes in Wetland P1 for an 11-year simulation under current climate and enhanced greenhouse gas climate conditions. Temperature and precipitation adjustments for the enhanced greenhouse gas climate were from the GISS general circulation model. The entire wetland was dry at approximately 557.7 meters above sea level. (From Poiani and Johnson, 1993b). 101

63A. Map showing model output of emergent vegetation cover and open-water distributions for years 1, 4, 7, and 11 of an 11-year simulation for semipermanent Wetland P1 under current climate. Simulations were on August 1 of each year using unrestricted seed germination. (From Poiani and Johnson, 1991) 102
63B. Map showing model output of emergent vegetation cover and open-water distributions for years 1, 4, 7, and 11 of an 11-year simulation for semipermanent Wetland P1 under an enhanced greenhouse gas climate as projected by the GISS general circulation model. Simulations were on August 1 of each year using unrestricted seed germination. (From Poiani and Johnson, 1991) 103
64. Maps showing model output of emergent vegetation cover and open-water distributions for years 1, 4, 7, 8, 10, and 11 of an 11-year simulation for semipermanent Wetland P1 under an enhanced greenhouse gas climate as projected by the GISS general circulation model. Simulations were on August 1 of each year. Seed germination was limited according to the timing of the drawdown. 104
65 Maps showing model output of emergent vegetation cover and open-water distributions for eight 5-year water-depth simulations for Wetland P4. Results are shown for October of year 5. 106

TABLES

1. Summary of pH and major ion data for five wetlands of the Cottonwood Lake area. Values presented are medians for 1984 to 1987 ... 39
2. Summary statistics of pH and major-ion data for 21 ground-water wells and specific data for selected wells in the Cottonwood Lake area. Values presented for summary statistics are for 1984 to 1987 and represent a total of 36 water samples ... 41
3. Median value of the coefficient of variation for each date on which water samples were collected for chemical characteristics of five wetlands in the Cottonwood Lake area, 1984-87. ... 45
4. Crustacean microinvertebrate species found in the water column of selected wetlands in the Cottonwood Lake area, 1984-87. ... 46
5. Species composition, occurrence (percent), and average canopy cover for vegetation in mesic upland sites in the Cottonwood Lake area in July 1989. Canopy cover values range from 1 to 7; 1 = <1 percent, 2 = 1 percent - 4 percent, 3 = 5 percent - 24 percent, 4 = 25 percent - 49 percent, 5 = 50 percent - 74 percent, 6 = 75 percent - 94 percent, and 7 = 95 percent - 100 percent. ... 89
6. Species composition, occurrence (percent), and average canopy cover for vegetation in xeric upland sites in the Cottonwood Lake area in July 1989. Canopy cover values range from 1 to 7; 1 = <1 percent, 2 = 1 percent - 4 percent, 3 = 5 percent - 24 percent, 4 = 25 percent - 49 percent, 5 = 50 percent - 74 percent, 6 = 75 percent - 94 percent, and 7 = 95 percent - 100 percent. ... 90
7. Species composition, occurrence (percent), and average canopy cover for vegetation in north aspect upland sites in the Cottonwood Lake area in July 1989. Canopy cover values range from 1 to 7; 1 = <1 percent, 2 = 1 percent - 4 percent, 3 = 5 percent - 24 percent, 4 = 25 percent - 49 percent, 5 = 50 percent - 74 percent, 6 = 75 percent - 94 percent, and 7 = 95 percent - 100 percent. ... 91
8. Species composition, occurrence (percent), and average canopy cover for vegetation in south aspect upland sites in the Cottonwood Lake area in July 1989. Canopy cover values range from 1 to 7; 1 = <1 percent, 2 = 1 percent - 4 percent, 3 = 5 percent - 24 percent, 4 = 25 percent - 49 percent, 5 = 50 percent - 74 percent, 6 = 75 percent - 94 percent, and 7 = 95 percent - 100 percent. ... 92
9. Species composition, occurrence (percent), and average canopy cover for vegetation in east aspect upland sites in the Cottonwood Lake area in July 1989. Canopy cover values range from 1 to 7; 1 = <1 percent, 2 = 1 percent - 4 percent, 3 = 5 percent - 24 percent, 4 = 25 percent - 49 percent, 5 = 50 percent - 74 percent, 6 = 75 percent 94 percent, and 7 = 95 percent - 100 percent. ... 93
10. Species composition, occurrence (percent), and average canopy cover for vegetation in west aspect upland sites in the Cottonwood Lake area in July 1989. Canopy cover values range from 1 to 7; 1 = <1 percent, 2 = 1 percent - 4 percent, 3 = 5 percent - 24 percent, 4 = 25 percent - 49 percent, 5 = 50 percent - 74 percent, 6 = 75 percent - 94 percent, and 7 = 95 percent - 100 percent. ... 94
11. Rules for changes in vegetation submodel. COV = vegetation type, WDC = water-depth category, MON = month, LENWDC = time period in water-depth category (months), LOC = cell location. Water-depth categories: (1) <-55 cm, (2) -55 to -10 cm, (3) -9 to 3 cm, (4) 4 to 19 cm, (5) 20 to 55 cm, and (6) >55 cm. OW = open water, DM = deep-marsh emergents, MSM = wet-meadow/shallow-marsh emergents, UPL = upland vegetation, SEEDL = seedlings, MIXPLT = mixed young plants, MIXEM = mixed species of shallow- and deep-marsh emergents, EXPSOIL = exposed soil. ... 98
12. Adjustments to daily temperature and precipitation data as projected by the GISS general circulation model for Jamestown, North Dakota. Data from Takle and Zhong (1990). Details in Poiani and Johnson (1993b) ... 100
13. Percentage of deep-marsh emergents and open water and area of wet-meadow/shallow-marsh emergents. Values are for end of 5-year management scenarios for Wetland P4 ... 105

CONVERSION FACTORS AND VERTICAL DATUM

Multiply	By	To obtain
	Length	
inch (in.)	2.54	centimeter
inch (in.)	25.4	millimeter
foot (ft)	0.3048	meter
mile (mi)	1.609	kilometer
mile, nautical (nmi)	1.852	kilometer
yard (yd)	0.9144	meter
	Area	
acre	4,047	square meter
acre	0.4047	hectare
acre	0.4047	square hectometer
acre	0.004047	square kilometer
square foot (ft^2)	929.0	square centimeter
square foot (ft^2)	0.09290	square meter
square inch (in^2)	6.452	square centimeter
section (640 acres or 1 square mile)	259.0	square hectometer
square mile (mi^2)	259.0	hectare
square mile (mi^2)	2.590	square kilometer
	Volume	
barrel (bbl), (petroleum, 1 barrel = 42 gal)	0.1590	cubic meter
ounce, fluid (fl. oz)	0.02957	liter
pint (pt)	0.4732	liter
quart (qt)	0.9464	liter
gallon (gal)	3.785	liter
gallon (gal)	0.003785	cubic meter
gallon (gal)	3.785	cubic decimeter
million gallons (Mgal)	3,785	cubic meter
cubic inch (in^3)	16.39	cubic centimeter
cubic inch (in^3)	0.01639	cubic decimeter
cubic inch (in^3)	0.01639	liter
cubic foot (ft^3)	28.32	cubic decimeter
cubic foot (ft^3)	0.02832	cubic meter
cubic yard (yd^3)	0.7646	cubic meter
cubic mile (mi^3)	4.168	cubic kilometer
acre-foot (acre-ft)	1,233	cubic meter
acre-foot (acre-ft)	0.001233	cubic hectometer
	Flow rate	
acre-foot per day (acre-ft/d)	0.01427	cubic meter per second
acre-foot per year (acre-ft/yr)	1,233	cubic meter per year
acre-foot per year (acre-ft/yr)	0.001233	cubic hectometer per year
foot per second (ft/s)	0.3048	meter per second
foot per minute (ft/min)	0.3048	meter per minute
foot per hour (ft/hr)	0.3048	meter per hour
foot per day (ft/d)	0.3048	meter per day

CHAPTER 1

GEOHYDROLOGIC SETTING OF THE COTTONWOOD LAKE AREA

Thomas C. Winter, U.S. Geological Survey, Denver, Colorado

ABSTRACT

Geologic deposits in the Cottonwood Lake area consist largely of silty, clayey glacial till that contains numerous fractures and small, randomly distributed sand and gravel deposits. The sand deposits can have a substantial effect on ground-water flow between wetlands in the area and can cause some to drain while others have relatively stable inflow. Direct precipitation and runoff from snowmelt are the primary sources of water to the wetlands and evaporation accounts for the largest loss of water from the wetlands. The wetlands in the study area have a range of functions with respect to their interaction with ground water. Some of the seasonal wetlands recharge ground water and others recharge ground water and receive ground-water discharge. The semipermanent wetlands receive ground-water discharge much of the time, but some have reversals of flow between them and the ground-water system nearly every year. Ground-water flow toward the wetlands is caused by recharge in the uplands and by focused recharge near the wetland perimeters. Flow from the semipermanent wetlands to the ground-water system occurs when the wetland water levels are higher than the contiguous water table, resulting in bank storage, and when evapotranspiration directly from the ground-water system causes seepage around the wetland perimeters. Substantial climate variability during the study period caused the wetlands to range from being completely dry to having such high water levels that some of the wetlands merged to become large lakes.

INTRODUCTION

A geohydrologic framework is the foundation of aquatic ecosystems. Landforms, geologic deposits, and the movement of water over and through a geologic landscape determine the types and positions of aquatic features that are present in the landscape. Geochemical interactions of rocks and water determine the general chemical characteristics of the aquatic features and plants and animals respond to the presence (or absence) of water and its chemical characteristics. The purpose of this chapter is to describe the geohydrologic framework of the Cottonwood Lake area to set the stage for discussion of the chemical and biological responses that have been observed in the area for more than 30 years, from the mid-1960s to the late 1990s.

GEOLOGIC ORIGIN AND PHYSIOGRAPHIC FEATURES

The Cottonwood Lake area is located near the eastern edge of the Missouri Coteau in Stutsman County, east-central North Dakota (fig. 1). The Missouri Coteau is a large glacial stagnation moraine that transects North Dakota from the northwest corner to the south-central part of the State. It lies north and east of the Missouri River. During the Pleistocene, continental glaciers moved south from Canada, overriding and incorporating bedrock consisting of Precambrian igneous and metamorphic rocks, early Paleozoic sandstones, limestones, and dolomites, and Cretaceous shales and siltstones (Carlson, 1969). The Pierre Formation was exposed at the surface in a large

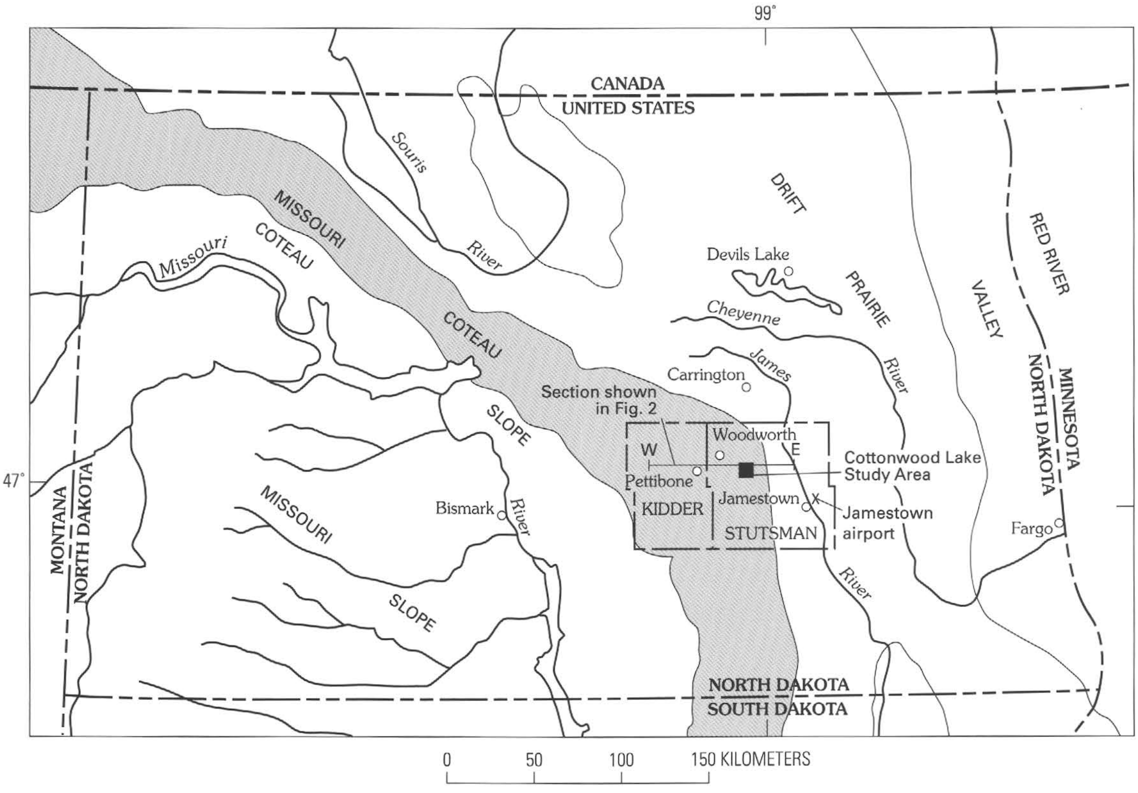


Figure 1. Physiographic regions of North Dakota, location of the Cottonwood Lake area, locations of National Weather Service stations, and location of geohydrologic section shown in figure 2.

part of the area over which the glaciers moved before reaching the Cottonwood Lake area, and incorporation of the fine-grained bedrock resulted in the very silty and clayey glacial till in the area.

The Missouri Coteau rises more than 100 m above the surrounding terrain along much of its length. The Cottonwood Lake area, situated on one of the higher parts of the eastern edge of the Missouri Coteau, lies about 120 m higher than the James River lowland to the east and about 30 m higher than a small lowland within the Missouri Coteau about 4 km to the west (location of Eric Lake in figure 2). Woodworth, about 16 km to the northwest, is situated on the highest part of the Missouri Coteau in the general vicinity of the Cottonwood Lake area.

Local relief within the 80 ha that constitute the Cottonwood Lake area is about 33 m (fig. 3). The area is very hummocky and has many closed depressions, most of which contain wetlands. The wetlands range in altitude from about 577 m for seasonal Wetland T8 to about 551 m for semipermanent Wetland P9. Wetland P11 lies about 4 km west of the Cottonwood Lake area (near Eric Lake) (fig. 4) at an altitude of about 542 m. Because of the silty and clayey characteristics of the till, land slopes are as much as 80 percent in many places in the Cottonwood Lake area.

CHARACTERISTICS OF GEOLOGIC DEPOSITS

Depositional processes characteristic of terminal and stagnation moraines, such as the Missouri Coteau, result in highly heterogeneous geologic deposits commonly referred to as drift. In the Missouri Coteau, most of the drift consists of till, a mixture of clay through boulder-size rocks, that was deposited directly by glaciers. However, meltwater streams flowing from the glaciers also resulted in the deposition of discrete fluvial deposits of well-sorted clay, silt, sand, and gravel that then were buried by minor advances of the glaciers. Therefore, fluvial deposits within the till are common, have limited extent, are highly variable in size and shape, and are randomly distributed.

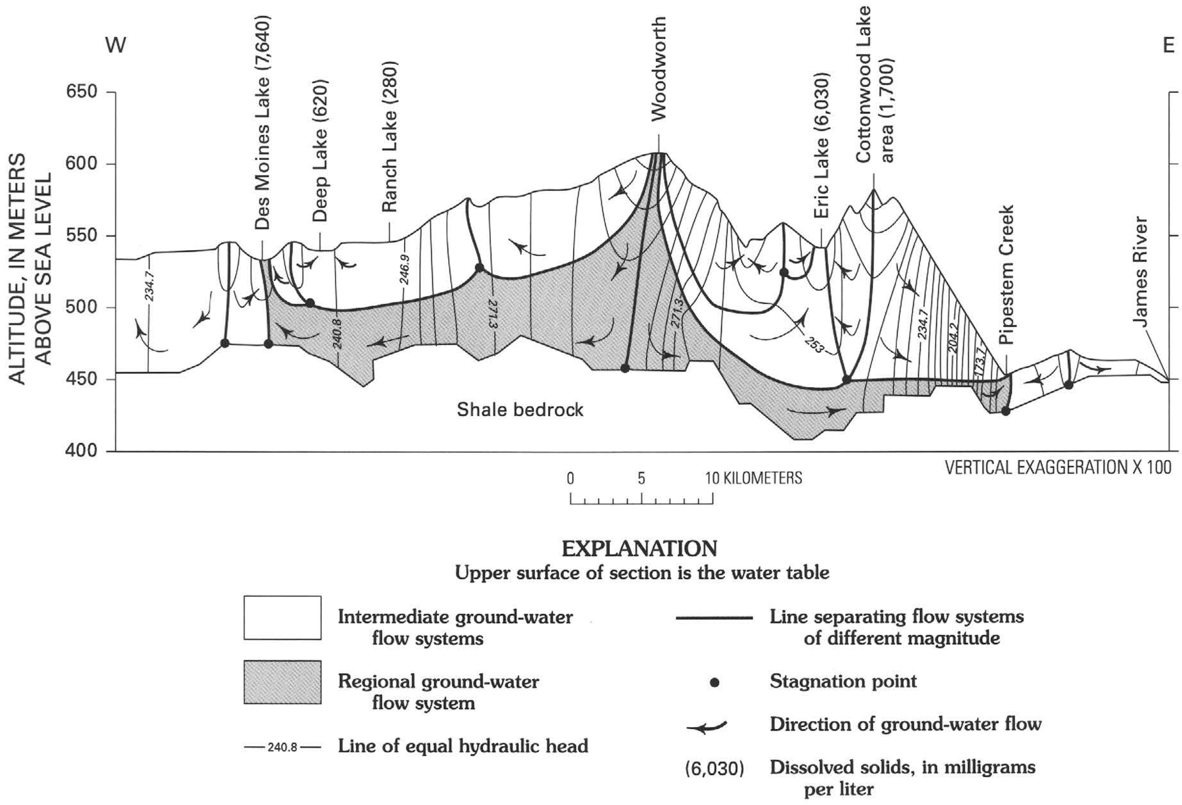
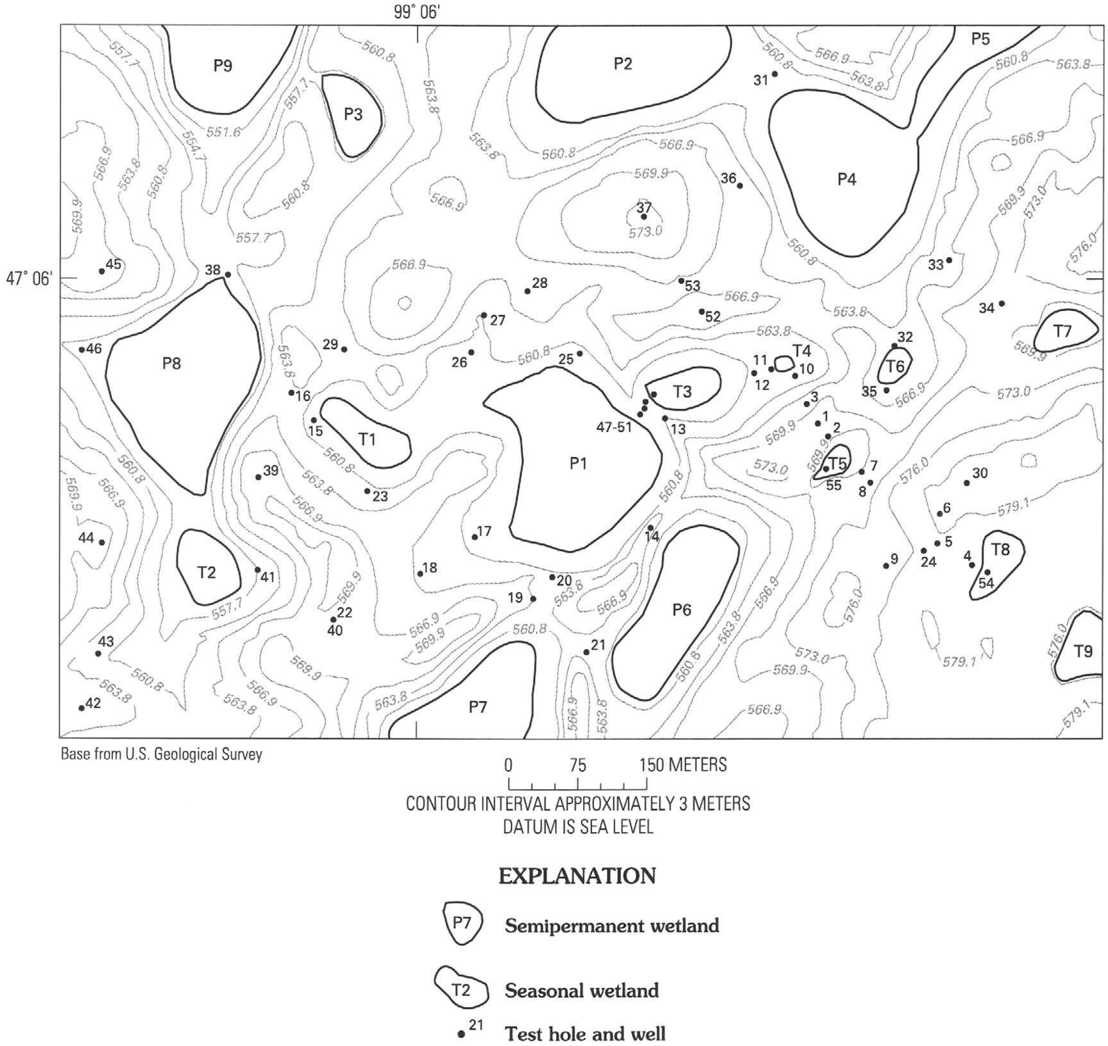


Figure 2. Hydrogeologic section showing the Cottonwood Lake area with respect to regional geology and numerical simulation of intermediate and regional ground-water flow systems. Line of section shown in figure 1. (Modified from Winter and Carr, 1980).

DISTRIBUTION AND PHYSICAL CHARACTERISTICS OF GEOLOGIC DEPOSITS

About 55 test holes were drilled in the Cottonwood Lake area (fig. 3). Most of the test holes were drilled using a power auger, but one (near test hole 15) was drilled to bedrock, a depth of 133 m, by the mud-rotary method. The test drilling indicated that most of the drift in the Cottonwood Lake area is silty, clayey till containing a considerable number of rocks as large as boulders. However, fluvial sand and silt deposits were encountered in a number of the test holes. Although the fluvial deposits in the drift have complex shapes and are somewhat random in size and distribution, mapping of the sand intervals on the basis of their upper-surface altitudes (Winter, 1975) indicated that one or more continuous buried sand deposits are present in the area (fig. 5). To aid in the visualization of the three-dimensional distribution of the sand deposits, a number of cross-sections are shown in figure 6.

Many of the test holes drilled in the western part of the study area encountered sand intervals that have upper-surface altitudes of 556 m to 559 m. (See test holes 16, 41, 42, 43, 44, and 46 in figs. 5 and 6, sections A-A’, B-B', and C-C'.) Recognizing the uncertainty of correlating subsurface fluvial deposits in the drift, it nevertheless is conceivable that the sand intervals encountered in the test holes drilled in the western and southern part of the study area are a single continuous deposit. Sand intervals that have similar upper-surface altitudes were encountered in test holes 1, 14, 19, and 24 in the southern part of the study area. These sand intervals could be isolated deposits or they could be an extension of the same deposit that occurs at the surface near Wetland T2 in the western part of the study area. If they are an extension of the same deposit, they would need to be part of a long sinuous deposit that extends to the east through the vicinity of test holes 14 and 19 and then continues to the southeast to the vicinity of test holes 1 and 24. That the sand deposit would need to be sinuous is dictated by the number of test holes in the southern part of the study area, such as test holes 17, 18, 20, and 21, and in the southeast part of the study area, such as test holes 2, 3, 7, and 30 (figs 5 and 6, sections A-A' and B-B'), that penetrated deeper than 556 m in altitude but did not penetrate sand. The test holes that did not penetrate sand indicate that, if the sand intervals encountered in test holes 1, 14, 19, and 24 are an extension of the deposit that occurs in the western part of the study area, the deposit would need to bifurcate northeast of Wetland P6, with one arm extending to the vicinity of test hole 1 and the other extending to the vicinity of test hole 24. The deposit may extend beyond test hole 24, but the extent could not be defined because test holes 4, 5, 6, and 54 were not drilled deeply enough. Much of the sand in the deposit in the southern part of the study area is fine to medium grained, and the deposit contains fine gravel in some locations. As will be discussed later in this chapter, the continuity of the sand deposit has important implications for the hydrologic function of some of the wetlands in the Cottonwood Lake area.



Base from U.S. Geological Survey

Figure 3. Locations of wetlands and locations of test holes and ground-water wells in the Cottonwood Lake area.

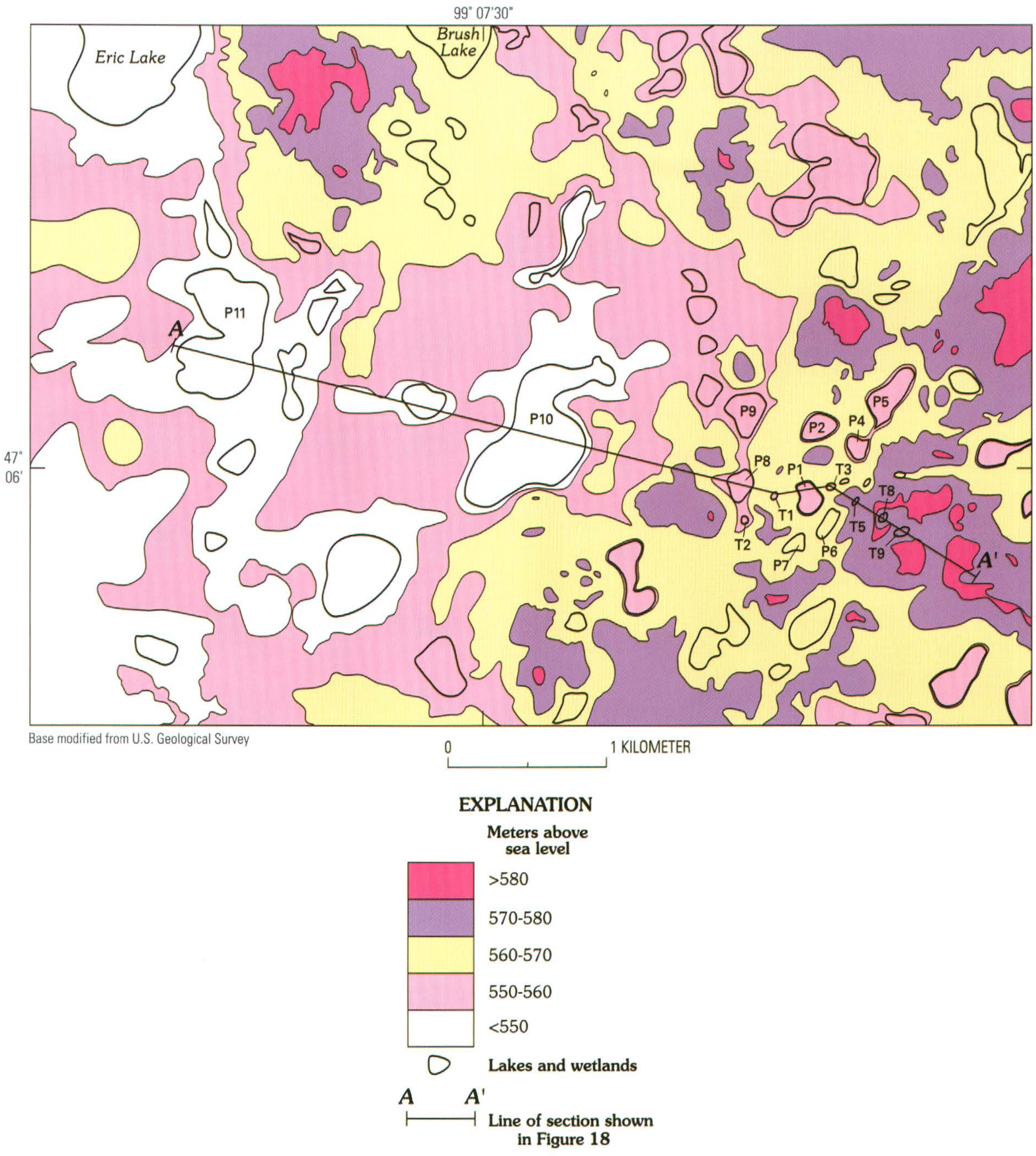


Figure 4. Hypsometric map of the Cottonwood Lake area and the regional topographic low occupied by Wetland P11 and Eric Lake.

Another smaller buried sand deposit is present at a higher altitude in the eastern part of the study area. Test holes 6, 30, and 34 penetrated sand intervals in that area that have upper-surface altitudes of 566 m to 569 m (figs. 5 and 6, section D-D'). Much of the sand in the deposit in the eastern part of the study area is very-fine to fine grained and is quite silty. Other sand intervals in the study area, particularly north of Wetland P1, appear to be thin isolated deposits (figs. 5 and 6, section A-E). Sand also is present at the surface in the vicinity of test holes 29 and 36.

Relatively thick silt deposits are present at the surface in two small valleys within the watershed of Wetland P1. In the valley southwest of Wetland P1, silt extends to depths of 1 m at test hole 17 and 4.9 m at test hole 18. In the valley northwest of Wetland P1, silt extends to depths of 1.2 m at test hole 26 and 4.3 m at test hole 27.

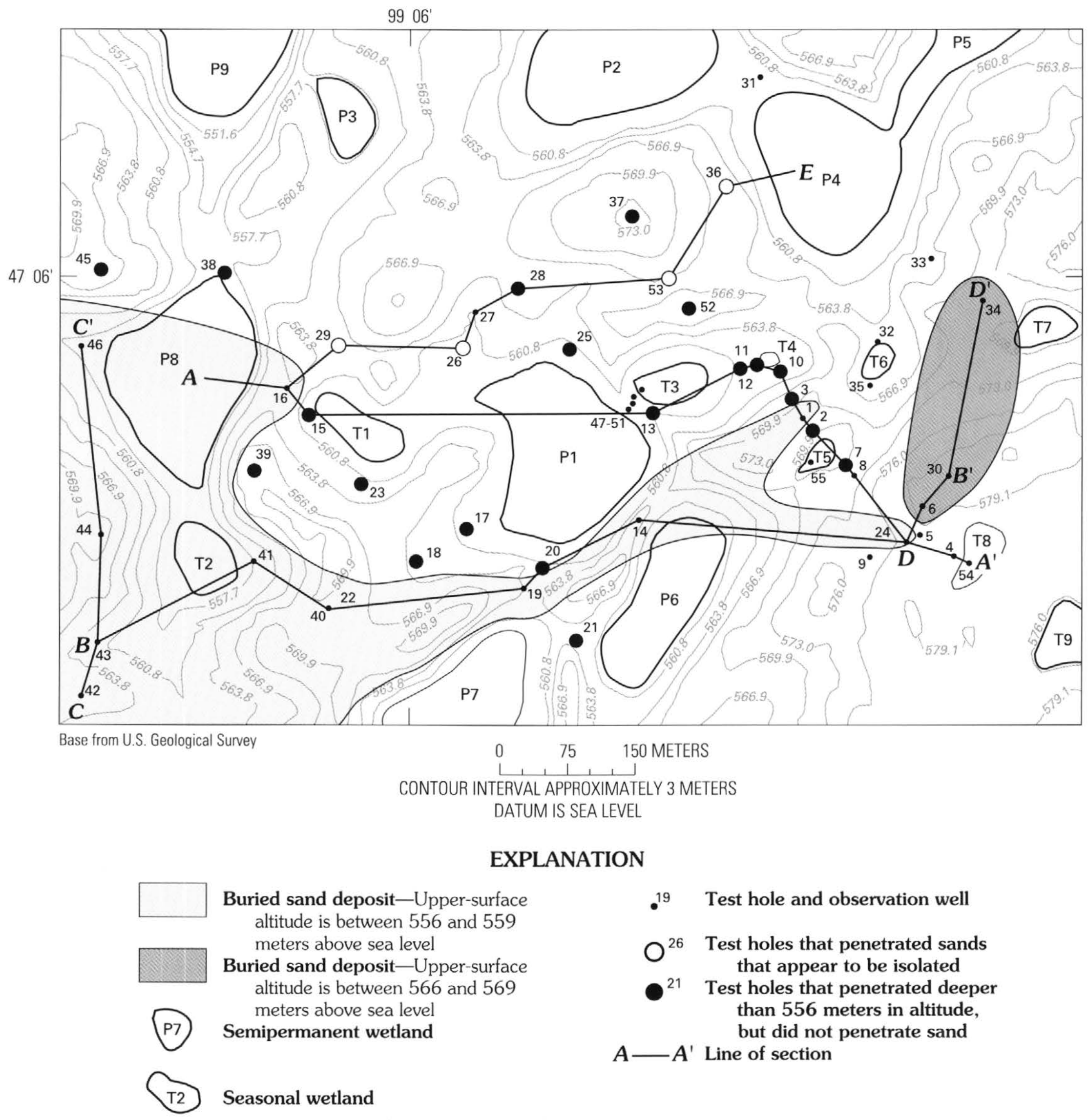


Figure 5. Distribution of buried sand deposits in the Cottonwood Lake area and locations of geologic sections shown in figure 6.

Fractures are common in the till in the study area. The large clay content of the till in the Missouri Coteau causes the till to crack upon drying, and results in the numerous fractures (Meyboom and others, 1966; Grisak and Cherry, 1975; Keller and others, 1986). To determine the presence and characteristics of fractures in the till in the Cottonwood Lake area, soil pits 3 m x 1 m in size were dug to a depth of 2.2 m at the top, side, and base of the hillslope northwest of Wetland P1 (Swanson, 1990). Fractures observed in the till in the soil pits have a spacing of about 10 cm and openings of various sizes; some are hairline fractures, but others have openings as great as 1 to 2 mm (Swanson, 1990). Many of the fractures are lined with gypsum crystals that are 1 to 2 mm in diameter, and some of the weathering rinds are as much as 2 cm wide. The depth to which the fractures extend in the study area is not known.

Single-well slug tests to determine the hydraulic properties of the till also indicated that fractures are common in the till in the study area. The fractured till proved to be relatively permeable, and hydraulic conductivity values were in the 10^{-4} to 10^{-7} cm s^{-1} range. These values are considerably greater than the hydraulic conductivity values that would be expected from a solid block of till; Hendry (1988) reported values to be about 10^{-8} cm s^{-1} for a similar till in Canada.

The middle soil pit confirmed the presence of the thick silt deposit in the vicinity of test hole 27, and soil augering in the floor of the pit revealed the presence of saturated white marl containing abundant gastropod shells from 35 to 60 cm below the pit bottom [about 2.5 m below land surface (Swanson, 1990)]. These data indicate that the water level of Wetland P1 probably was about 2 m higher and that the wetland covered a larger area at some time in the past compared to the time the pits were dug and mapped in 1990.

MINERALOGY OF GLACIAL DEPOSITS

The mineralogy of the drift in the Cottonwood Lake area reflects the mineralogy of the bedrock over which the glaciers moved. Igneous and metamorphic rocks derived from the Canadian Shield make up a large percentage of the rocks in the drift. Many of these rocks have large amounts of quartz and feldspar. Calcite and dolomite derived from the lower Paleozoic rocks north of the area are common. Shale particles derived from the Pierre Formation, and lignite, are abundant. Minor amounts of pyrite are also present in the drift. Smectite is the most common clay mineral (Swanson, 1990).

Gypsum is very abundant as a secondary mineral, both in fracture fillings, as mentioned previously, and disseminated in the drift. Crystals as large as 2 cm long and 1 cm in diameter were recovered from drill cuttings of the silt deposit southwest of Wetland P1. Calcite, largely in the form of fine crystals, also occurs as a secondary mineral near the wetland perimeters (Swanson, 1990; Arndt and Richardson, 1993). Iron oxide staining is common, particularly near the wetland perimeters, and iron oxide concretions were recovered from some drill cuttings of the till.

HYDROLOGIC CHARACTERISTICS OF WETLANDS

Although biological studies in the Cottonwood Lake area began in the 1960s, hydrological studies did not begin until 1979. In that year, the first test holes were drilled, and deep piezometers and water-table wells were constructed. The water-table wells were constructed by inserting well screen and casing into the test holes discussed in the previous section of this chapter. Therefore the number designations for the wells are the same as for the test holes. In addition, staff gages were installed in the wetlands, a recording stage gage was placed in Wetland Pl, and a climate station was established near Wetland Pl. Climate, surface-water, and ground-water data have been collected at these hydrologic installations since 1979, but hydrologic information for only the 20-year period from 1979 to 1998 is presented in this report.

INTERACTION OF WETLANDS AND ATMOSPHERIC WATER

Precipitation is the primary source of water to wetlands in the study area. During the winter, the precipitation is stored on the land surface as snow. The snow commonly is deepest in the wetlands because the wetlands are more protected from the

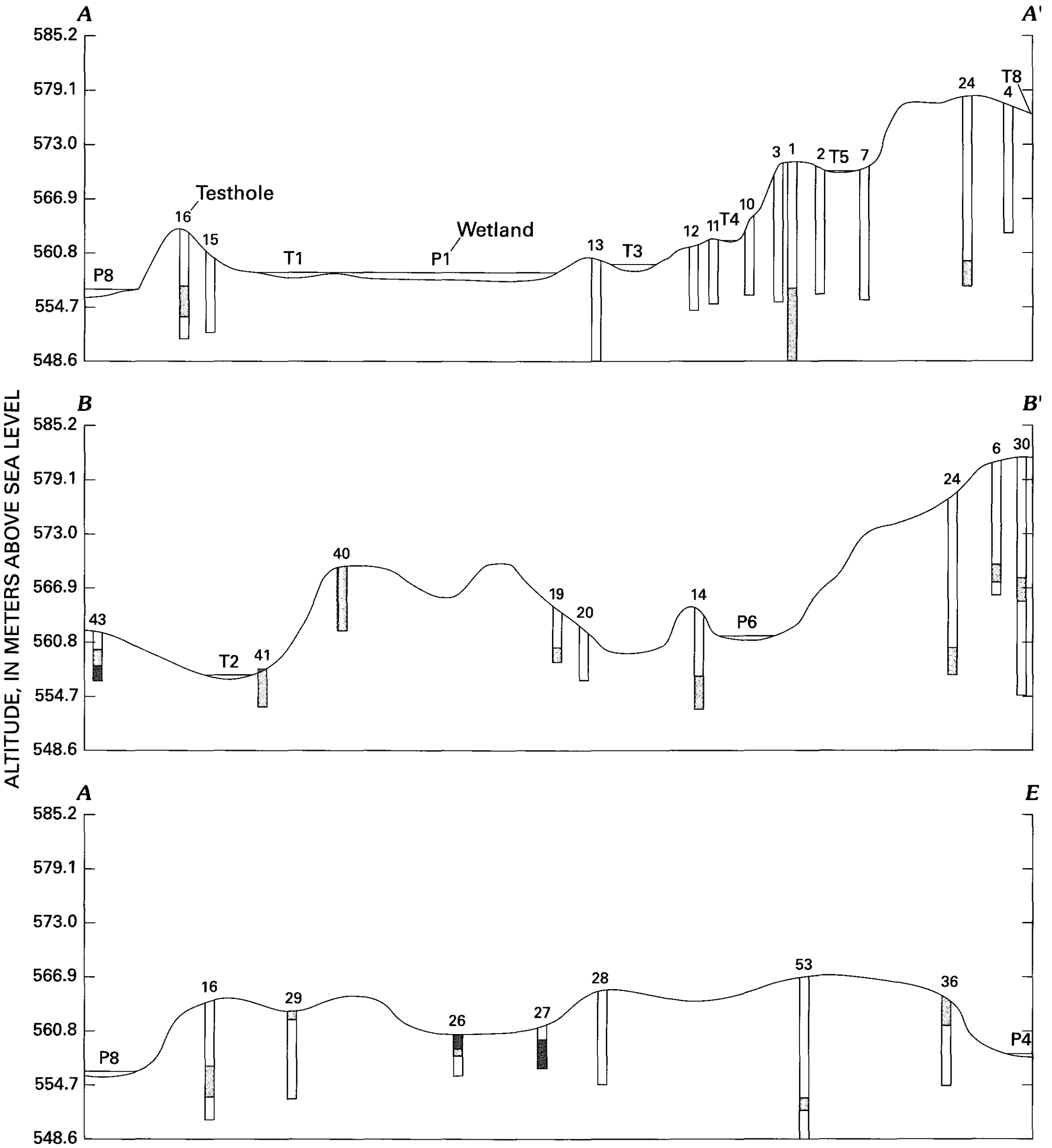


Figure 6. Geological sections of the Cottonwood Lake area. Lines of sections shown in figure 5.

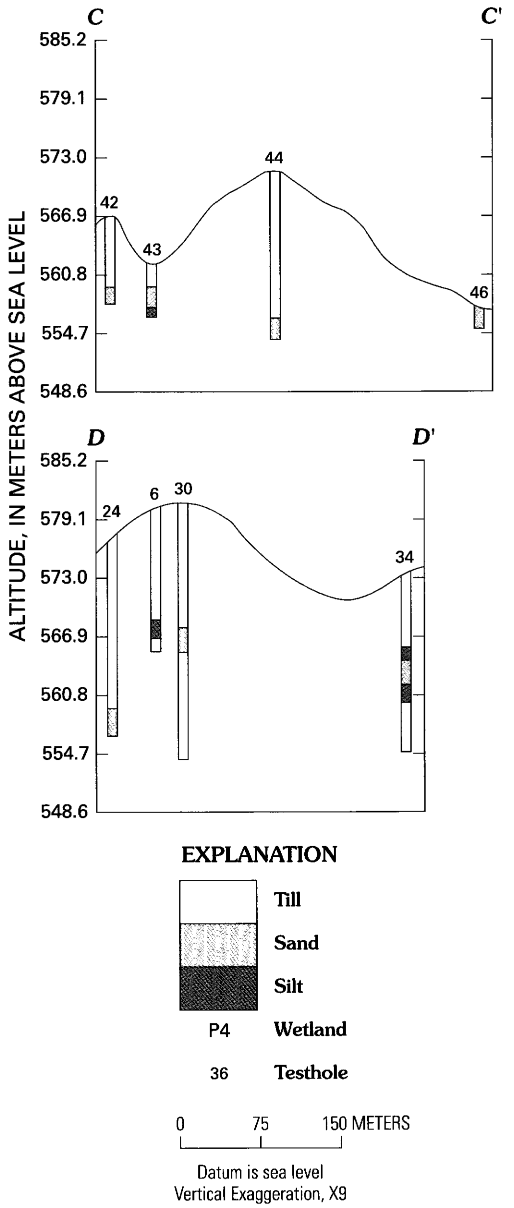


Figure 6. Geological sections of the Cottonwood Lake area. Lines of sections shown in figure 5 (continued).

wind than the uplands and the tall wetland plants trap more snow than the shorter upland plants. Because soil frost impedes infiltration during the winter, snowmelt from the uplands usually enters the wetlands as surface runoff during a relatively short time in the spring while the soils are still frozen. The flux of water, including meltwater from the snow in the wetlands, results in a sharp rise in wetland water levels, and the water levels generally reach the highest levels of the year in late April and May. Spring rainfall also commonly contributes to the high water levels at that time of year. During the growing season, the only precipitation that contributes water to the wetlands generally is that which falls directly on the water surface. Most of the water that falls on the uplands infiltrates into the soil zone and is transpired. Only during prolonged or intense summer rainstorms does precipitation that falls on the uplands infiltrate past the root zone to recharge ground water. Precipitation following killing frosts in the fall can infiltrate past the root zone to recharge ground water, but this precipitation usually results in only moderate rises in ground-water levels. In some years, water from late-fall rain is stored over the winter in the soil zone as ice, and the water contributes to ground-water recharge or wetland water the following spring (Winter and Rosenberry, 1995). Further information on the characteristics of precipitation in the study area is given by Rosenberry (Chapter 2 of this report).

Evaporation from wetlands in the study area is driven by radiation energy. When this study began, the loss of water by evaporation from the wetlands in the prairie environment had not been studied sufficiently well to estimate evaporation from network data, such as from National Weather Service stations. Therefore, instruments were placed at Wetland P1 to determine evaporation by the energy-budget method, which generally is considered to be one of the most accurate methods for determining evaporation (Harbeck and others, 1958; Gunaji, 1968). The instruments included sensors to measure the incoming solar radiation, atmospheric radiation, air temperature, vapor pressure, windspeed, and temperature of the wetland water surface. A further purpose of the energy-budget studies was to provide evaporation values against which empirical methods of determining evaporation could be evaluated so that an acceptable simpler and cheaper method could be used for long-term monitoring of evaporation.

Results of the energy-budget studies, which were conducted for 6 years (1982-87), indicated that evaporation varied considerably from season to season, as expected, and also from year to year (Parkhurst and others., 1998). For example, the highest midsummer high rate of evaporation was 7.0 mm d^{-1} in 1987, and the lowest midsummer high rate was 4.4 mm d^{-1} in 1982. Other midsummer high rates of evaporation were 5.3 mm d^{-1} in 1983, 4.9 mm d^{-1} in 1984, and 5.6 mm d^{-1} in 1985. These evaporation rates apply only to the open water of Wetland P1; the difference between these rates and transpiration by aquatic plants in the vegetated part of the wetland has yet to be determined. Most of the semipermanent wetlands in the Cottonwood Lake area are as shallow as Wetland P1; therefore, it is assumed that evaporation rates for the other semipermanent wetlands in the area are similar to the rates for Wetland P1.

WETLAND WATER LEVELS

Wetland water levels usually followed a similar annual pattern and were highest in the spring following snowmelt and spring rainfall (fig. 7). During the remainder of the open-water period, the water levels gradually declined because evaporation exceeded rainfall and ground water contributed a relatively small amount of water to the wetlands. Heavy rains during the open-water periods caused the water levels to rise temporarily, but the water levels usually resumed their downward trend soon after the rainy period.

Since this study began, the Cottonwood Lake area has experienced highly variable to extreme climate conditions (Rosenberry, Chapter 2 of this report). Therefore, the interannual and long-term fluctuations of the wetland water levels followed a much more unpredictable pattern than the annual pattern. Although precipitation was below normal during the first 9 years of the study (1979-87), the wetland water levels had relatively minor interannual variations (fig.7, A-D). Relatively high water levels in 1979 were followed by 2 years of low levels and a return to high levels in 1982. The water levels then increased for the next 2 years, 1983 and 1984, and then declined substantially in 1985. The water levels increased again for the next 2 years, and, in 1987, reached the highest levels for the period of record at that time. The water levels declined precipitously in 1988, and some of the semipermanent wetlands became dry. The dry conditions that began in 1988 continued for the next 4 years, and 1988-92 became the second worst drought of the 20th century for this part of North Dakota (Winter and Rosenberry, 1998). During those 5 years, Wetland P1 dried up every summer (fig. 7A), Wetland P11 dried up for the first time in 1990 and again in 1991 and 1992 (fig. 7D), and Wetland P8 dried up for the first time in 1991 and again in 1992 (fig. 7E). Wet conditions returned during the spring of 1993 and all of the wetlands contained water, but the great deluge that began in July 1993 caused the water levels to rise to unprecedented levels. The wet period continued to 1998 and caused water levels to rise to the point where some of the wetlands merged to become single lakes (fig. 8). For example, Wetland P1 merged with Wetland T3 in 1995 (fig. 7A), and Wetland P2 merged with Wetland P4 in 1997 (fig. 7C). The time at which the wetlands merged to become single lakes is shown in figure 7 where hydrographs for the individual wetlands begin to plot on top of hydrographs for the other wetlands.

All of the hydrographs shown in figure 7, B-D, are for wetlands that are enclosed by surface watersheds that are considerably higher than the normal wetland water levels. The hydrographs for those wetlands show the interannual variability of water levels even during the wet years from 1993 to 1998. Other wetlands in the Cottonwood Lake area have low points on their surface watersheds that allowed the wetlands to spill to adjacent wetlands only when the water levels become high enough. Wetlands that spill when their water levels are only slightly higher than normal will spill to adjacent wetlands fairly frequently, usually following spring snowmelt and (or) periods of abundant rainfall. Hydrographs for those wetlands (fig. 7, A, E, F, and H) show a characteristic plateau at which a spill is likely to occur. Wetland T3 frequently spilled to Wetland P1 prior to the drought that began in 1988 and before the two wetlands merged in 1995 (fig. 7A). Wetland P8 frequently spilled to Wetland P9 except during the driest years (fig. 7E), and Wetland P3 spilled to Wetland P9 only during the wet years that began in 1993 (fig. 7E). Some seasonal wetlands, such as Wetland T6 (fig. 7F) and Wetlands T5 and T7 (fig. 7H), spilled most years except during the drought when they seldom contained water. Other seasonal wetlands, such as Wetlands T8 and T9, rarely spilled even during the wettest years (fig. 7G). Wetlands T8 and T9 apparently have a greater elevation difference between their normal water levels and the water level at which a spill occurs because those wetlands rarely overflowed.

INTERACTION OF WETLANDS AND GROUND WATER

The high topographic position of the Cottonwood Lake area precludes the wetlands in the area from receiving ground-water inflow from regional ground-water flow systems, therefore, the wetlands are associated largely with local ground-water flow systems. Although some of the recharge in the study area contributes to the recharge of regional flow systems, most of the recharge is to the local flow systems. Winter and Carr (1980) indicated that wetlands in the study area serve the full range of functions with respect to ground water; some recharge ground water, some receive ground-water discharge but also recharge ground water (termed flow-through), and some receive ground-water discharge (fig. 9). For example, Wetlands T8 and T5 do not receive ground-water discharge, but they do recharge ground water during the brief period of the year that they hold water. Water-table gradients are always away from those two wetlands, and the water table declines as much as 2 m below the bottoms of the wetlands during dry times of the year.

Seasonal wetlands that are topographically lower and at an intermediate altitude in the study area, such as Wetlands T3 and T4, are flow-through wetlands most of the time. Semipermanent wetlands that are at an intermediate altitude, such as Wetland P1, receive ground-water discharge most of the time. However, reversals of flow between the wetlands and the ground water around the wetland perimeters are common. The flow reversals are caused by focused recharge and transpiration directly from ground water, as discussed later. The topographically lowest wetlands, such as Wetland P8, nearly always receive ground-water discharge, but they also may have transpiration-induced outflow to ground water.

The 20-year records of wetland water levels and ground-water levels indicate that the annual and long-term interannual fluctuation patterns of the ground-water levels were similar to those of the wetland water levels (figs. 10 and 11). The annual pattern showed high levels in the spring and an overall decline for the

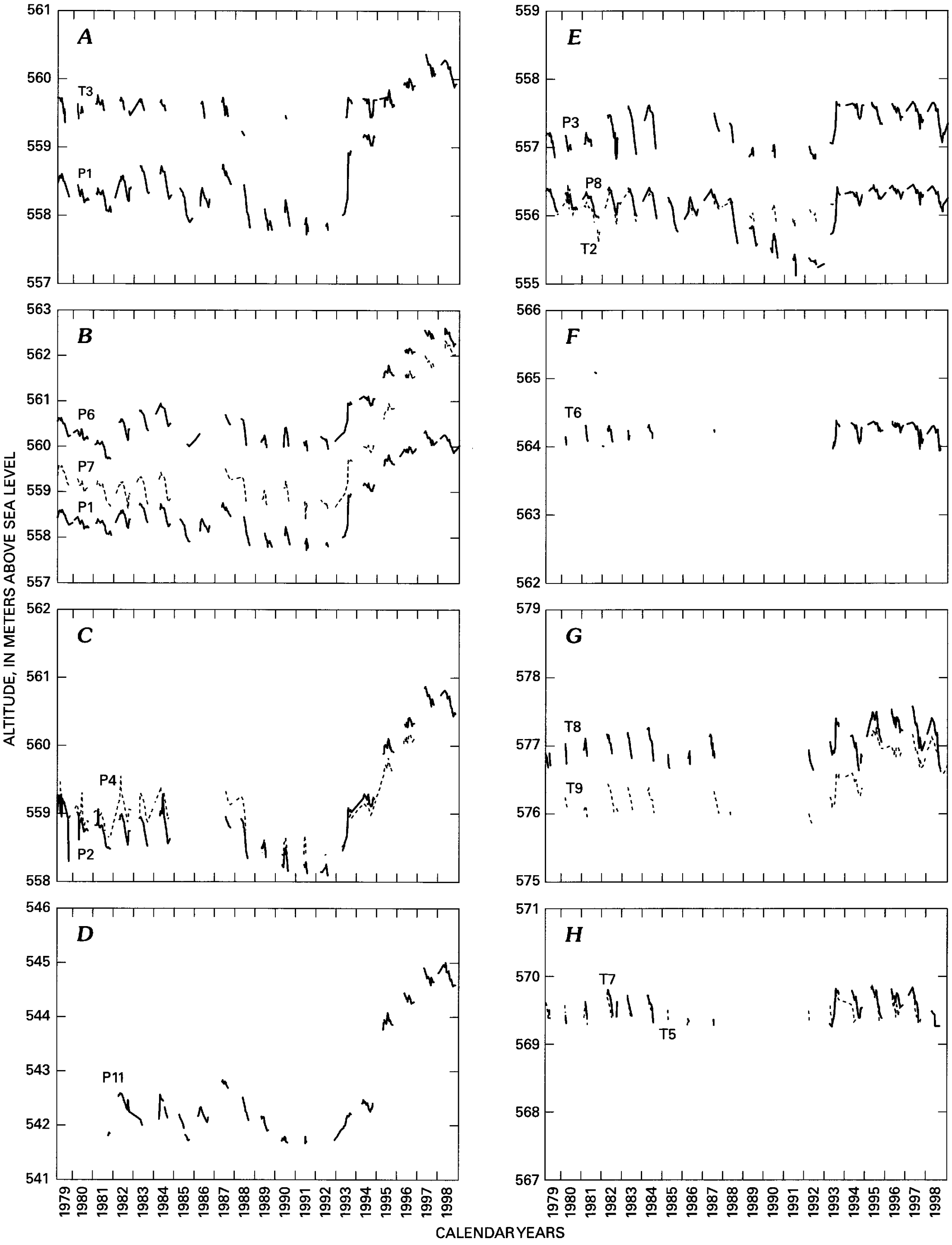


Figure 7. Wetland water levels, 1979-98. Wetlands P1 and T3 (A), Wetlands P1, P6, and P7 (B), Wetlands P2 and P4 (C), Wetland P11 (D), Wetlands P3, P8, and T2 (E), Wetland T6 (F), WetlandsT8 and T9 (G), Wetlands T5 and T7 (H).

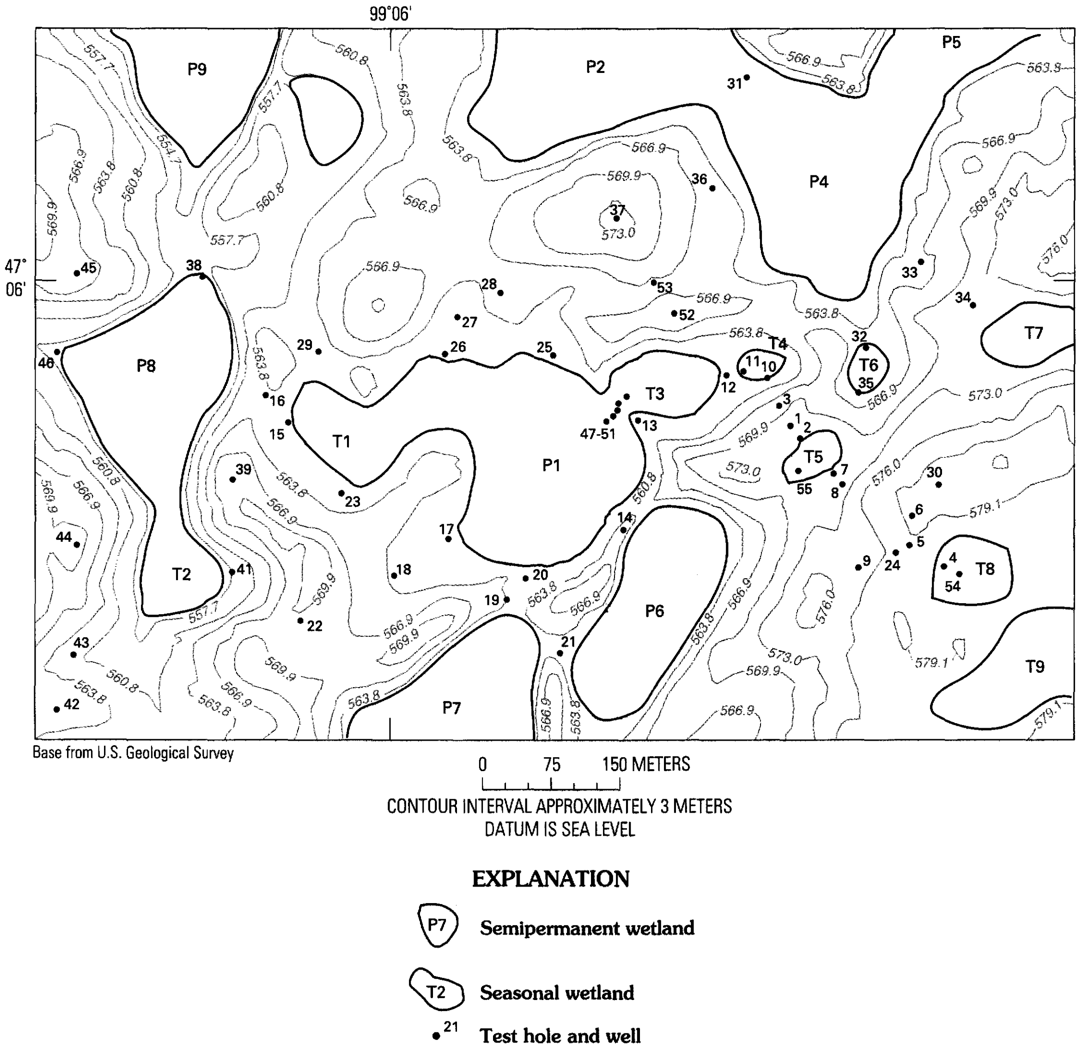


Figure 8. Extent of open water in wetlands in the Cottonwood Lake area in the fall of 1996 following 4 years of unusually wet climate conditions. All wetlands are larger than shown in figure 3, and a number of wetlands merged to form single water bodies. (From Winter and Rosenberry, 1998)

remainder of the year. The long-term interannual pattern showed minor variations during the first 9 years (1979-87), an overall decline during the drought (1988-92), and a substantial rise during the deluge (1993-98).

Although the general patterns of highs and lows were similar, the magnitudes of the fluctuations in the ground-water levels were much larger than those in the wetland water levels, and the magnitudes differed between wells. A given amount of water added to a porous media will result in a greater increase of hydraulic head than the same amount of water added to an open-water surface. Because the water fills only the pore spaces between the solid material, 1 cm of water added to earth materials having an effective porosity of 20 percent would result in a water-table rise of 5 cm; whereas, 1 cm of water added to an open-water surface would result in a water-level rise of 1 cm. Where water tables are shallow, such as near surface-water bodies that are connected to the ground-water system, infiltrated water that recharges ground water causes transient water-table mounds to form directly adjacent to the surface water. This process is referred to as focused recharge (Winter, 1983). The transient water-table mounds generally have hydraulic heads greater than the hydraulic head of the surface water. However, in the same areas of shallow water tables, plant roots can reach the capillary fringe above the water table and transpire water from the ground-water system. Consequently, the plants act as pumps, lowering the water table and causing cones of depression near the wetland perimeters (Meyboom, 1967; Winter and Rosenberry, 1995).

Given the transient relations between the ground-water and surface-water hydraulic heads, a typical annual interaction between a wetland and contiguous ground water is as follows. When the water table near the wetland is higher than the wetland water level, it is usually because a given amount of ground-water recharge resulted in higher water levels than the equal amount of water added to the open-water surface. Wetland water levels are sometimes higher than ground-water levels for a brief time in the early spring when water from snowmelt and (or) spring rains on the uplands runs into the wetland over frozen soil. The runoff results in less water being available for ground-water recharge in the uplands and more water being available for focused recharge in the lowlands and for the wetland itself. When the soil thaws, the ground-water levels generally rise higher than the wetland water levels because of focused recharge. As the season progresses, evapotranspiration directly from the ground-water system by plants that have roots deep enough to reach the capillary fringe lowers the water table. The resulting gradient causes seepage from the wetland, but the seepage is transpired by plants and does not recharge the ground-water system. At the same time, ground water continues to move toward the wetland from higher parts of the ground-water flow system, but much of that water also is transpired before it reaches the wetland.

The highly variable climate conditions that occurred during the last 2 decades of the 20th century provided an opportunity to evaluate the effect of changing climate conditions on the generally expected relation between the wetlands and ground water in the Cottonwood Lake area. The following discussion focuses primarily on the interaction of ground water with Wetland P1 because that wetland was selected for the most detailed study of water and chemical budgets and has the most wells within its watershed.

The hydrographs of water levels in upland wells within the watershed of Wetland P1 were always higher than the wetland water level (fig. 10), indicating that ground-water gradients are toward the wetland. This relation held true for the relatively normal climate conditions during the first 9 years of the study as well as during the drought and deluge. Using data from only the upland wells would indicate that Wetland P1 is a ground-water discharge wetland under all climate conditions. However, the relation between the wetland water levels and the water levels in the lowland wells near the wetland was more complex.

For most years, the water levels in the wells nearest the wetland were higher than the wetland water levels in spring and early summer and lower than the wetland water levels in late summer and fall (fig. 11). However, during the drought, the ground-water levels declined further each year to where spring recharge did not always raise the levels to the bottom of the wetland. In contrast, during the first 2 years of the deluge, the ground-water levels were higher than

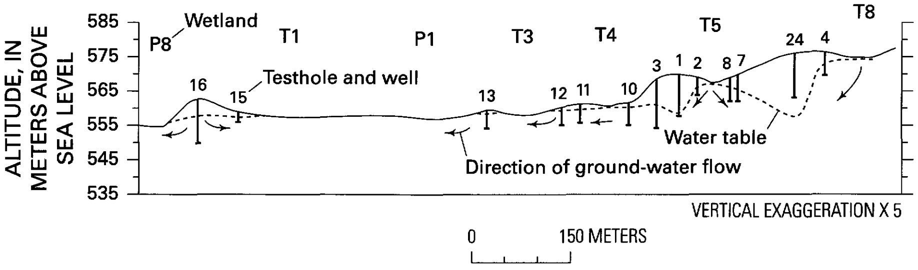


Figure 9. Hydrologic section through the Cottonwood Lake area showing the relation of wetlands to the water-table profile. (Modified from Winter and Carr, 1980)

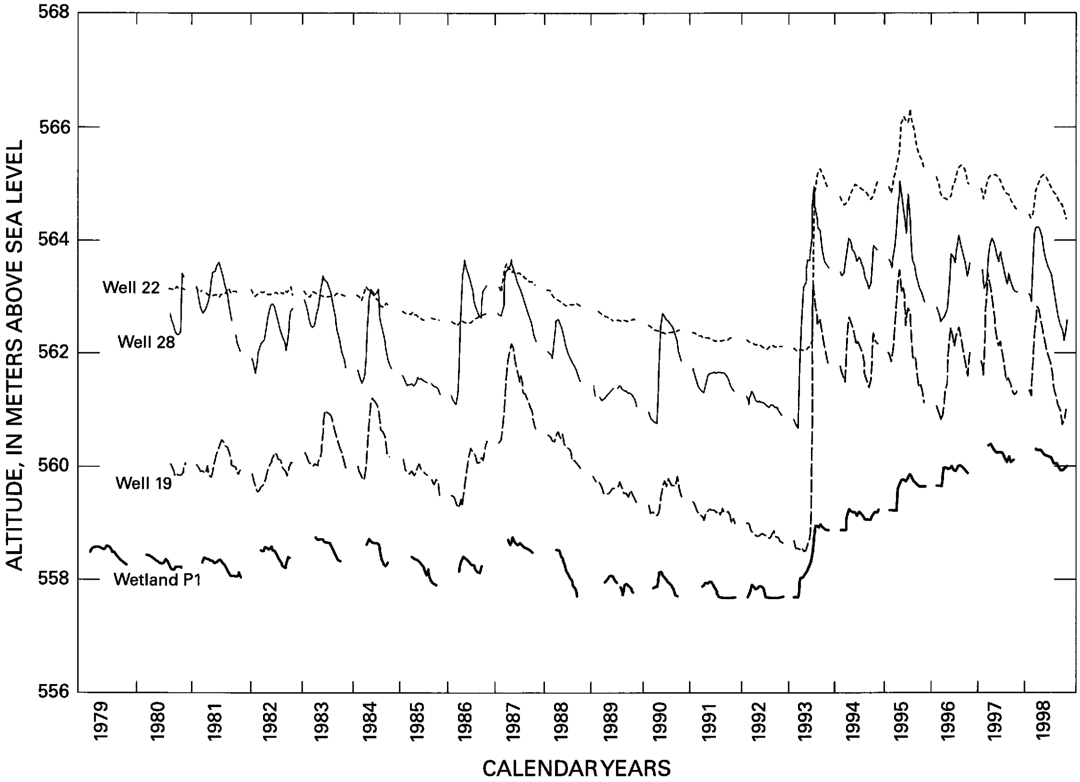


Figure 10. Water level of Wetland P1 and water levels in selected ground-water wells in the uplands, 1979-98.

the wetland water levels throughout the year. By 1995, the wetland expanded to the vicinity of well 25, and the wetland water levels and the water level in well 25 coincided in subsequent years. As the high water levels persisted, the seasonal reversals of flow became reestablished, as indicated by the hydrographs for the wetland and well 20 (fig. 11). These data indicate that reversals of flow between the wetland and ground water occur even when the wetland expands beyond the zones of wetland plants and the wetland perimeter is in direct contact with upland plants.

Hydrographs of the water levels in Wetland P1 and of the water table in the vicinity of wells 20 and 25 provide a time-series view of the relation between the wetland and only two of the wells near the wetland. To provide an areal view of the relation between the wetland and to the ground water in the wetland watershed, water-table maps were prepared for several dates to indicate the range of conditions that occurred during the study period. The configuration of the water table during a wet period is shown in figure 12. Ground-water levels in all wells were greater on that date than the wetland water level, indicating that ground water was discharging to the wetland around its entire perimeter. In contrast, during the drought, transpiration from ground water caused cones of depression to form around much of the wetland perimeter (fig. 13), and seepage from the wetland moved toward the depression. This seepage then was transpired along with the ground water that moved toward the wetland from higher in the flow system. The configuration of the water table in and around Wetland P1 has many variations between the two extremes. For example, cones of depression formed nearly every summer in some areas around the wetland perimeter, but the depressions commonly were not as continuous as shown in figure 13 and did not always form in the same place. The directions of flow, either toward the wetland or away from the wetland toward the cones of depression, are shown in figure 14 for the periods of high and low water levels for each year from 1981 to 1990.

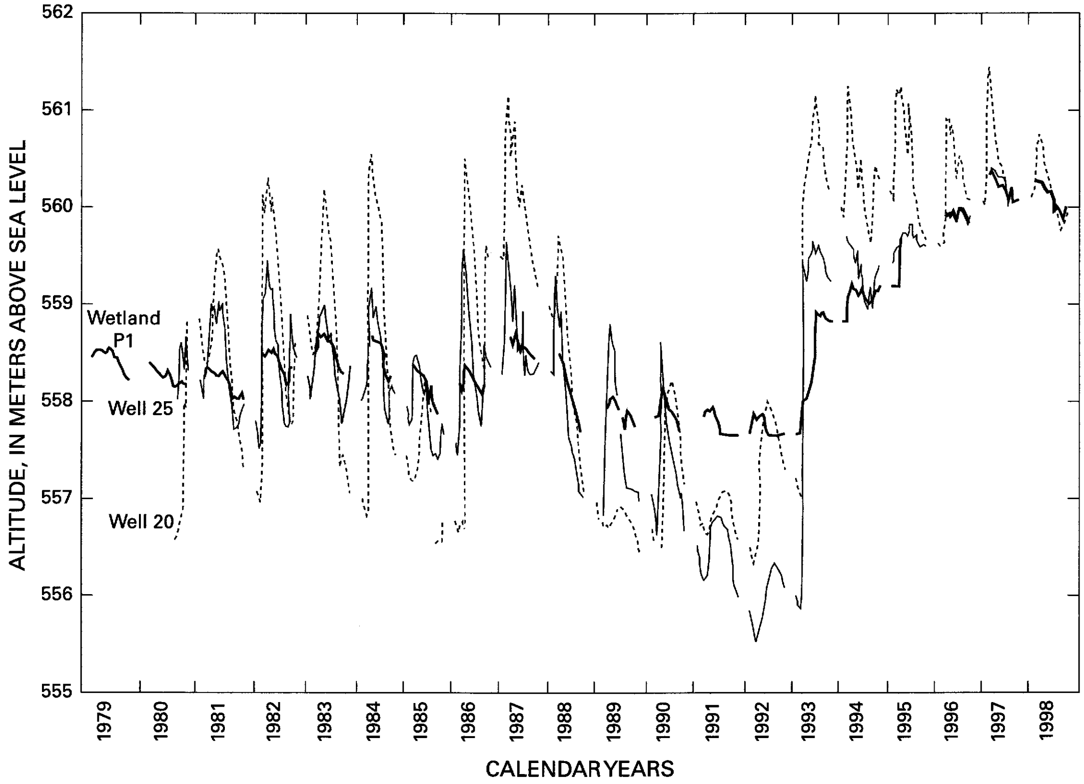


Figure 11. Water level of Wetland P1 and water levels in selected ground-water wells in the lowlands near the wetland, 1979-98.

To gain an increased understanding of the transient flow processes near the wetland perimeters, a number of water-table wells were installed along a transect from Wetland T3 to Wetland P1. The wells were instrumented with continuous recorders to document the small-scale time and space effects of focused recharge and transpiration from ground water on the configuration of the water table and to assess the effect of those processes on the flow of ground water between the wetlands. Data were collected for a 5-year period from 1989 to1993. As a result, data for 4 of the 5 years were collected during the drought, data collection was terminated when the wells became flooded during the deluge that began in 1993.

The data indicate that when Wetland T3 contained water, seepage from the wetland moved through the ground-water system and discharged to Wetland P1. During those few times that Wetland T3 contained water over the four dry years of the 5-year period (fig. 7A), infiltration of precipitation resulted in the formation of transient water-table mounds between the two wetlands. The mounds interrupted the ground-water flow from Wetland T3 to Wetland P1, but the mounds persisted for only a few days (Rosenberry and Winter, 1997).

When Wetland T3 was dry, ground-water gradients commonly were away from Wetland P1 toward transpiration-induced cones of depression. However, infiltration of snowmelt and precipitation still caused the formation of transient water-table mounds, but they generally were below the bottom of Wetland T3. The magnitude and duration of the mounds depended on the timing and amount of the rainfall. Rainfall in spring or early summer usually created large water-table mounds that were located near the center of the upland between the two wetlands, and rainfall in late summer or early fall more often created small water-table mounds that were located adjacent to the lower wetland. On two occasions, the late-season water-table mounds formed adjacent to the lower wetland and then migrated away from the wetland as the height of the mounds dissipated. Although water-table mounds formed frequently following rainfall during the 5-year period

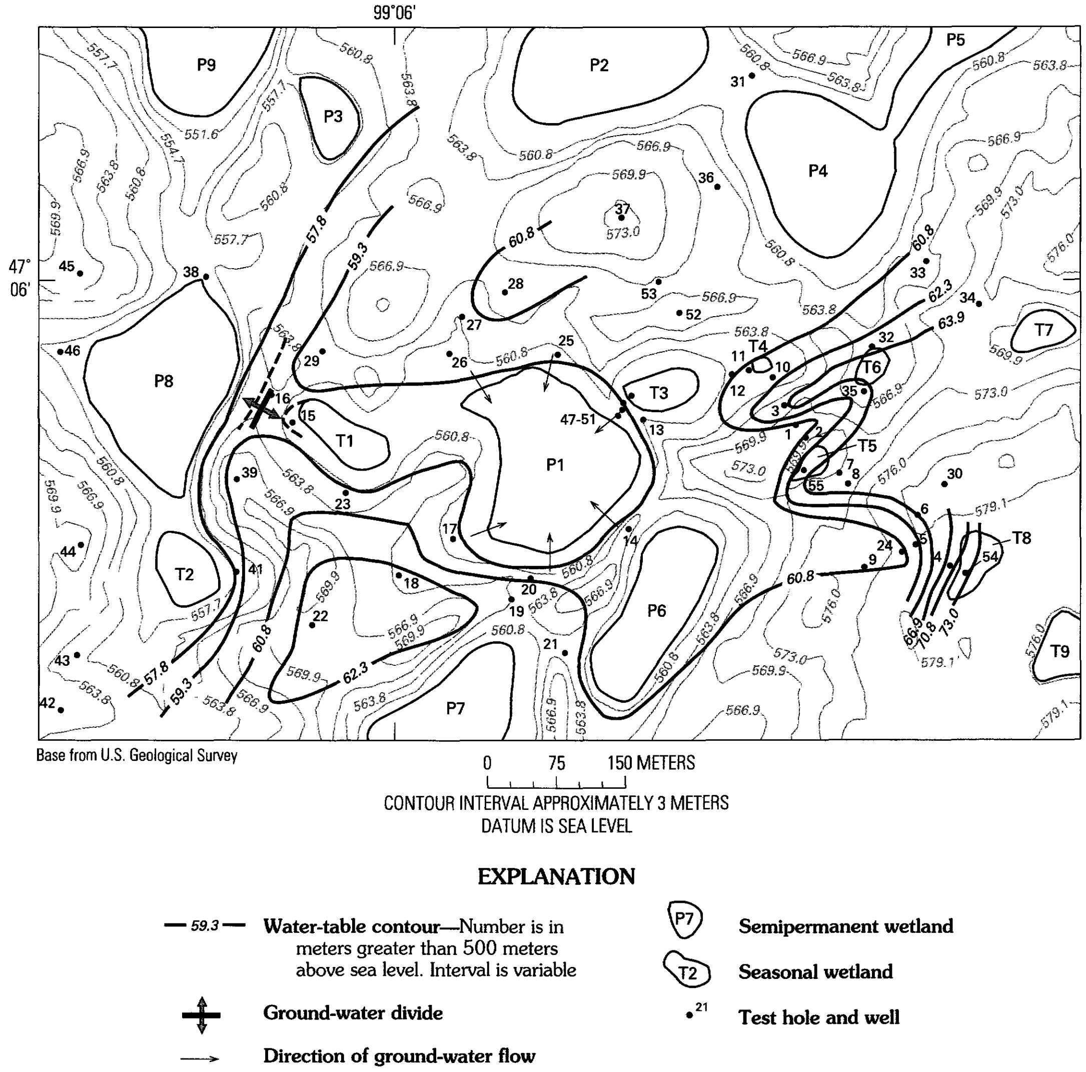


Figure 12. Configuration of the water table in the Cottonwood Lake area, May 31, 1987, indicating that ground water was discharging to Wetland P1 around its entire perimeter. (From Winter and Rosenberry, 1995)

of data collection, two examples, one for early summer and one for late summer, are shown in figure 15. The early-summer series (fig. 15, A-E) shows water-table configurations before and after rainfall of 51 mm on June 14 and 30 mm on June 28-30, 1991. The late-summer series (fig. 15, F-J) shows water-table configurations before and after rainfall of 52 mm on August 18 and 43 mm on August 31-September 3, 1989. Before the recharge event in both cases (fig. 15, A and F), a cone of depression was present adjacent to the wetland. Because the antecedent water table was higher in early summer than in late summer, the equivalent amount of rainfall resulted in higher and longer lasting mounds in early summer. For example, the early-summer mound was as much as 1.3 m higher than the water level of Wetland P1 (fig. 15B), and the mound persisted for about 12 days before a trough reformed near well 51 on June 28 (fig. 15C). The highest late-summer mound formed following the second period of late-summer rainfall and was 0.5 m higher than the wetland water level (fig. 15I). That mound persisted for only about 6 days (Rosenberry and Winter, 1997).

Data from the long-term records of wetland water levels and ground-water levels throughout the Cottonwood Lake area and from the shorter-term instrumented record of water levels between Wetlands T3 and P1 indicate that several generalizations can be

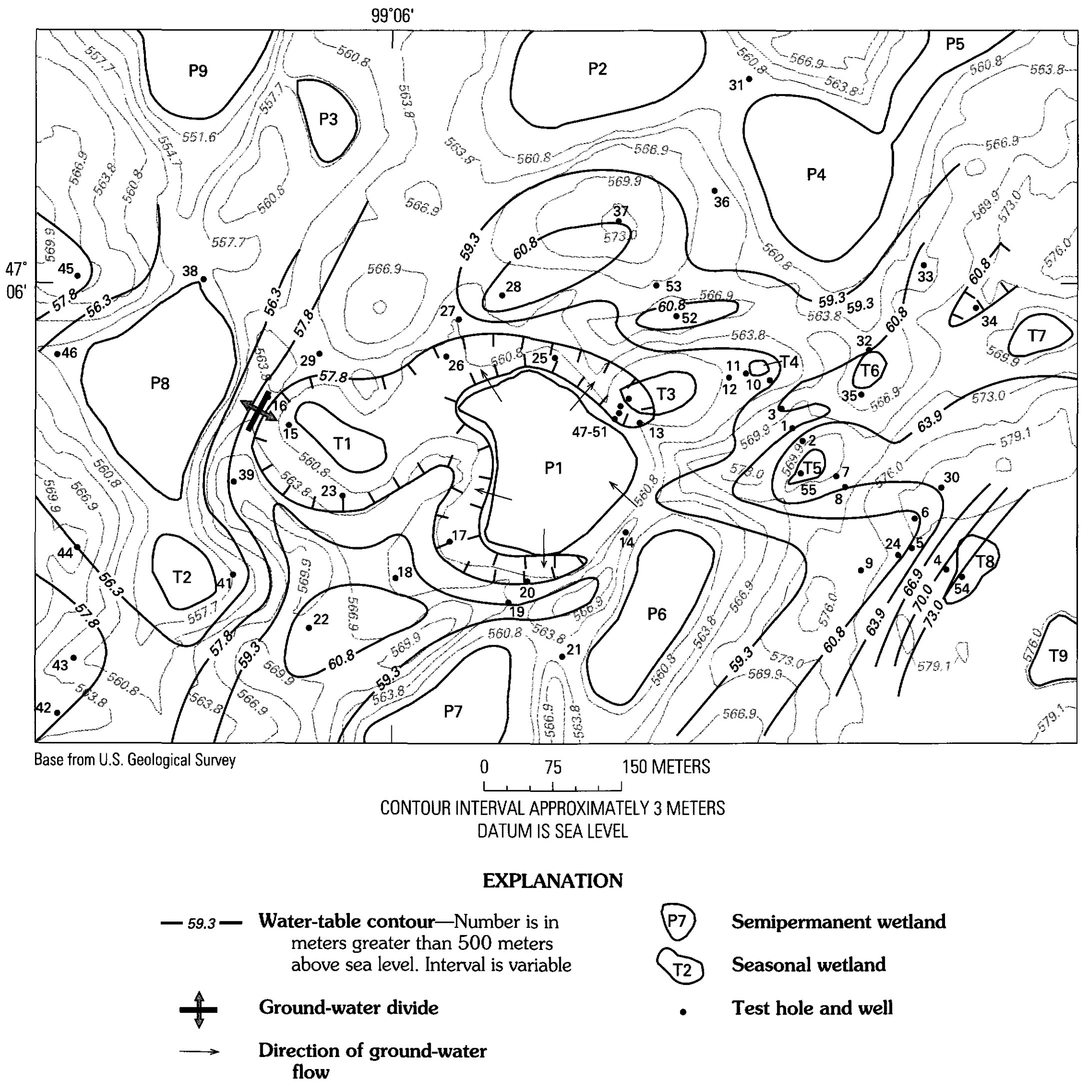


Figure 13. Configuration of the water table in the Cottonwood Lake area, August 31, 1989, showing the cones of depression caused by transpiration directly from ground water around much of the perimeter of Wetland P1. (From Winter and Rosenberry, 1995)

made with respect to the interaction of the wetlands with ground water: (1) Flow reversals between the wetlands and ground water are common; (2) during high-water conditions, ground-water gradients are toward the wetlands most of the time; and (3) during low-water conditions, ground-water gradients are away from the wetlands toward transpiration-induced cones of depression much of the time, particularly from midsummer through the fall.

Data for the Cottonwood Lake area also provide insight into several other features of the geohydrologic setting of the wetlands. These features are: (1) the transient characteristics of the major ground-water divides separating the wetlands and the rates of ground-water flow from wetland to wetland, (2) the effect of highly permeable ground-water drains on ground-water flow near the wetlands, (3) the superposition of ground-water flow systems, and (4) the characteristics of the wetland soils.

With respect to the first feature, a ground-water divide separates the ground-water basins of Wetlands P1 and P8 most of the time. The ground-water basin of Wetland P1 extends from the vicinity of well 16 (figs. 12 and 13) to Wetland T8 and is bounded to the north and south by water-table highs underlying the land-surface ridges contiguous to Wetland P1. The only part of the divide that is occasionally lower than Wetland P1, especially during drought conditions, is near wells 15 and 16. When the divide is not present, ground water can move from the basin of Wetland P1

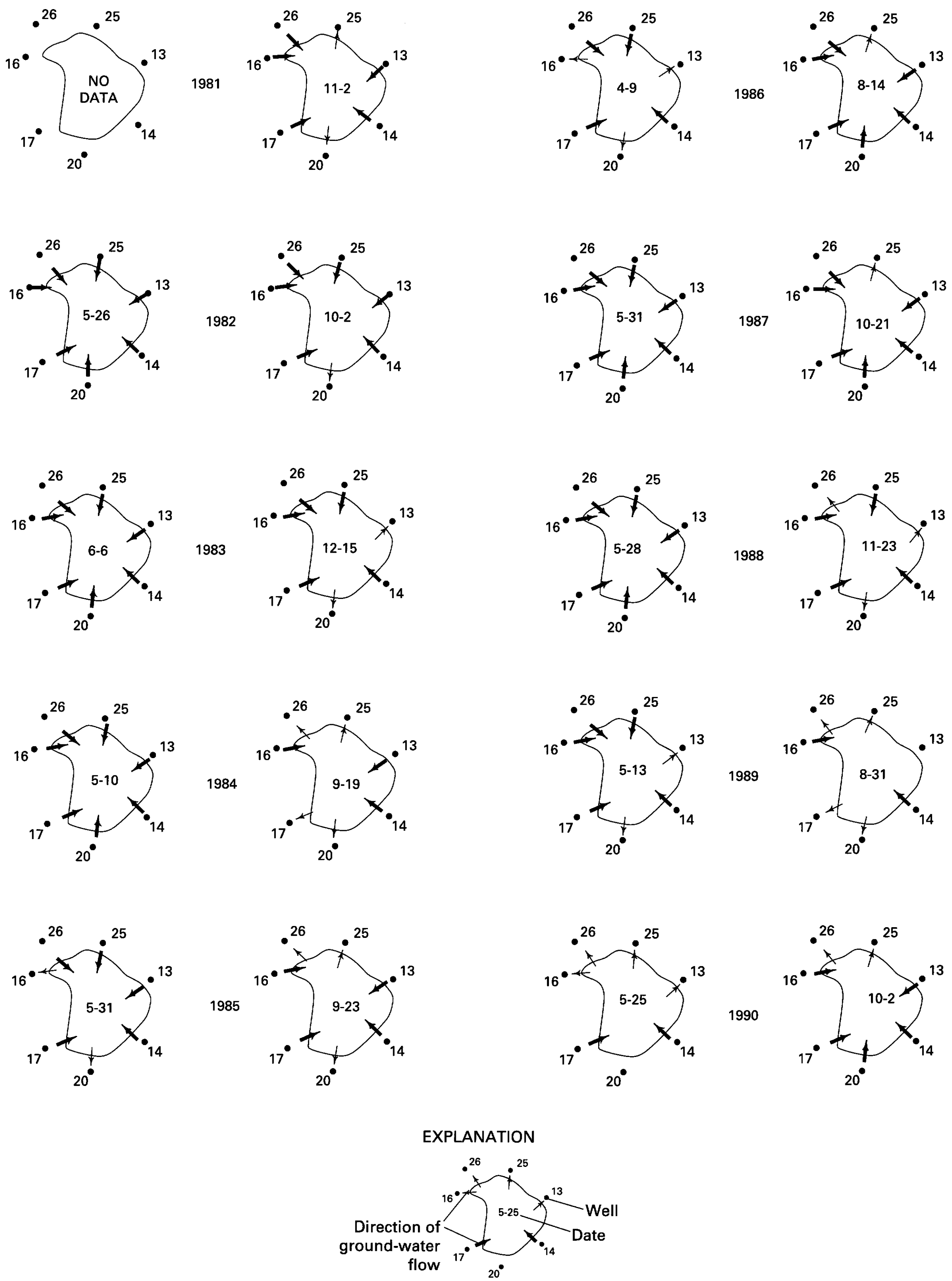


Figure 14. Direction of flow between Wetland P1 and nearby ground-water wells for the periods of high and low water levels of each year from 1981 to 1990. (From Winter and Rosenberry, 1995)

to that of Wetland P8 (fig. 16). However, the low hydraulic conductivity of the till allows only a small amount of ground water to transfer from one ground-water basin to the other. Using 0.016 for the hydraulic gradient of the water table between the two wetlands and an effective porosity of 0.2, the average linear pore-water velocity calculated for the movement of ground water between the two wetlands ranges from 0.025 m yr^{-1} if the hydraulic conductivity is 10^{-6} cm s^{-1} to 2.5 m yr^{-1} if the hydraulic conductivity is 10^{-4} cm s^{-1}. These rates of ground-water flow through the till probably are typical of rates throughout the Cottonwood Lake area.

With respect to the role of ground-water drains, a cone of depression is present between Wetlands T5 and T8 and between Wetlands T4 and T5 (fig. 9) for all climate conditions. Theoretical numerical modeling studies of ground-water flow have indicated that zones of high permeability in the subsurface can cause increased downward gradients over the upgradient parts of the zones (Freeze and Witherspoon, 1967; Winter, 1976). For example, figure 17 shows that increased hydraulic gradients toward the highly permeable zone on the side toward the ground-water divide cause flow to converge into the permeable zone. Conversely, on the side of the permeable zone toward the ground-water discharge area, gradients are the opposite and flow diverges away from the permeable zone. The upgradient side of the permeable zone can be thought of as a drain. The mechanism of enhanced flow toward a ground-water drain could be responsible for the persistent cone of depression between Wetlands T5 and T8 and Wetlands T4 and T5. If the subsurface sand deposit in the southwest part of the study area extends as a continuous deposit as far east as wells 1 and 24, as shown in figure 5, the deposit could cause the enhanced downward gradients that essentially would drain the ground-water system between the two wetlands.

With respect to the superposition of ground-water flow systems, the Cottonwood Lake area provides a field example of the effect of superposition on the ecological characteristics of prairie pothole wetland complexes (See Swanson and others, Chapter 4 of this report). The configuration of the water table in the area is highly irregular. As a result, some of the wetlands are enclosed by local ground-water flow systems where water cannot move from wetland to wetland by way of the ground-water system. However, other wetlands recharge ground water, and some of that water moves through the ground-water system and discharges to wetlands at a lower altitude. For example, because of the known ground-water divides between some of the wetlands, it is unrealistic to view the ground-water flow field from Wetland T8 to Wetland P11 as a continuous flow system where water flows from one wetland to the next lower wetland through the ground-water system. A more realistic flow field would show that ground water discharging to Wetland P11 would be receiving ground water that was recharged within its own local flow system as well as from ground water that was recharged in the highest part of the Cottonwood Lake area. Some of the ground water recharged in the higher part of the Cottonwood Lake area would flow as an intermediate ground-water flow system, passing at depth beneath the local flow systems associated with Wetlands P1, P8, P10, and several unnamed wetlands before discharging into Wetland P11 (fig. 18).

With respect to wetland soils, Arndt and Richardson (1993) indicated that evapotranspiration from ground water is a key part of the process that concentrates salts in the subsurface around wetland perimeters. Stolte and others (1992) also discussed the role of evapotranspiration from ground water as part of the process that concentrated salts in soils around the perimeter of a ground-water-recharge wetland in Manitoba. Evapotranspiration from ground water results in wetland water and solutes being drawn into the subsurface during dry times of the year. The annual flushing of the subsurface in the spring apparently does not completely dissolve and remove the salts. The process that concentrates salts in the subsurface around wetland perimeters, repeated over thousands of years, has resulted in the presence of large amounts of gypsum and calcite crystals along parts of the perimeter of Wetland P1 (Swanson, 1990; Arndt and Richardson, 1993). The storage of salts in the subsurface is probably the reason that Wetland P1 is not more saline (LaBaugh and Swanson, Chapter 3 of this report). As indicated earlier, the ground-water basin of Wetland P1 is a closed local flow system most of the time, and except for the outseepage caused by evapotranspiration, the basin would have outseepage only during the times that the ground-water divide near well 16 is absent. As indicated earlier, the loss of water and solutes from the basin of Wetland P1 to Wetland P8 by way of ground water is minimal and could not account for a large loss of solutes from Wetland P1.

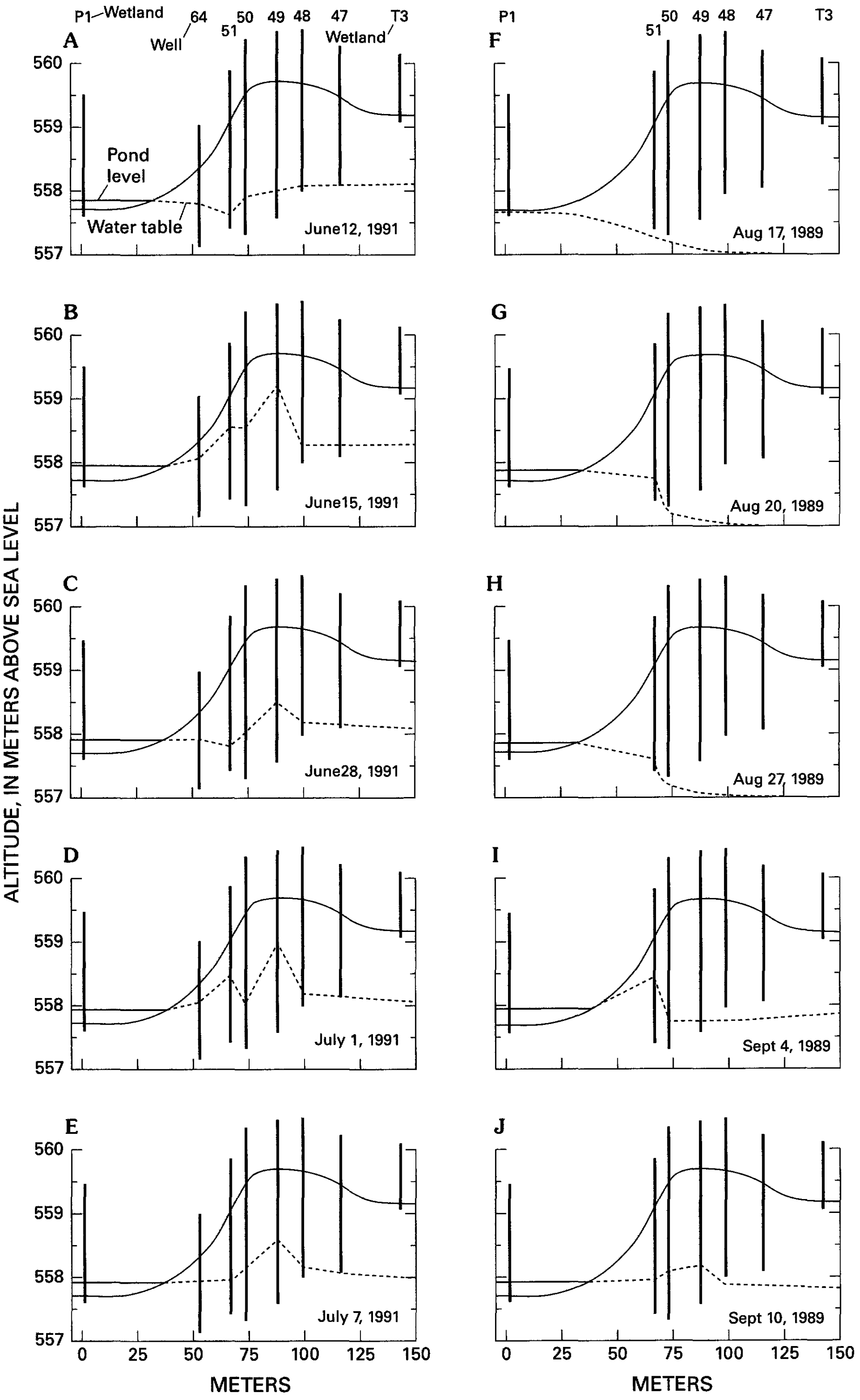


Figure 15. Hydrologic sections showing water-table profiles between Wetlands T3 and P1 indicating the formation of water-table mounds in response to early-summer rainfall (A-E) and in response to late-summer rainfall (F-J). (From Rosenberry and Winter, 1997)

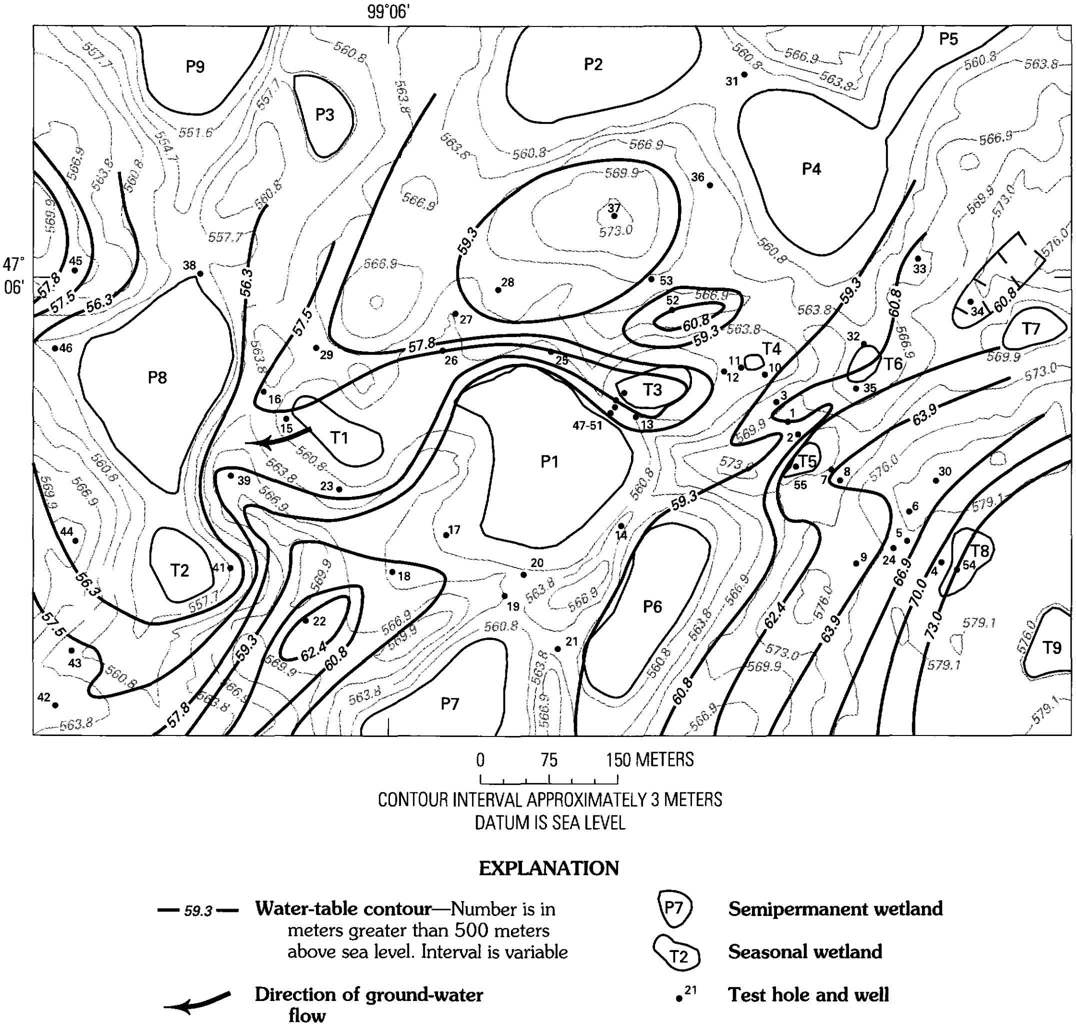


Figure 16. Configuration of the water table in the Cottonwood Lake area, May 25, 1990, indicating one of the few times during the study when a ground-water divide was not present between Wetlands P1 and P8.

Mapping of the wetland soils in the Cottonwood Lake area also has provided useful information for the general delineation of wetlands. In mapping the soils throughout the watershed of Wetland P1, James Arndt (oral and written commun., 1993) found wetland soils on the hillsides that were about 2 m above the level of Wetland P1 prior to the deluge that began in 1993. The outer limit of the calciaquoll wetland soils (fig. 19) is similar to the present area of open water in Wetland P1 (fig. 8). The area of open water in the wetland is at least as extensive at present (2002) as it was 150 years, and perhaps 500, years ago (Winter and Rosenberry, 1998). Thus, the soils indicated that Wetland P1 had been as large in the past as it is at present, and probably was that large many times in the past. This information indicates that mapping of wetland soils is perhaps the most useful way to delineate wetlands because the soils integrate highly variable climate and hydrologic conditions over many millenia.

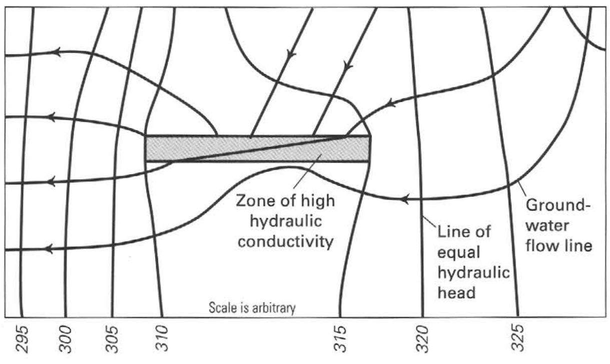


Figure 17. Numerical simulation of ground-water flow in the vicinity of a highly conductive aquifer of limited extent within a porous media having lower hydraulic conductivity. (Modified from Winter, 1976)

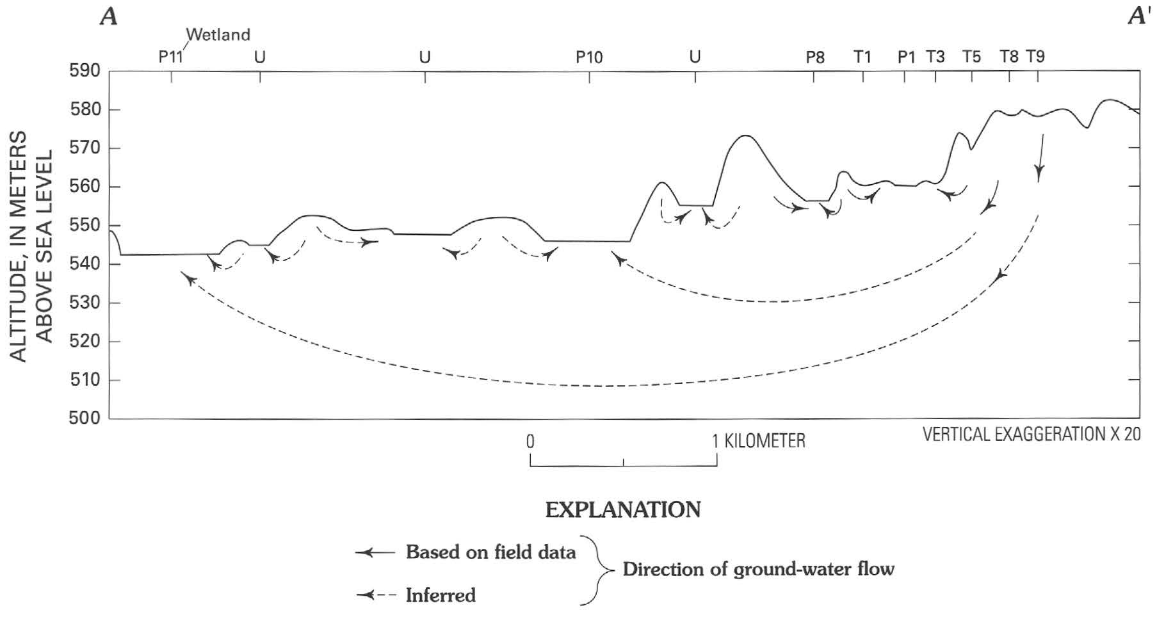


Figure 18. Hydrologic section showing intermediate ground-water flow systems passing at depth beneath local ground-water flow systems associated with selected wetlands. Note the local and intermediate flow systems discharging into Wetland P11. The intermediate flow system is also shown in figure 2 where ground water moves from the Cottonwood Lake area to Eric Lake. Wetland names are shown along top of figure. U indicates unnamed. Line of section shown in figure 4.

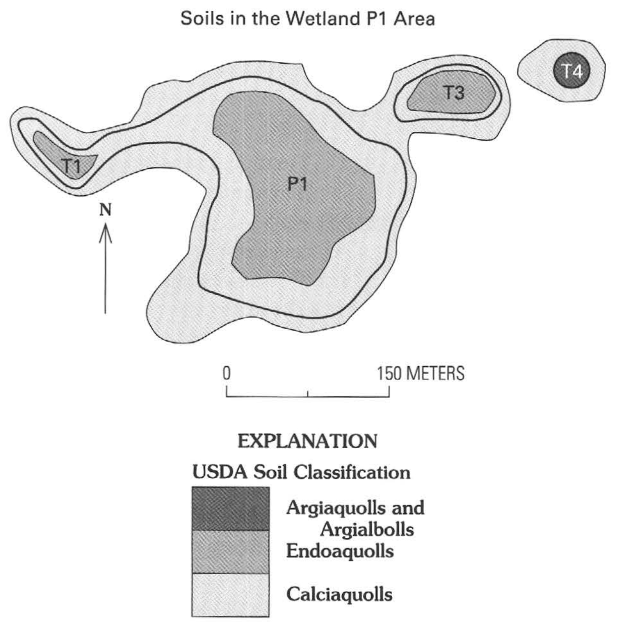


Figure 19. Generalized distribution of soils in the Cottonwood Lake area. (Map courtesy of Dr. James Arndt, then of North Dakota State University)

REFERENCES

Arndt, J.L., and Richardson, J.L., 1993, Temporal variations in the salinity of shallow ground water from the periphery of some North Dakota wetlands (USA): Journal of Hydrology, v. 141, p. 75-105.

Carlson, C.G., 1969, Bedrock geologic map of North Dakota: North Dakota Geological Survey Miscellaneous Map 10.

Freeze, R.A., and Witherspoon, P.A., 1967, Theoretical analysis of regional ground water flow. 2, The effect of water-table configuration and subsurface permeability variation: Water Resources Research, v. 3, p. 623-634.

Grisak, G.E., and Cherry, J.A., 1975, Hydrologic characteristics and response of fractured till and clay confining a shallow aquifer: Canadian Geotechnical Journal, v. 12, p. 23-43.

Gunaji, N.N., 1968, Evaporation investigations at Elephant Butte Reservoir in New Mexico: International Association of Scientific Hydrology Publication No. 78, p. 308-325.

Harbeck, G.E., Jr., and others, 1958, Water-loss investigations. Lake Mead studies: U.S. Geological Survey Professional Paper 298, 100 p.

Hendry, M.J., 1988, Hydrogeology of clay till in a prairie region of Canada: Ground Water, v. 26, p. 607-614.

Keller, C.K., Van der Kamp, G., and Cherry, J.A., 1986, Fracture permeability and ground water flow in clayey till near Saskatoon, Saskatchewan: Canadian Geotechnical Journal, v. 23, p. 229-240.

Meyboom, P., 1967, Groundwater studies in the Assiniboine River drainage basin, Part II, Hydrologic characteristics of phreatophytic vegetation in south-central Saskatchewan: Geological Survey of Canada Bulletin 139, 64 p.

Meyboom, P., van Everdingen, R.O., and Freeze, R.A., 1966, Patterns of ground water flow in seven discharge areas in Saskatchewan and Manitoba: Canadian Geological Survey Bulletin 147, 57 p.

Parkhurst, R.S., Winter, T.C., Rosenberry, D.O., and Sturrock, A.M., 1998, Evaporation from a small prairie wetland in the Cottonwood Lake area, North Dakota—an energy budget study: Wetlands, v. 18, no. 2, p. 272-287.

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

Stolte, W.J., Barbour, S.L., and Eilers, R.J., 1992, A simulation of the mechanisms influencing salinity development around prairie sloughs, *In* Robards, R.D., and Bothwell, M.L., eds., Aquatic Ecosystems in Semi-Arid Regions, Implications for Resource Management: The National Hydrology Research Institute Symposium Series No. 7, Environment Canada, Saskatoon, Saskatchewan, Canada, p. 165-177.

Swanson, K.D., 1990, Chemical evolution of ground water in clay till in a prairie wetlands setting in the Cottonwood Lake area, Stutsman County, North Dakota: MS Thesis, University of Wisconsin, Madison, 229 p.

Winter, T.C., 1975, Delineation of buried glacial-drift aquifers: U.S. Geological Survey Journal of Research, v. 3, no. 2, p. 137-148.

Winter, T.C., 1976, Numerical simulation analysis of the interaction of lakes and ground water: U.S. Geological Survey Professional Paper 1001, 45 p.

Winter, T.C., 1983, The interaction of lakes with variably saturated porous media: Water Resources Research, v. 19, no. 5, p. 1203-1218.

Winter, T.C., and Carr, M.R., 1980, Hydrologic setting of wetlands in the Cottonwood Lake area, Stutsman County, North Dakota: U.S. Geological Survey Water-Resources Investigations Report 80-99, 42 p.

Winter, T.C., and Rosenberry, D.O., 1995, The interaction of ground water with prairie pothole wetlands in the Cottonwood Lake area, east-central North Dakota, 1979-1990: Wetlands, v. 15, no. 3, p. 193-211.

_____1998, Hydrology of prairie pothole wetlands during drought and deluge: A 17-year study of the Cottonwood Lake wetland complex in North Dakota in the perspective of longer term measured and proxy hydrological records: Climatic Change, v. 40, no. 2, p. 189-209.

CHAPTER 2
CLIMATE OF THE COTTONWOOD LAKE AREA

Donald O. Rosenberry, U.S. Geological Survey, Denver, Colorado

ABSTRACT

The climate of central North Dakota is continental, with typically long, cold, dry winters and short, mild, variably wet summers. The average annual temperature is 4°C, and average annual precipitation is 440 mm. Central North Dakota receives an average annual 59 percent of possible sunshine. Annual windspeed averages 4.5 m s^{-1}, and prevailing winds are from the northwest. The number of daylight hours in a 24-hour period ranges from less than 9 hours in December to more than 16 hours in June. This large range contributes to the large seasonal temperature changes; extreme temperatures range from –47 to 48°C. Normally, 17 days each year have temperatures that exceed 32°C, 56 days each year have temperatures below –18°C, and 195 days have temperatures below 0°C. November through February are the driest months, and average precipitation during those months ranges from 12 to 14 mm per month. Average annual snowfall is 865 mm, and average maximum snow depth is 300 mm. Snow normally covers the area from December 4 to March 24. June is normally the wettest month of the year and has an average 91 mm of rainfall. Thunderstorms produce most of the rainfall during summer. Average annual lake evaporation is 810 mm per year, almost twice the average annual precipitation. Spring runoff, overland flow, and ground-water seepage make up the difference between evaporation and precipitation. Wetland water levels respond markedly to seasonal and annual climatic perturbations.

Conditions at the Cottonwood Lake area were warmer and drier than normal for the first 14 years of the study period and were especially dry during a drought that lasted from 1988 through 1992. The cumulative precipitation deficit, relative to normal, during the 14-year period was 635 mm. Conditions were much wetter than normal from 1993 through 1998; during that time, the cumulative precipitation excess, relative to normal, was 885 mm. This wet period was the wettest of the century for central North Dakota.

INTRODUCTION

The hydrology, geochemistry, and biology of the Cottonwood Lake area are being studied to improve the understanding of wetland processes. Knowledge of the climate of the Cottonwood Lake area is paramount to understanding the hydrology, which drives the geochemical and biological processes. The climate of the area is continental and is characterized by large temperature changes over daily and annual time scales (Jensen, 1972). The area receives light to moderate precipitation and nearly continuous wind. Air masses arrive from polar, Pacific, and Gulf of Mexico sources. The Pacific air masses typically are moderate and pleasant, but the Gulf of Mexico and polar air masses generally bring extreme climatic conditions to the area.

Annual evaporative losses in the area are almost twice as large as precipitation amounts (Eisenlohr and others, 1972). For many of the prairie wetlands, surface runoff and ground-water seepage are the only hydrologic fluxes available to make up the difference between evaporation and precipitation. Therefore, many wetlands in the area dry up during prolonged periods of drought when evaporative and transpirative losses are not compensated for by precipitation, runoff, and ground-water inflow.

Information on the normal climatic conditions for central North Dakota is presented in the first part of this chapter. This information is followed by a more detailed description of climatic conditions for the Cottonwood Lake area based on data collected at the site since 1979.

METHODS

Temperature and precipitation data from three National Weather Service stations near the Cottonwood Lake area were used to represent monthly and annual normal conditions for the study area. Normals were calculated for the 30-year period from 1961 to 1990 using data collected at the Carrington, Jamestown airport, and Pettibone stations (fig. 1). These stations are located 39 km north, 39 km southeast, and 32 km west of the Cottonwood Lake area. Weighted averages were determined to represent normal conditions for the area. Other climatic characteristics of the area were summarized from data collected at National Weather Service stations at Bismarck, Devils Lake, and Fargo (Jensen, 1972).

Climate data have been collected during open-water periods from a raft or platform in the center of Wetland P1 and at a land station adjacent to the wetland since 1979. Climate parameters that were monitored for all of the period from 1979 to 1998 include air temperature, relative humidity, windspeed, and precipitation. Incident shortwave solar radiation and incident longwave atmospheric radiation were monitored for part of the period. Wetland surface-water temperature was monitored for the entire period. Bottom-water temperature and sediment temperature at 0.5- and 1.0-m depths below the sediment-water interface were monitored for part of the period. Since 1981, the climate data have been recorded by a digital data logger and exist as hourly and daily averages or totals of scans made at 1-minute intervals. During the open-water periods of 1979 and 1980, temperature, humidity, and windspeed data were collected by analog instruments. Rainfall during the open-water periods was monitored with a standard 8-in National Weather Service gage, monitored weekly, and an 8-in.-diameter tipping-bucket gage with 0.01 inch resolution. The tipping-bucket gage was monitored continuously during open-water periods by a land-based data recorder. Evaporation during 1982 to 1987 was determined using the energy-budget method (Parkhurst and others, 1998).

REGIONAL CLIMATE OF CENTRAL NORTH DAKOTA

The climate of central North Dakota, is continental, with typically long, cold, dry winters and short, mild, variably wet summers. The average annual temperature is 4°C and average annual precipitation is 440 mm. Large seasonal differences in the climate are related to the number of daylight hours in a 24-hour period. This number ranges from less than 9 hours in December to more than 16 hours in June. The large range in the number of daylight hours contributes to the large seasonal temperature changes. Extreme temperatures in central North Dakota range from –47 to 48°C and are nearly as great as the statewide extremes of –51 and 49°C. The freeze-free period normally lasts 119 days from May 20 to September 15.

Winter is typically cold and dry; normally, 56 days each year have temperatures below –18°C, and 195 days have temperatures below 0°C. January is the coldest month and has an average temperature of –13.5°C (fig. 20). The diurnal temperature range is smallest from November through March and averages 11.5°C. Based on data from the Jamestown airport station, soil frost normally reaches a depth of 1.4 m although depths as great as 1.8 m have been recorded. November through February are the driest months; average precipitation during those months ranges from 12 to 14 mm per month (fig. 20). Average annual snowfall is 865 mm, the average maximum snow depth is 300 mm, and an average snowpack of at least 25 mm covers central North Dakota from December 4 to March 24. On average, two blizzards, usually originating in either Alberta, Canada or Colorado, occur in North Dakota each year. Blizzards that originate in Alberta generally pose a greater hazard than those that originate in Colorado because they tend to be faster moving and often approach with little advance warning.

A maximum mean monthly temperature of 20.5°C occurs in July, but August is nearly as warm (fig. 20). During a normal year, 17 days have temperatures that exceed 32°C. The chance of extended warm periods is greatest from July 19 to August 1. The diurnal temperature range is greatest during summer, and a maximum average monthly difference of 16.5°C is reached in August. June is normally the wettest month of the year and has an average of 91 mm of rainfall. Most summer rainfall is generated by thunderstorms. From April to October, an average of 30 thunderstorms can be expected; and, during June through August, 7 to 8 thunderstorms occur each month.

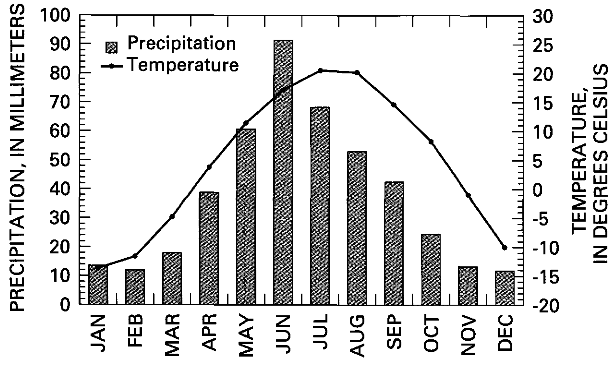


Figure 20. Normal (1961-90) monthly precipitation and temperature for the Cottonwood Lake area based on data from three nearby National Weather Service stations.

On average, 72 days each year have measurable precipitation. Most precipitation events are light; 48 percent result in 3 mm of precipitation or less. Only 4 percent of the precipitation events result in more than 25 mm of precipitation during a 24-hour period. The chance for precipitation is greatest from 6 to 9 a.m., the chance reaches 30 percent at 8 a.m. during the winter and 13 percent at 6 a.m. during the summer. The chance for precipitation is smallest during midafternoon in the winter and during midday in the summer. The chance for precipitation is uniformly small during the fall, and averages about 12 percent throughout the day.

Relative humidity is generally highest near 6 a.m. and lowest during midafternoon and has a much greater diurnal range in the summer than in the winter. Mean monthly maximum values range from 71 percent in January to 86 percent in July. Mean monthly midafternoon minimum values range from 67 percent in January to about 50 percent in July. Typically, daily-average relative humidity is lowest during midspring and early fall.

On an average annual basis, central North Dakota receives 59 percent of total possible sunshine. This value is a ratio of incoming solar radiation measured on the ground and the amount of solar radiation that the earth would receive at that latitude if there were no clouds. Based on data from the Bismarck and Fargo stations, July is the sunniest month and receives an average of 74 percent of possible sunshine. November is the cloudiest month and receives an average of only 43 percent of possible sunshine. Central North Dakota averages about 210 clear or partly cloudy days each year, monthly totals range from an average of 24 days during July to about 14 days during November through February.

Wind is one of the more noticeable features of the climate of central North Dakota. Wind prevails from the northwest during all seasons at an average speed of 4.5 m s^{-1}. Average monthly windspeed is greatest during late winter through early spring and reaches a maximum of 5.4 m s^{-1} in April. The July monthly windspeed averages 4.0 m s^{-1}. Monthly maximum windspeeds are normally greatest during July and August and usually accompany thunderstorm activity. However, monthly maximum windspeeds associated with winter cold fronts often are large also.

Whereas precipitation generally decreases from east to west across central North Dakota, evaporation increases from northeast to southwest. Average annual lake evaporation is 810 mm near the study area and ranges from 760 mm 80 km northeast of the study area to 860 mm 80 km southwest of the study area (Eisenlohr and others, 1972).

LOCAL CLIMATE OF THE COTTONWOOD LAKE AREA

Many characteristics of climate are highly variable spatially, and areally averaged data often do not provide accurate information for a specific site. Also, few wetlands are instrumented with climate stations, and the climate over a wetland can be different from the climate over an area where wetlands are not present. Therefore, to obtain accurate, site-specific data for estimating evaporation using the energy-budget method, climate data have been collected for the Cottonwood Lake area since 1979 (Sturrock and others, 1986; 1987; Parkhurst and others, 1994, 1998). These data also allow a more site-specific characterization of the climate over a wetland. For example, monthly average air temperatures calculated as weighted means of data from the Carrington, Jamestown airport, and Pettibone stations were compared to monthly average air temperatures measured at the study area for June, July and August 1982-85 (fig. 21). The average of the differences between the National Weather Service data and the study area data for the 12 months was only 0.1°C, but the differences for the individual months ranged from 0.3°C during June 1982 to 2.7°C during August 1985. These differences can cause error when network data are used to estimate evaporation for a specific site. Also, most network climate stations provide only air temperature and precipitation data, and daily-average air temperature data often are determined by averaging the daily maximum and minimum values. However, for the Cottonwood Lake area, data were collected every minute, and 1,440 values were averaged each day to provide a more accurate daily-average air temperature.

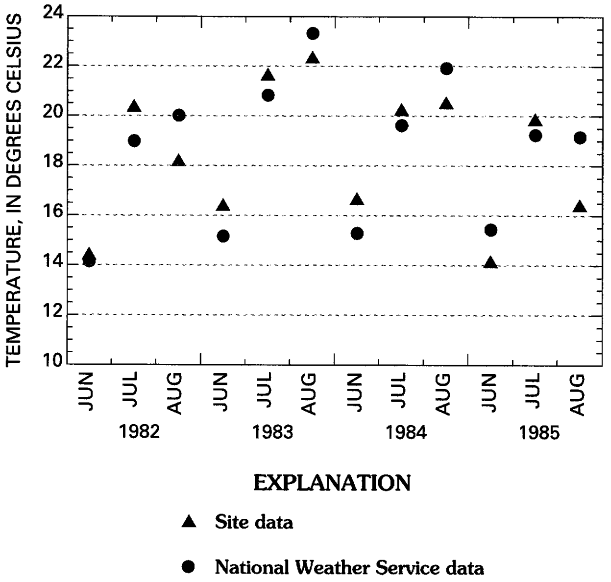


Figure 21. Summer monthly average air temperatures measured at the Cottonwood Lake area and monthly average air temperatures calculated as weighted means of data from the Carrington, Jamestown airport, and Pettibone National Weather Service stations, 1982-85.

Daily maximum and minimum values for many of the climate variables, and the times that the values occurred, were collected for the study area. The monthly mean hours of occurrence for the maximum and minimum air temperatures are shown in figure 22. These monthly means do not include days when the maximum occurred during nighttime hours or when the minimum occurred between noon and midnight; the means represent typical days, when the maximum occurs sometime during the day and the minimum occurs sometime during the night or morning. The monthly mean hour of occurrence for the maximum air temperature was about 4 p.m. The maximum usually occurred between 2 and 6 p.m., and the time was fairly consistent throughout the summer. The hour of occurrence for the maximum air temperature varied the most during May, and occurred earliest during May and latest during July. The monthly mean hour of occurrence for the minimum air temperature was about 4:15 a.m., and the minimum usually occurred between 2 and 6:30 a.m. The hour of occurrence for the minimum air temperature varied little between May and September, and the minimum occurred earliest during July and latest during May.

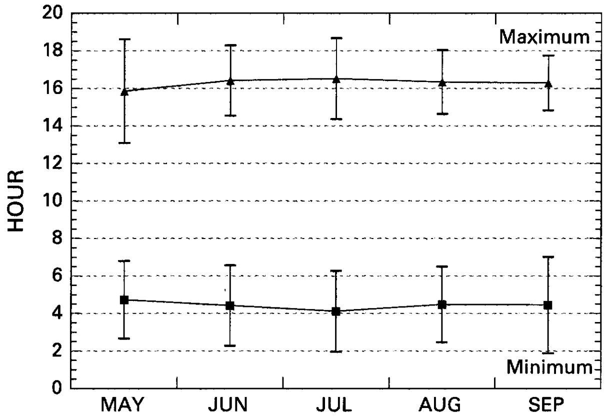


Figure 22. Monthly mean hours of occurrence for daily maximum and minimum air temperatures, and one standard deviation from the monthly mean, for the Cottonwood Lake area, 1982-85.

Incident solar and atmospheric radiation for the Cottonwood Lake area were monitored from 1982 to 1987. Longwave atmospheric radiation varies primarily with air temperature, but shortwave solar radiation varies primarily due to changes in cloud cover. The daily total incident shortwave solar radiation for the study area and the theoretical maximum total value assuming a clear sky are shown in figure 23. The shortwave solar radiation had considerable variability from year to year. For example, the springs of 1984 and 1986 appear to have been relatively cloud free based on the high values of solar radiation relative to the maximum possible values. The summers and falls of 1982 and 1983 appear to have been more cloudy than the other years. The monthly average percent of clear-sky shortwave solar radiation for 1982 to 1987 indicates that radiation was greatest during May through July; the monthly average ranged from 68 percent in July, to slightly less than 50 percent during October and

November (fig. 24). This range in average monthly solar radiation is somewhat less than the range based on data from the Bismarck and Fargo stations that was previously reported in this chapter.

Windspeed also was highly variable on a daily, seasonal, and annual basis and also varied spatially. During 1982 to 1991, the annual average windspeed at Wetland P1, measured during May to October each year, varied from 2.3 m s^{-1} during 1991 to 3.6 m s^{-1} during 1986. Monthly average values during the same period indicate that the windiest conditions occurred during May and the calmest conditions occurred during August (fig. 25).

A focus on the climatic conditions over a wetland is essential to understanding the variability of the temperature of the water in the wetland. Therefore, to obtain water temperature data, thermistor thermometers were installed at the center of Wetland P1 at the wetland water surface and at the wetland water bottom. In addition, thermistor thermometers were installed in the wetland sediment at 0.5 and 1.0 m below the sediment-water interface. The water depth of Wetland P1 ranged from 0.3 to 1.2 m during the period for which the temperature data were collected. The data indicate that during the open-water season the average temperature of the entire water column was greater than the average air temperature (fig. 26). Monthly average surface-water temperatures ranged from 16.6°C during September to 23.7°C during July. Monthly average air temperatures were 2.6°C (August) to 4.6°C (May) lower than the surface-water temperatures, and monthly average bottom-water temperatures at were 1.4 °C (June) to 3.1°C (May) lower than the surface-water temperatures. Wetland water temperatures peaked during July, but the much colder sediment temperatures peaked during August and September. Wetland sediments warmed at an average rate of slightly less than 0.1°C day^{-1} throughout the spring and summer.

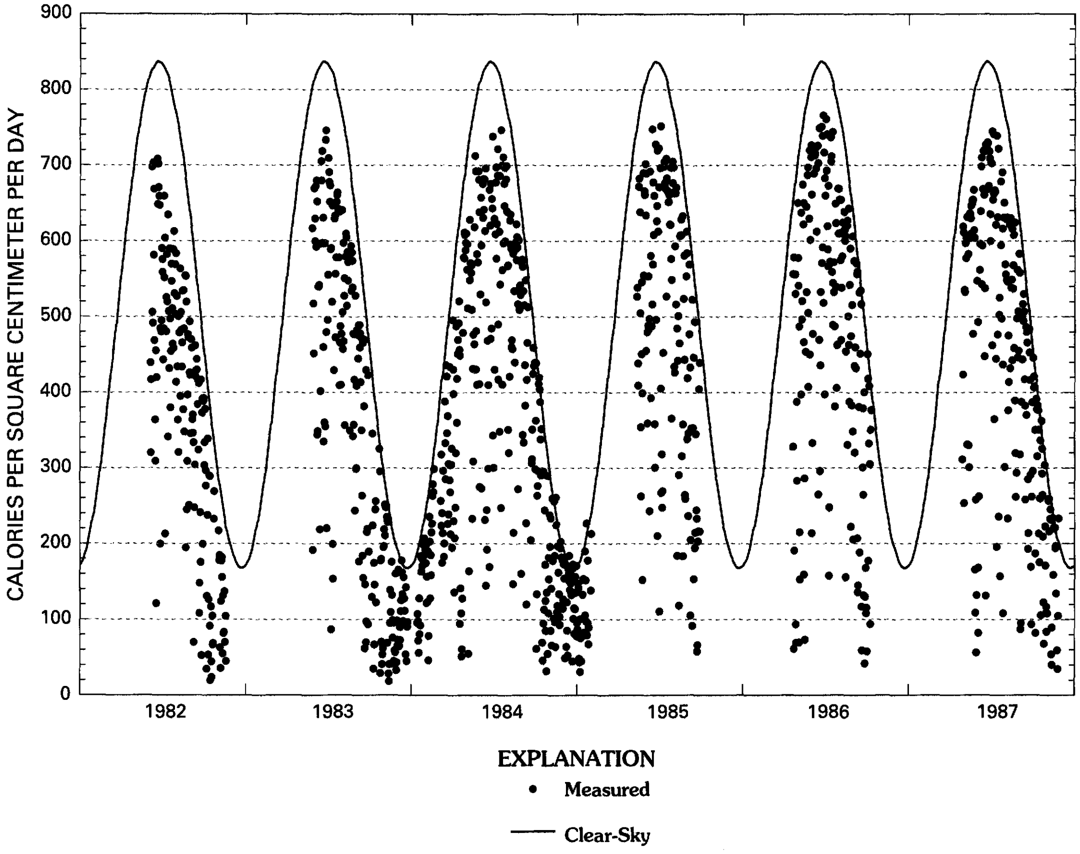


Figure 23. Measured daily total incident shortwave solar radiation at the Cottonwood Lake area from 1982 to 1987 and clear-sky shortwave solar radiation at 47 degrees north latitude.

Air temperature and precipitation are the most commonly used parameters for characterizing the climate of an area, and onsite collection of these data provides information about variations in the climate relative to conditions normal for the area. The cumulative departures from normal monthly average values for both air temperature and precipitation from 1978 to 1998 for the Cottonwood Lake area are shown in figure 27. The plots were created by calculating monthly averages, determining the departures from normal for each monthly average, and then determining the running sum of the departures from the normal monthly averages. Onsite data were used when available; otherwise, the temperature data were the weighted averages for the Carrington, Jamestown airport and Pettibone stations; precipitation data were from the Woodworth station. Normal monthly values are those shown in figure 20. In figure 27, segments of the curves that have a positive slope represent periods of above-normal temperature or precipitation, and segments of the curves that have a negative slope represent periods of below-normal temperature or precipitation. If conditions averaged out to be normal for the study period, the lines would end near their respective zero points by the end of 1998. The figure indicates that, for the first 14 years of the study, conditions were warmer and drier than normal, and, for the last 6 years of the study, conditions were slightly cooler and much wetter than normal.

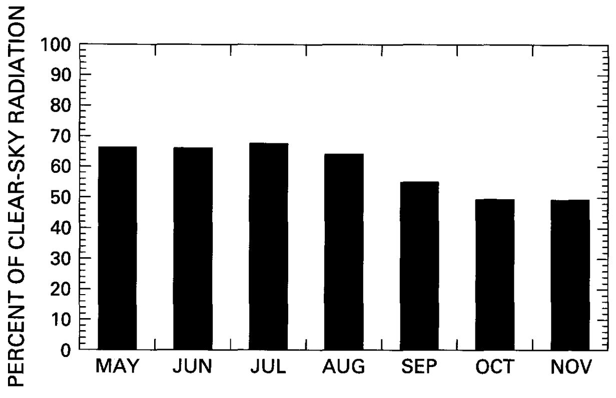


Figure 24. Monthly average percent of clear-sky shortwave solar radiation for the Cottonwood Lake area, 1982-87.

The air temperature averaged out to be about normal for the first 9 years shown in figure 27. From 1986 through 1992 the air temperature was much greater than normal (with the exception of 1989 when the air temperature was about normal for the year). Much of the 6-year period of above-normal air temperatures coincided with a severe drought that lasted from 1988 through 1992. From 1993 through 1998, the air temperature was below normal for 3 years.

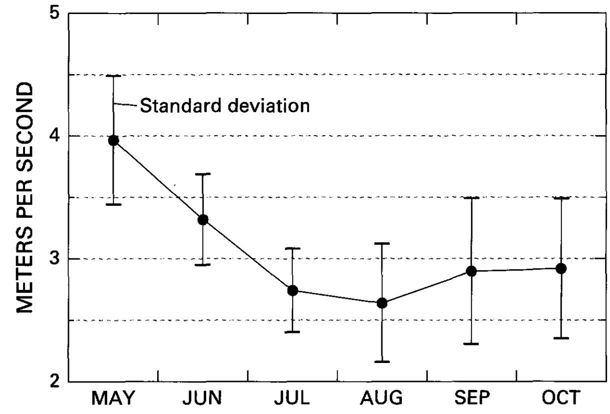


Figure 25. Monthly average windspeed, and one standard deviation from the monthly average, for the Cottonwood Lake area, 1982-91.

Precipitation was below normal for 9 of the first 15 years shown in figure 27; the cumulative precipitation deficit, relative to normal, was 635 mm for the 15-year period. Precipitation was above normal for only 3 of those 15 years. During an extended drought that began in 1988 and lasted through 1992, precipitation was less than normal by 575 mm, an amount 1.3 times the normal total annual precipitation for the Cottonwood Lake area. For 1993 through 1998, the remaining 6 years of the 21-year period shown in figure 27, precipitation was much greater than normal. The cumulative precipitation excess, relative to normal, was 885 mm during the extremely wet period.

The severe drought that occurred from 1988 through 1992 had a great impact on the wetland water levels in the Cottonwood Lake area. The water level of Wetland P1 fluctuated slightly less than 1 m during the first 10 years shown in figure 28, although precipitation was below normal during most of that period. However, the wetland dried up during every year of the 5-year drought and dried up earlier each year as the drought persisted. The extremely wet period that began in 1993 had an even greater impact on the water level of Wetland P1. During the 6 years of greater-than-normal precipitation from 1993 through 1998, the wetland water level rose to more than 1.5 m above the highest water level recorded during the first 15 years of the study, and the wetland went from being dry early in 1993 to a maximum depth of 2.7 m in 1997.

The Palmer Drought Severity Index (PDSI) is an indicator of periods of above- or below-normal moisture available in the soil for crop production (Palmer, 1965). The PDSI can be used to put into perspective the recent drought and wet period in the Cottonwood Lake area relative to a long-term record that extends back to 1895. The PDSI is an indicator of meteorologic drought. Some have disputed its use as an indicator of hydrologic drought (Alley, 1985) and some have disputed the spatial comparability of its definitions of severe and extreme drought (Guttman and others, 1992). Nevertheless, the PDSI is appropriate for showing the severity and duration of wet or dry meteorologic conditions, such as the warm and dry conditions in the Cottonwood Lake area from 1988 through 1992 and the extremely wet conditions from 1993 through 1998, relative to normal conditions over periods of months to years.

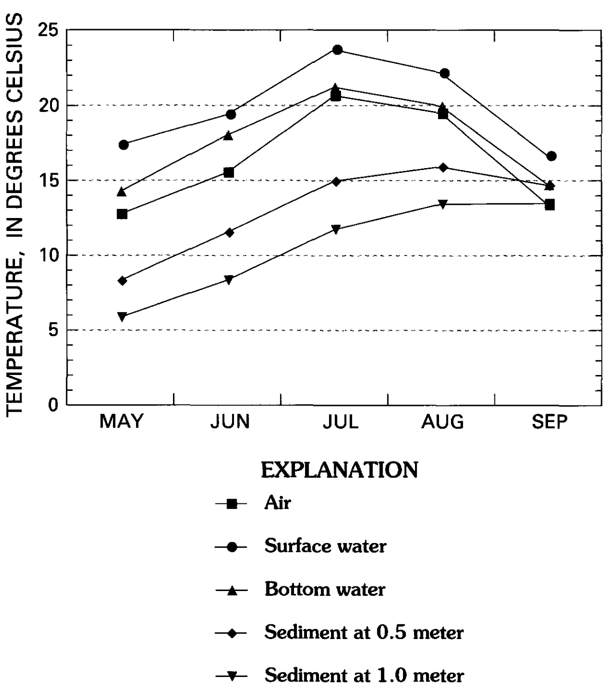


Figure 26. Monthly average temperatures of air, surface water, bottom water, and sediment at 0.5 meter and 1.0 meter below the sediment-water interface at the center of Wetland P1, 1982-85.

The PDSI data for central North Dakota for 1900 to 1998 are shown in figure 29. Values above zero indicate wet periods, and values below zero indicate dry periods. The greater the value, the greater the degree of wetness or dryness. For example values of –3 to –4 indicate severe drought, and values of less than –4 indicate extreme drought. According to the PDSI data, central North Dakota experienced a drought from late 1988 to early 1993 that was matched in severity only during the late-1930s. Periods of drought also occurred more frequently during the latter years shown in figure 29, leading to a hypothesis that the long-term climate of central North Dakota may be becoming drier with time. Todhunter (1993) presented data from Jamestown that support this hypothesis. Todhunter used a simple linear regression model to show that the air temperature at Jamestown is increasing at a rate of 1.3°C per century and that precipitation is decreasing at a rate of 1.7 mm per century. The extremely wet period from 1993 through 1998 was the wettest of the century, according to the PDSI data (figure 29). Winter and Rosenberry (1998) cite data from Devils Lake that indicate the wet period was the wettest in the past 130 years and perhaps the wettest in the past 500 years.

COMPARISON OF EVAPORATION AND PRECIPITATION AT THE COTTONWOOD LAKE AREA

On average, evaporation at the Cottonwood Lake area is slightly greater than 800 mm/yr, or about 1.8 times the average annual precipitation (Eisenlohr and others, 1972). During a normal year, precipitation, runoff from snowmelt in the spring, overland flow after high-intensity rainfall events, and groundwater seepage combine to offset evaporative losses. During years when precipitation is below normal, or when below-normal snowfall results in diminished snowmelt, water levels can decline substantially, even to the point of wetlands drying up. During the warm and dry period from 1988 through 1992 Wetland P1 dried up during mid to late summer every year.

Monthly total evaporation, determined by the energy-budget method, and precipitation for Wetland P1 are shown in figure 30. Problems with instrumentation prevented evaporation estimates for 1986. The evaporation/precipitation (E/P) ratios ranged from 1.0 during May 1987 to 34.0 during July 1985. The median ratio for the 25-month comparison was 2.3. Shjeflo (1968), in a 2-year study (1963-64) of a nearby wetland, reported an average monthly E/P ratio of 1.92 during the May-October months. The average monthly evaporation rate during Shjeflo's study was 114 mm; the average monthly evaporation rate during this 5-year comparison was 108 mm. The likely

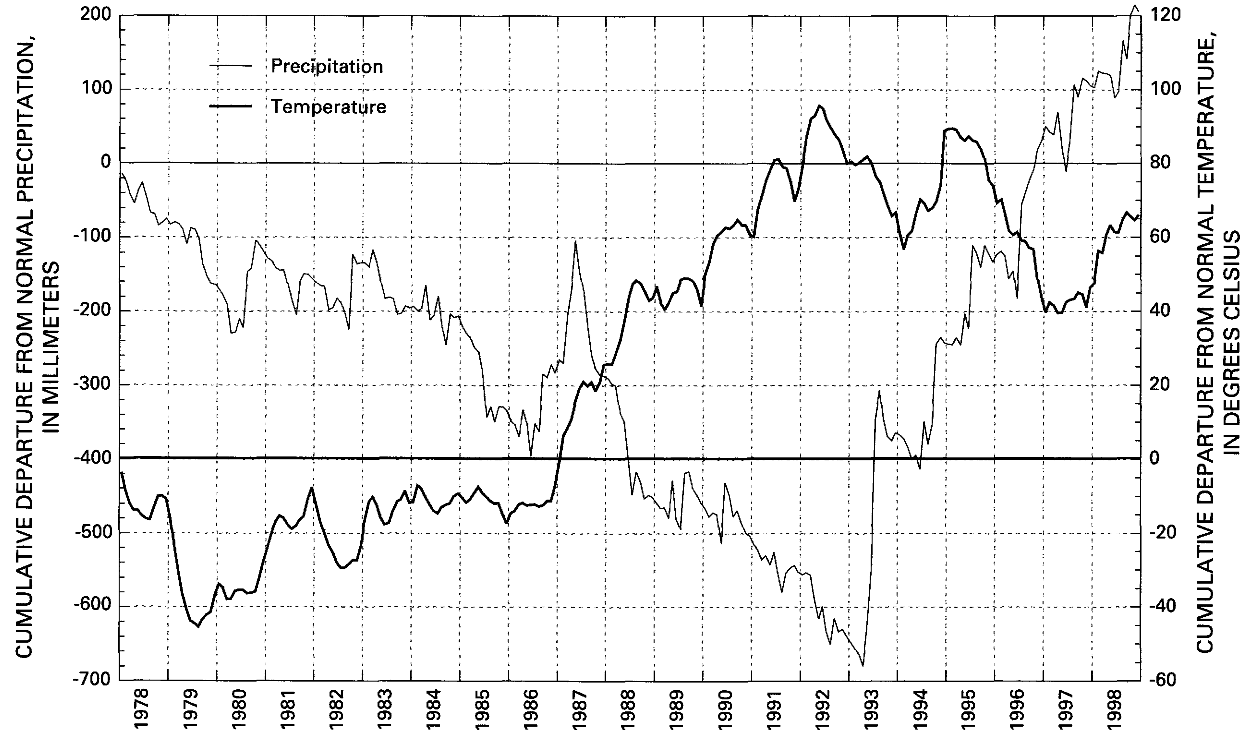


Figure 27. Cumulative departure from normal monthly average air temperature and cumulative departure from normal monthly total precipitation for the Cottonwood Lake area, 1978-98.

explanation for the greater E/P ratio for this comparison is the below-normal precipitation for the period. During 1982-87, with the exception of 1986, precipitation was only 61 percent of normal.

Evaporative loss was normally greatest during July, and the greatest difference between evaporation and precipitation normally occurred during July (fig. 31). Wetlands normally lost water during that month, and losses from Wetland P1 during July were usually large. The greatest difference between evaporation and precipitation recorded during this study occurred during July 1985 when evaporation was 150 mm greater than precipitation (fig. 30). During that time, the water level of Wetland P1 declined nearly 200 mm, indicating that other processes also were acting to remove water from the wetland. The energy-budget method used for estimating evaporation assumes an open-water body devoid of emergent vegetation; this was not the case for Wetland P1, which contained a slowly encroaching perimeter of cattails and hardstem bullrush. Possibly, transpiration by these plants was acting to increase the amount of water removed from the wetland. Stannard and Rosenberry (1991) showed that for a shallow open lake in Nebraska, evapotranspiration from an area of emergent hard-stem bullrush was twice as great as evaporation from open water. However, Shjeflo (1968) indicated that evapotranspiration from wetlands covered with emergent vegetation was no greater than evaporation from open-water wetlands. His assessment was that as transpiration increases, evaporation decreases a like amount due to diminished windspeeds at the water surface. Shjeflo also reported that transpiration occurred mainly during June-August, while the conditions contributing to diminished wind speeds occurred even after the plants were dormant.

Perhaps transpirational losses at the Cottonwood Lake area are more significant than indicated by Shjeflo. Or perhaps ground-water seepage had a net effect of removing water from the wetland. Winter (Chapter 1, of this report) and Rosenberry and Winter (1997) have shown that transpiration-induced cones of depression commonly exist around much of the perimeter of Wetland P1, inducing seepage of water from the wetland to the contiguous ground-water system and increasing the overall loss of water from the wetland.

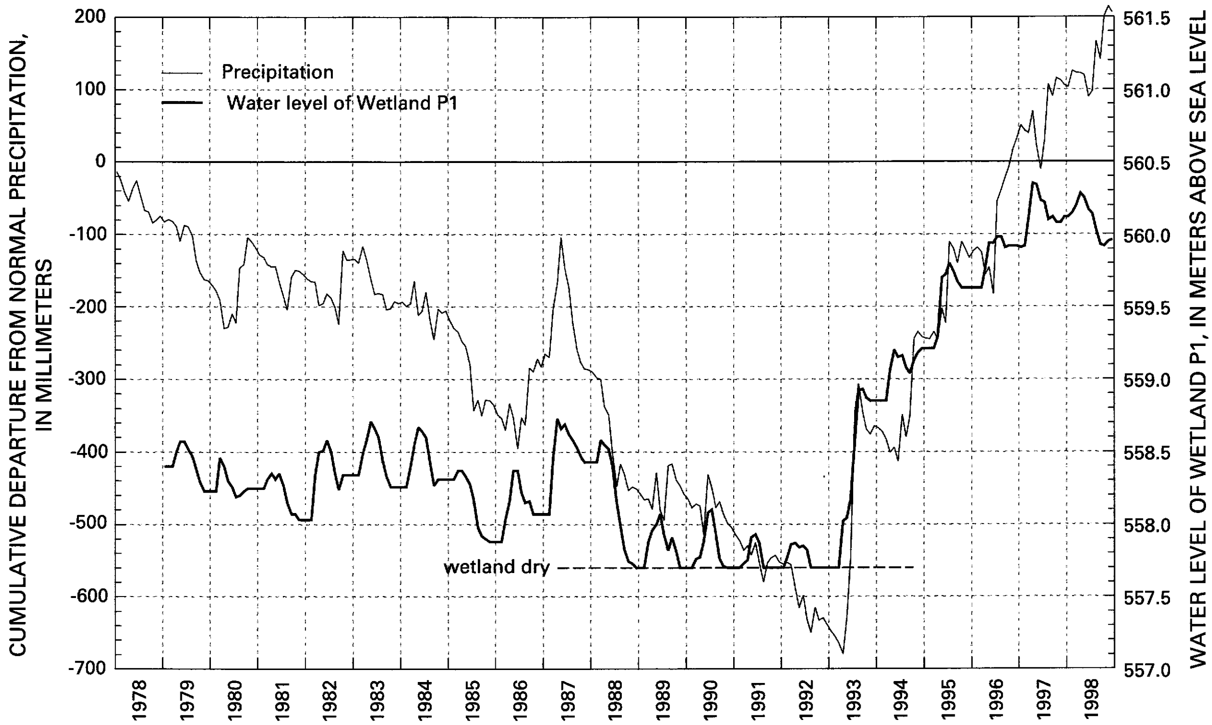


Figure 28. Cumulative departure from normal monthly total precipitation and water level of Wetland P1, 1978-98.

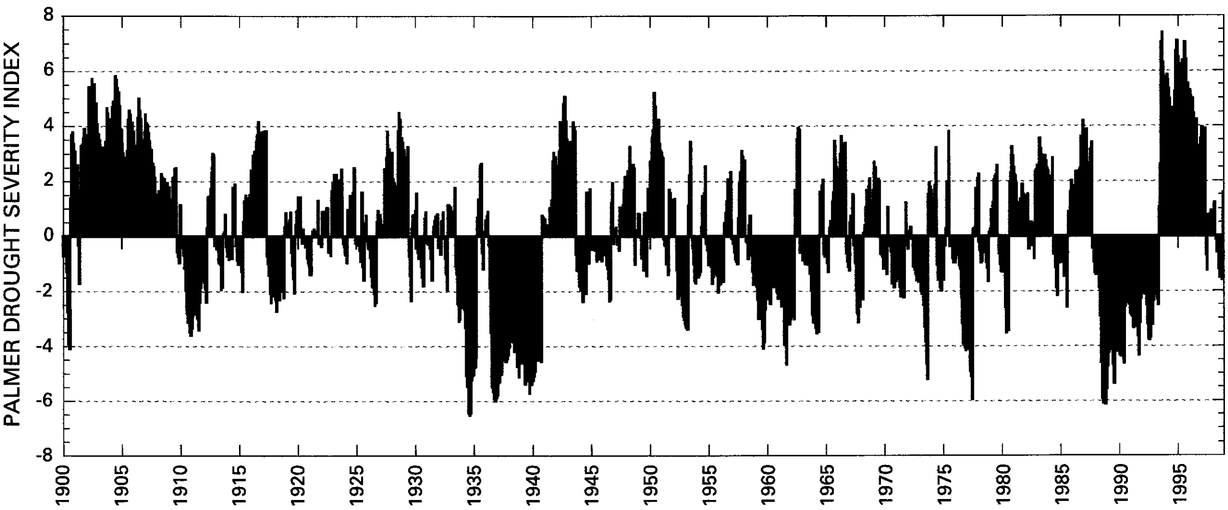


Figure 29. Palmer Drought Severity Index (PDSI) for climate region 5, North Dakota, 1900-98.

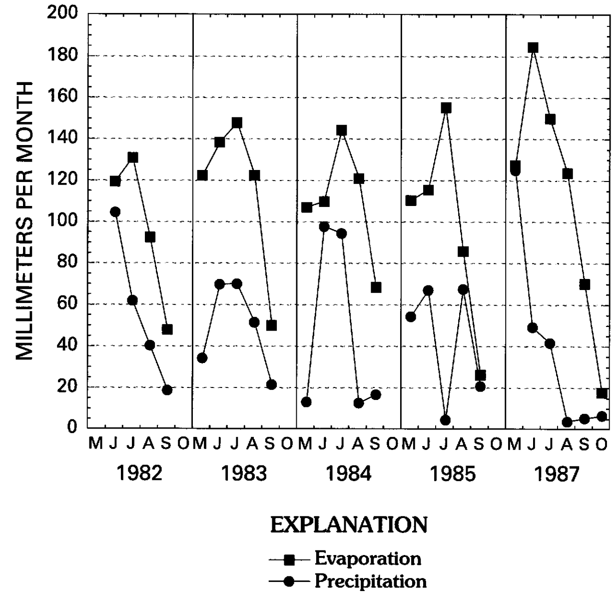


Figure 30. Monthly total evaporation and precipitation for Wetland P1 during the open-water season, 1982-85, and 1987.

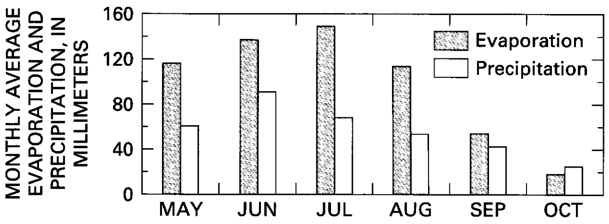


Figure 31. Monthly average evaporation from Wetland P1 (1982-87) and normal (1961-90) monthly precipitation for May-October.

ACKNOWLEDGMENTS

The author thanks John Enz and Chris Brenk, North Dakota State University, Fargo, North Dakota, for providing climate data collected at the Carrington, Jamestown airport, and Pettibone stations.

REFERENCES

Alley, W.M., 1985, The Palmer Drought Severity Index as a measure of hydrologic drought: Water Resources Bulletin, v. 21 no. 1, p. 105-114.

Eisenlohr, W.S., Jr., and others, 1972, Hydrologic investigations of prairie potholes in North Dakota, 1959-68: U.S. Geological Survey Professional Paper 585-A, 102 p.

Guttman, N.B., Wallis, J.R., and Hosking, J.R.M., 1992, Spatial comparability of the Palmer Drought Severity Index: Water Resources Bulletin, v. 26, no. 6, p. 1111-1119.

Jensen, R.E., 1972, Climate of North Dakota: North Dakota State Water Commission, 48 p.

Palmer, W.C., 1965, Meteorologic drought: U.S. Weather Bureau Research Paper no. 45, 58 p.

Parkhurst, R.S., Sturrock, A.M., Rosenberry, D.O., and Winter, T.C., 1994, Climatic and lake temperature data for Wetland P1, Cottonwood Lake area, Stutsman County, North Dakota, 1982-1987: U.S. Geological Survey Open-File Report 94-546, 40 p.

Parkhurst, R.S., Winter, T.C., Rosenberry, D.O., and Sturrock, A.M., 1998, Evaporation from a small prairie wetland in the Cottonwood Lake area, North Dakota – an energy budget study: Wetlands, v. 18, no. 2, p. 272-287.

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

Shjeflo, J.B., 1968, Evapotranspiration and the water budget of prairie potholes in North Dakota: U.S. Geological Survey Professional Paper 585-B, 49 p.

Stannard, D.I., and Rosenberry, D.O., 1991, A comparison of short-term measurements of lake evaporation using eddy correlation and energy-budget methods: Journal of Hydrology, v. 122, p. 15-22.

Sturrock, A.M., Hanson, B.A., Scarborough, J.L., and Winter, T.C., 1986, Climatic data for the Cottonwood Lake area, Stutsman County, North Dakota, 1982: U.S. Geological Survey Open-File Report 86-477, 24 p.

_____1987, Climatic data for the Cottonwood Lake area, Stutsman County, North Dakota, 1983: U.S. Geological Survey Open-File Report 87-216, 28 p.

Todhunter, P., 1993, Historical temperature and precipitation trends at Jamestown, North Dakota: Proceedings, North Dakota Academy of Science, v. 47, p. 5.

Winter, T.C., and Rosenberry, D.O., 1998, Hydrology of prairie pothole wetlands during drought and deluge: A 17-year study of the Cottonwood Lake wetland complex in North Dakota in the perspective of longer term measured and proxy hydrologic records: Climatic Change, v. 40, no. 2, p. 189-209.

CHAPTER 3

SPATIAL AND TEMPORAL VARIABILITY IN SPECIFIC CONDUCTANCE AND CHEMICAL CHARACTERISTICS OF WETLAND WATER AND IN WATER COLUMN BIOTA IN THE WETLANDS IN THE COTTONWOOD LAKE AREA

James W. LaBaugh, U.S. Geological Survey, Reston, Virginia
George A. Swanson, U.S. Fish and Wildlife Service (Retired), Jamestown, North Dakota

ABSTRACT

Five wetlands in the Cottonwood Lake area were the subject of a detailed chemical and biological study during 1984 to 1987. The study was part of a larger investigation of longer duration to understand the relation between the hydrology of the wetlands and their use by waterfowl. Chemical characteristics of water in the wetlands varied considerably, particularly for major ions, and were related to the interaction of the wetlands with ground water and atmospheric exchange (precipitation and evaporation). Plant nutrients, such as phosphorus, nitrogen, and silica, varied more spatially within the wetlands than did major ions. The algal communities of the wetlands included numerous species and differed among the wetlands. Chlorophyll *a*, which is a measure of the amount of algae in the wetlands, varied as much spatially as phosphorus, nitrogen, and silica. However, no distinct seasonal pattern in chlorophyll *a* was evident for the seasonal wetlands. Chlorophyll *a* concentrations in the semipermanent wetlands usually followed a seasonal pattern of (1) declining concentrations following spring thaw, when the open-water zones contained little submerged vegetation, (2) remaining small through mid summer, when submerged vascular vegetation was abundant, and (3) increasing in the fall before ice formation, when submerged vascular vegetation in the open-water zones was senescent. The periods of large concentrations were usually coincident with the use of the wetlands by migrating waterfowl. The microinvertebrate communities of the wetlands, as constituted by representatives of Cladocera, Copepoda, and Rotifera, included some species common to all five wetlands. Copepoda generally were the most abundant and Rotifera the least abundant members of the microinvertebrate communities. Replicate samples were required to characterize seasonal differences in algal and microinvertebrate communities due to spatial variation.

INTRODUCTION

The prairie wetlands in mid North America are an important resource for migrating waterfowl (Swanson and Duebbert, 1989). The chemical composition of water in these wetlands (LaBaugh, 1989), as well as vegetation (Stewart and Kantrud, 1972; Kantrud, Millar, and van der Valk, 1989), varies according to differences in the hydrologic setting (Sloan, 1972; LaBaugh and others, 1987), hydroperiod (van der Valk, 1981), and soils (Arndt and Richardson, 1993). Although prairie wetlands have been the focus of hydrological, chemical, and ecological studies by scientists in Canada and the United States over the past half-century (van der Valk, 1989), most studies have dealt with vegetation and waterfowl. Less is known about the microscopic plants and animals that inhabit the wetlands. Crumpton (1989) pointed out the lack of information on algae, and studies of microscopic invertebrates are rare (Bataille and Baldassare, 1993). Thus, not much is known about the spatial distribution of the microorganisms within or among prairie wetlands, and only a few studies have documented how some of the microorganism populations vary over time (Barica, 1975; Kling, 1975).

Studies at the Cottonwood Lake area included the collection of algae and microinvertebrates from the water column of selected wetlands from 1984 to 1988. Collection of these organisms has coincided with concurrent research on hydrological and chemical properties of the wetlands. The main objective of the studies is to determine how the hydrogeologic setting and wetland-ground water interactions affect the chemical characteristics and biological communities of the wetlands. The purpose of this chapter is to present information about the chemical characteristics of water in the wetlands (and of relevant ground water) and the spatial and temporal variation in the algal and microinvertebrate communities of five selected wetlands. The data presented herein are for 1984 to 1987, a period for which detailed analyses of community characteristics are available. Ancillary chemical data collected between 1979 and 1998 are used to place the 4-year period of data collection that included biota in perspective with long-term changes in the study area.

METHODS

A tube water-column sampler (Swanson, 1978) having a minimum diameter of 10 cm was used to collect water samples from the wetlands. Each wetland was divided into three transects according to procedures described in LaBaugh, and others (1987). During 1984 to 1987, samples were collected from approximately the same location along each transect every month that the wetlands contained water and were ice free. On the rare occasions when the wetlands were very shallow, samples were collected from the middle of the wetland instead of along each of the three transects. The contents of the sampler were poured into a large polyethylene jug or large plastic bucket from which water was taken for processing. Multiple insertions were made when insufficient water was collected by a single insertion of the sampler into the water column.

Ground-water samples were collected for chemical analysis by pumping or bailing a well dry and then collecting the water that seeped into the well overnight. If the well yielded water readily when pumped, three casing volumes of water were removed before sampling.

Some of the water collected from the wetlands was used to determine the chlorophyll *a* concentration in the water column. A known volume of water was pumped through a glass-fiber filter using a hand-operated vacuum pump. The filter was placed in a glass vial, stored in ice, and then shipped in ice to the U.S. Geological Survey National Water Quality Laboratory in Arvada, Colorado. At the laboratory, the chlorophyll *a* concentration was determined by the high pressure liquid chromatographic and fluorometric technique described in Britton and Greeson (1988).

Water collected for algal analysis was put into a 1-L high-density polyethylene bottle and the contents were preserved with 10 mL of Lugol's solution. The composition of the solution and the prescribed proportion of preservative to sample are described in Vollenweider (1974). Algal samples collected in 1984 were examined to determine the algal species and their abundance. Algal samples collected during 1985 to 1987 also were examined to determine the biovolume represented by each species in addition to their abundance. Identification, enumeration, and biovolume determination of the algal species were done by Richard Dufford, Ft. Collins, Colorado, using standard inverted microscopic techniques.

Some of the water collected from the wetlands also was used to determine species identification and enumerate invertebrates found in the water column of the wetlands. For invertebrate samples, the total volume of water collected from a transect was measured using a 1-L graduated cylinder and then poured through an 80-m mesh Wisconsin plankton bucket. The total volume of water represented by the sample was recorded; usually this volume was between 2 and 6 L. The contents of the plankton bucket then were placed into a 250-mL high-density polyethylene bottle. Prior to preservation with 10 mL of 40-percent formalin, the organisms in the bottle were narcotized with soda water. Preserved samples were sent to Dr. William Taylor, Michigan State University, for analysis.

Water collected from the wetlands also was analyzed for physical properties and chemical inorganic constituents. The samples were analyzed for specific conductance, pH, and dissolved calcium, magnesium, sodium, potassium, sulfate, chloride, orthophosphate phosphorus, nitrate plus nitrite nitrogen, iron, manganese, and silica. Total alkalinity, kjeldahl nitrogen, and phosphorus concentrations also were determined. Details of the sample processing and analytical techniques used are described in LaBaugh and Swanson (1992).

SPECIFIC CONDUCTANCE AND CHEMICAL CHARACTERISTICS OF WETLAND WATER

Chemical characteristics of the water in the wetlands were not uniform, and specific conductance varied among the wetlands (fig. 32). The variation in specific conductance during the period when the wetlands were ice free, usually from April through October, reflected differences in the hydrologic functions of the wetlands. Water in Wetland T8, which is in an area of recharge to ground water and receives little, if any, ground water discharge, had smaller specific-conductance values than water in the remaining selected wetlands (Note that the range in specific-conductance values for Wetland T8 for 1984 to 1987 is small enough that the size of the symbols used to indicate values outside of the 10th and 90th percentiles in figure 32 mask the median and percentile symbols). The remaining selected wetlands received some ground-water discharge and water in those wetlands had larger specific-conductance values than water in Wetland T8. Among the wetlands receiving ground-water discharge, Wetland P8 had the smallest specific-conductance values, reflecting the fact that the wetland had an intermittent outlet by which water and solutes could be removed. Wetlands P1 and P11 did not have outlets during 1984 to 1987 and Wetland T3 spilled to Wetland P1 only occasionally in spring. In addition, ground water in part of the basin of Wetland P8 contained fewer solutes (specific conductance was less than 600 $\mu S\ cm^{-1}$) than typically found in ground water in the other wetland basins.

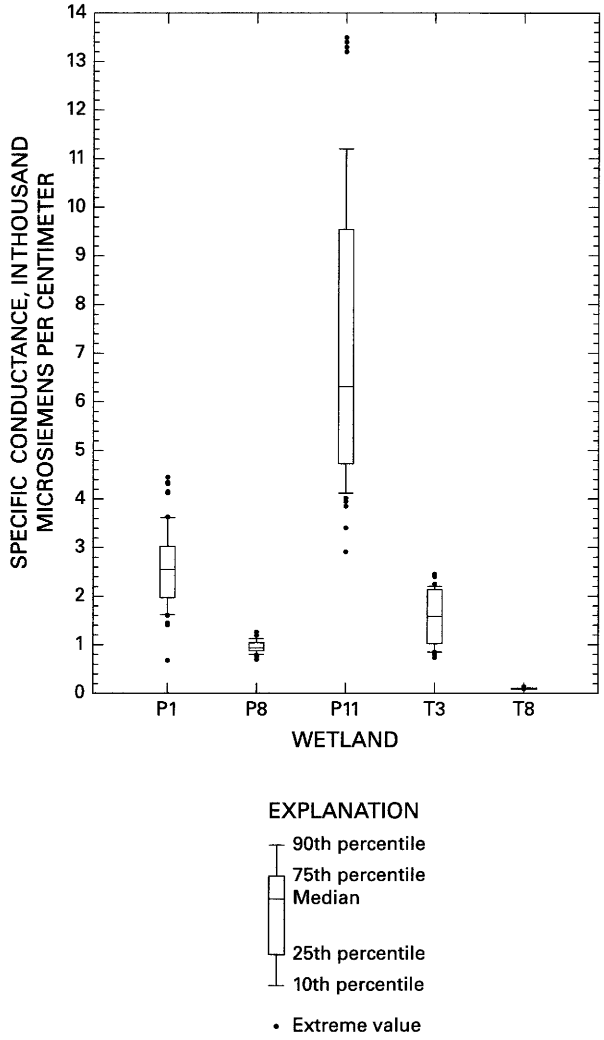


Figure 32. Summary of specific-conductance data for five wetlands for 1984 to 1987.

The specific conductance of water in each wetland also varied over time. An example of the seasonal changes in specific conductance for a semipermanent wetland is illustrated by data for Wetland P1 for 1984 to 1987 (fig. 33). Commonly, specific-conductance values were smallest in spring after ice melt and increased through the summer and into the fall as water levels declined. However, the general pattern of increased specific conductance from the spring to the fall was interrupted by episodes of decreased specific conductance as a result of dilution by rainfall. Specific-conductance values for each of the three transects in Wetland P1 are shown in figure 33. Each point in the figure represents the value for one transect. Therefore, three points are shown for each date. In most cases, values for each of the three transects are quite similar and many points overlie one another. However, as indicated in the figure, large differences exist among the values for October 1986. The seasonal changes in specific conductance for the seasonal wetlands were similar to those for the semipermanent wetlands; commonly, specific-conductance values were the smallest in spring after ice melt and largest in the summer prior to the complete loss of all standing water.

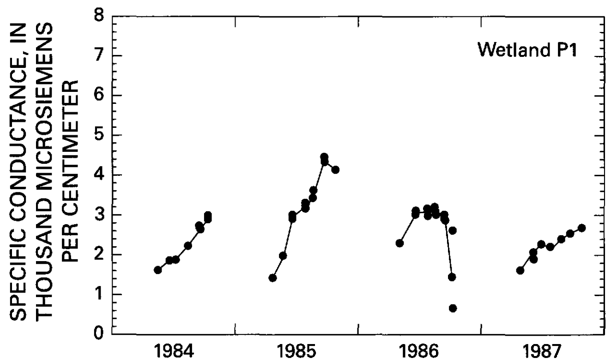


Figure 33. Specific conductance of water in Wetland P1 for the months when the wetland was ice free during 1984 to 1987. Gaps between lines are periods when the wetlands were ice covered. Lines connect median values. Points represent data from each of the three transects from which water samples were collected for chemical analysis. Many points overlie one another for individual dates.

Specific conductance of water in the wetlands varied from year to year in both the seasonal changes and the range of values. While the seasonal changes were related to episodic rainfall punctuating declines in wetland water levels, annual changes in the range of values was related to periods of generally wetter or drier conditions. A period of decreased rainfall in 1988 resulted in relatively larger specific-conductance values for Wetland P1 than those observed in the preceding years (fig. 34A). Between 1988 and 1992, wetland water levels declined to the point where, in each year, the wetland was dry in late summer; this condition previously was observed in 1976. A deluge in July 1993, followed by years in which more of the annual input of water from the atmosphere occurred during October to April than in earlier years, resulted in increased water levels and relatively smaller maximum specific-conductance values than those observed since 1979 when detailed hydrological studies began in the Cottonwood Lake area.

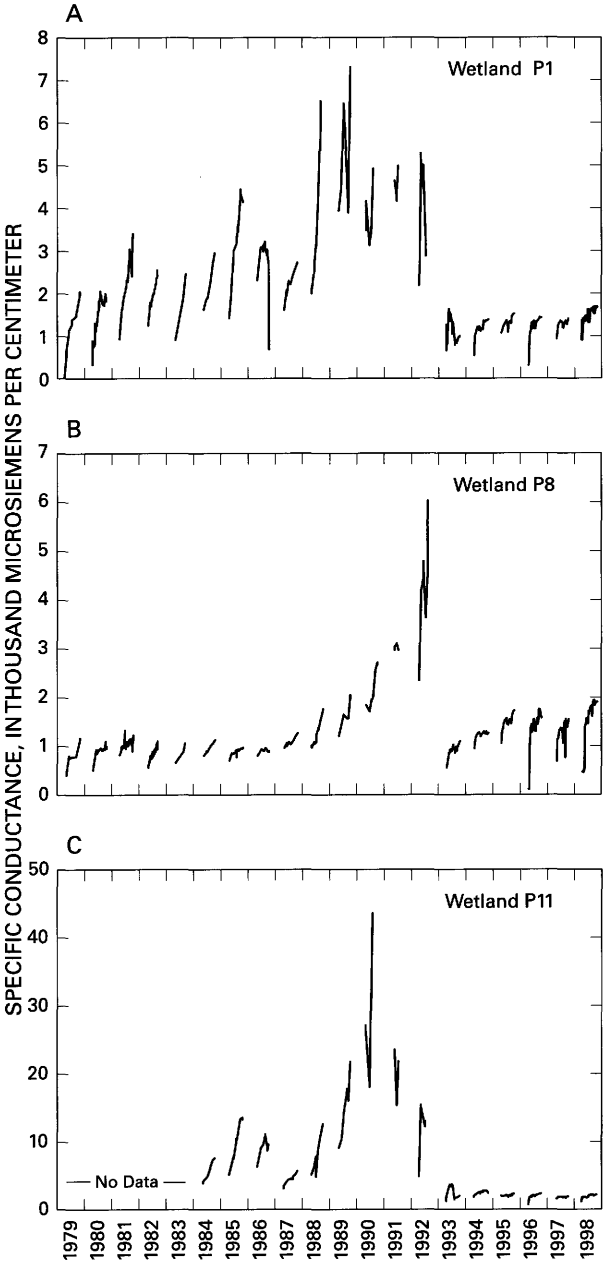


Figure 34. Specific conductance of water in semipermanent Wetlands P1 (A), P8 (B), and P11 (C), for the months when the wetlands were ice free during 1979 to 1998. Gaps between lines are periods when the wetlands were ice covered.

All semipermanent wetlands in the Cottonwood Lake area did not respond uniformly to wetter or drier conditions, although the wetlands are in close proximity. Specific conductance of the water in Wetland P8 continued to increase in succeeding years of the declining water levels from 1988 through 1992, whereas specific conductance of the water in Wetlands

P1 and P11 did not increase in succeeding years during that period (fig. 34). During the latter part of the relatively drier years between 1988 and 1992, the relation between Wetland P1 and ground water changed. At times, the ground-water levels adjacent to the wetland were lower than the wetland water levels so that the direction of flow was from the wetland to the ground-water system rather than from the ground-water system to the wetland. This change in the direction of flow provided a means for removing water and solutes from Wetland P1 that did not occur for Wetland P8 during the same time period. In the case of Wetland P11, the smaller specific-conductance values in 1991 and 1992 were related to the fact that when Wetland P11 became dry in 1990 and 1991, salts in the wetland were removed by wind action (deflation) in the fall and winter. When the wetland refilled with water in the springs of 1991 and 1992, fewer salts were present to dissolve so specific-conductance values were less than in the previous years of relatively dry conditions. While the focus in this chapter is on the chemical and biological data for 1984 to 1987, placing these years within the context of a 20-year period as shown in figure 34 points out the importance of recognizing that characteristics of the wetlands can be quite variable both spatially and temporally because of the relation between the wetlands and ground water and because of the response of the wetlands to changes in rainfall.

Water in the wetlands typically was alkaline although in wetlands P8, T3, and T8 circumneutral values were recorded between 1984 and 1987. The pH values were larger for the semipermanent wetlands than for the seasonal wetlands (table 1, fig. 35). The smaller pH values for the seasonal wetlands may be due to the large amounts of rain and snow inputs relative to ground-water inputs, decomposition of organic matter, or organic acids. The pH values for the semipermanent wetlands commonly were smallest in the spring after ice melt, increased during midsummer, and decreased in the fall. The pH values for each of the three transects in Wetland P11 are shown in figure 36. The differences between the data points, which represent the pH values measured on a specific day at each of the three transects, indicate pH was not uniform within the wetland on a given date of sample collection.

The wetlands differed not only in specific conductance and pH but also in the relative abundance of dissolved major ions (table 1). The most abundant cations were calcium or potassium in Wetland T8, calcium or magnesium in Wetland T3, magnesium in Wetlands P1 and P8, and sodium in Wetland P11. The most abundant anions were sulfate in Wetlands T3, P1, and P11, bicarbonate or sulfate in Wetland P8, and bicarbonate in Wetland T8 (most of the alkalinity reported in table 1 is due to the bicarbonate anion). The seasonal changes in concentration commonly were similar to the seasonal changes in specific conductance, particularly for the most abundant cation and anion. The major-ion composition generally reflected the influence of ground-water input. For example, those wetlands receiving some ground-water discharge had an increased abundance of magnesium, sodium, and sulfate.

Table 1. Summary of pH and major ion data for five wetlands of the Cottonwood Lake area. Values presented are medians for 1984 to 1987.

Wetland	Number of samples	Median pH (standard units)	Median concentration (milliequivalents per liter)						
			Calcium	Magnesium	Sodium	Potassium	Alkalinity	Sulfate	Chloride
P1	78	8.2	5.99	18.5	5.65	1.35	6.45	25.0	0.380
P8	78	8.1	2.77	6.00	2.04	0.715	7.41	2.81	0.479
P11	78	8.7	2.24	30.4	43.5	2.56	10.4	64.5	6.21
T8	27	7.0	0.349	0.312	0.017	0.460	0.979	0.333	0.053
T3	36	7.7	8.48	9.05	1.70	0.511	5.710	14.0	0.128

[1] At the pH values present in the wetlands, most of the alkalinity was due to the bicarbonate ion.

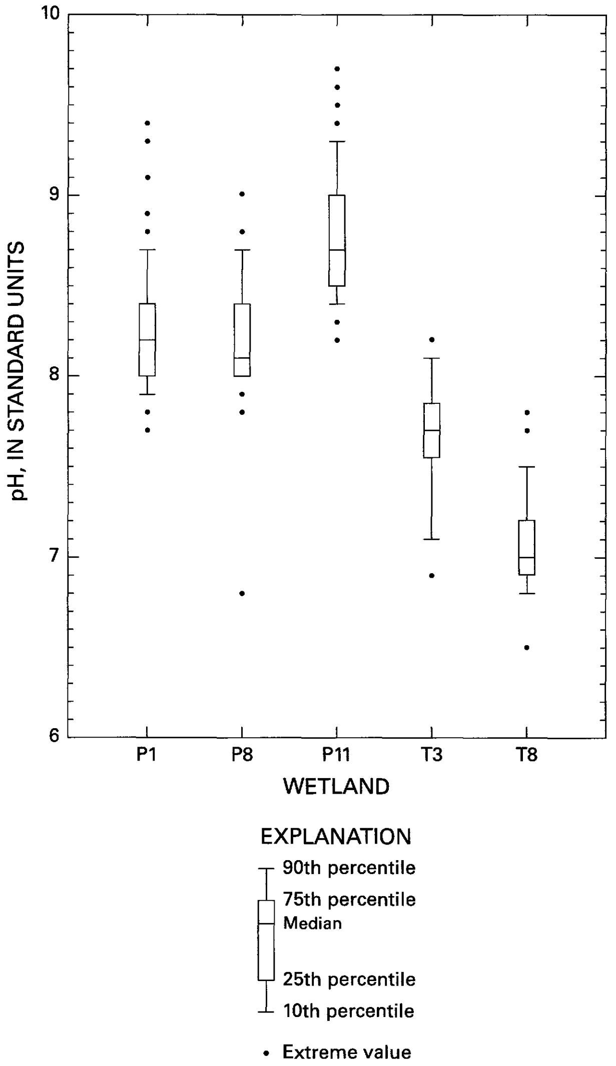


Figure 35. Summary of pH data for five wetlands for 1984 to 1987.

The relation of the chemical characteristics of the water in the wetlands also was examined by use of a modified Schoeller diagram (fig. 37). Values shown in figure 37A are for May 1986 for Wetland T8, June 1986 for Wetland T3, and August 1986 for the remaining wetlands. The May and June data for the seasonal wetlands were the last data obtained before the wetlands either went dry or became too shallow for the collection of a sufficient amount of water for chemical analysis. The differences in the concentrations for Wetland T8 and the concentrations for the remaining wetlands reflect the fact that the wetlands having larger concentrations than Wetland T8 received some ground-water discharge. As concentrations increase along ground-water flow paths, magnesium exceeds calcium as saturation levels are reached for calcium and bicarbonate minerals. Along flow paths where ground water is in contact with the till for some time, ion exchange can take place, making it possible for sodium concentrations to exceed magnesium concentrations. Weathering of sulfate minerals at the same time that saturation levels for bicarbonate minerals are reached results in sulfate concentrations exceeding bicarbonate concentrations. Thus, the concentrations of those major ions are larger for wetlands receiving some ground-water discharge than for Wetland T8, and the relative abundance of those major ions also reflects where the wetlands lie in relation to the ground-water flow systems.

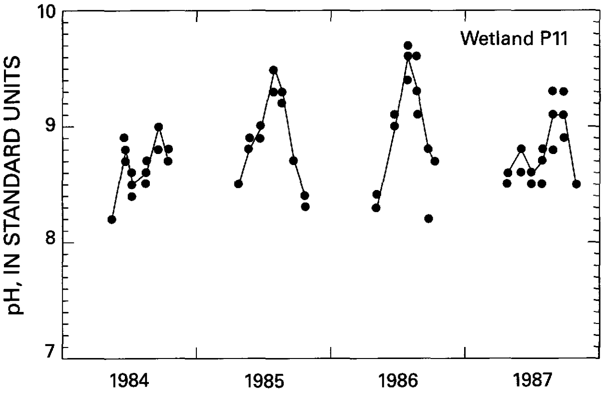


Figure 36. pH of water in Wetland P11 for the months when the wetland was ice free during 1984 to 1987. Gaps between lines are periods when the wetlands were ice covered. Lines connect median values. Points represent data from each of the three transects from which water samples were collected for chemical analysis. Some points overlie one another for individual dates.

To relate the chemical characteristics of water in the wetlands to the chemical characteristics of the ground water, samples were collected from four ground-water wells (wells 4, 12, 13, and 16) prior to 1983. Those wells were thought to represent different parts of the ground-water flow system within the Cottonwood Lake area. Between 1983 and 1987, additional samples were collected from wells 2, 3, 4, 7, 8, 10, 11, 13, 14, 15, 17, 18, 19, 20, 21, 22, 23, 25, 26, 27, 28, and 29, to determine the spatial variability of the chemical characteristics of the ground water in the vicinity of the wetlands. (See fig. 3 for the locations of the wells.) A summary of the ground-water chemical characteristics determined for 1984 to 1987, and specific data for selected wells, is presented in table 2. Ground water in the vicinity of the wetlands differed in the relative abundance of major ions. Calcium was the most abundant cation and bicarbonate was the most abundant anion in ground water having small major-ion concentrations and specific-conductance values of less than 900 µS·cm^{-1} (wells 2, 3, 7, 8, 10, 11, and 27). Data for well 11 (table 2, fig. 37B), a representative of that type of ground water, are characteristic of ground water in areas of ground-water recharge. Calcium was the most abundant cation and sulfate was the most abundant anion in ground water having large major-ion concentrations and specific-conductance values between 1,000 µS·cm^{-1} and 4,500 µS·cm^{-1} (Wells 4, 14, 15, 16, 22, 28, and 29). Data for well 16 (table 2, fig. 37B), a representative of that type of ground water, are characteristic of ground water between areas of ground-water recharge and areas of ground-water discharge to the wetlands. Magnesium was the most abundant cation and sulfate was the most abundant anion in ground water having specific-conductance values between 4,500 µS·cm^{-1} and 16,200 µS·cm^{-1} (wells 13, 17, 18, 19, 20, 21, 23, and 25). Data for well 17 (table 2, fig. 37B), a representative of that type of ground water, are characteristic of ground water in areas of ground-water discharge to the wetlands.

The relation of the chemical characteristics of the ground water to the chemical characteristics of the water in the wetlands also is evident from examination of figure 37. Wetland T8 recharges ground water and, therefore, water in that wetland is unlike ground water in the relative abundance and concentration of major cations. Wetlands T3, P1, P8, and P11 receive ground-water discharge and, therefore, water in those wetlands is similar to ground water in the concentration of major cations. The relative abundance of major ions in water in Wetlands T3, P1, and P8 is similar to the relative abundance of major ions in the different parts of the ground-water flow system represented by wells 11, 16, and 17. Ground-water samples were not collected in the vicinity of Wetland P11 because no wells were installed in that area. However, Wetland P11 contained water in which sodium was the most abundant cation, something not observed in the ground water collected elsewhere in the study area. Ion exchange in the ground water is a likely mechanism that could explain the major ion relations in Wetland P11.

In contrast to the major-ion concentrations, total phosphorus concentrations were larger for the seasonal wetlands than for the semipermanent wetlands (fig. 38). Vegetation in the shallow-marsh zones of the seasonal wetlands, and leaching from standing dead plants in those zones, likely provided sources of phosphorus not always present in the open-water zones of the semipermanent wetlands. Large orthophosphate phosphorus concentrations usually occurred in the water in seasonal Wetland T8 (fig. 39). Phosphorus in the water in each wetland varied seasonally, but no distinct seasonal pattern was evident.

Table 2. Summary statistics of pH and major-ion data for 21 ground-water wells and specific data for selected wells in the Cottonwood Lake area. Values presented for summary statistics are for 1984 to 1987 and represent a total of 36 water samples.

	pH (standard units)	**Concentration (milliequivalents per liter)**						
		Calcium	**Magnesium**	**Sodium**	**Potassium**	**Alkalinity**	**Sulfate**	**Chloride**
Median	7.3	16.9	16.0	4.35	0.383	7.79	41.6	0.224
Maximum	7.9	28.9	263	78.3	1.25	12.4	333	8.74
Minimum	6.9	3.04	1.56	0.11	0.025	4.95	0.158	0.019
			Specific data for selected wells					
Well 11[a]	7.8	3.04	1.56	1.26	0.194	5.05	0.158	0.070
Well 16[a]	7.0	26.4	16.4	5.65	0.588	5.33	43.7	0.705
Well 17[b]	7.1	17.9	263	78.3	0.869	11.7	333	8.741

[a] Date of sample collection was August 26, 1986.

[b] Date of sample collection was August 20, 1985.

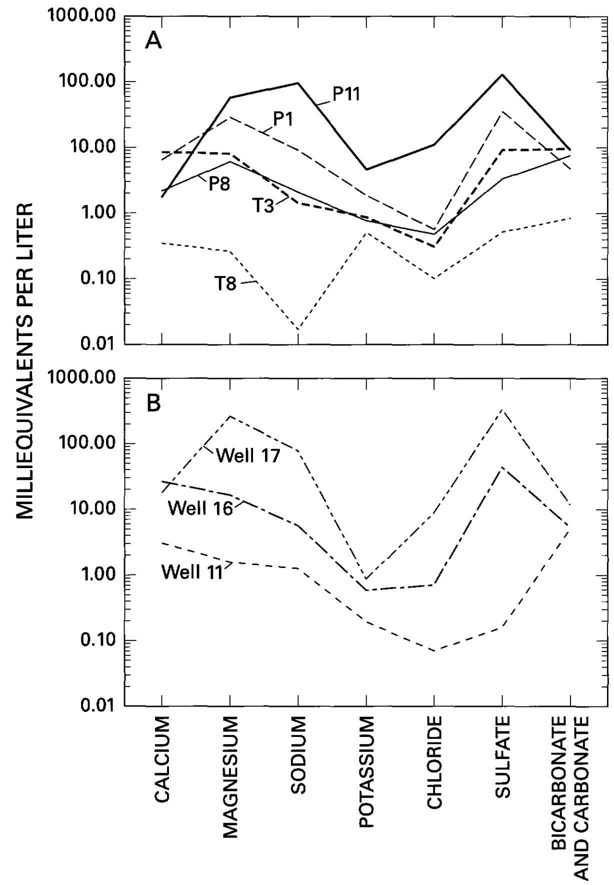


Figure 37. Modified Schoeller diagram of the abundance of major ions in water within five wetlands (A) and selected ground-water wells (B).

Total nitrogen concentrations were similar for all wetlands (fig. 40), and total nitrogen commonly varied more spatially in water in a wetland than temporally over a season. Dissolved inorganic nitrogen was usually a small fraction of the nitrogen content of water in the wetlands. Most of the dissolved inorganic nitrogen in the water was ammonia. Nitrate and nitrite typically were below detection levels, particularly in the water in Wetlands T3 and T8. The differences in ammonia and nitrate plus nitrite indicated nitrification probably was inhibited in the wetlands.

Chlorophyll *a* concentrations varied from less than 1 µg/L for all five wetlands to as much as 380 µg/L for Wetland T3 (fig. 41). No seasonal pattern in chlorophyll *a* was evident for the seasonal wetlands. For the semipermanent wetlands, chlorophyll *a* concentrations declined in the spring after ice melt, usually remained small through midsummer, and increased in September or October. Data for Wetland P11 provide an example of this seasonal pattern (fig. 42). Large chlorophyll *a* concentrations for the semipermanent wetlands usually coincided with periods when migrating waterfowl were present.

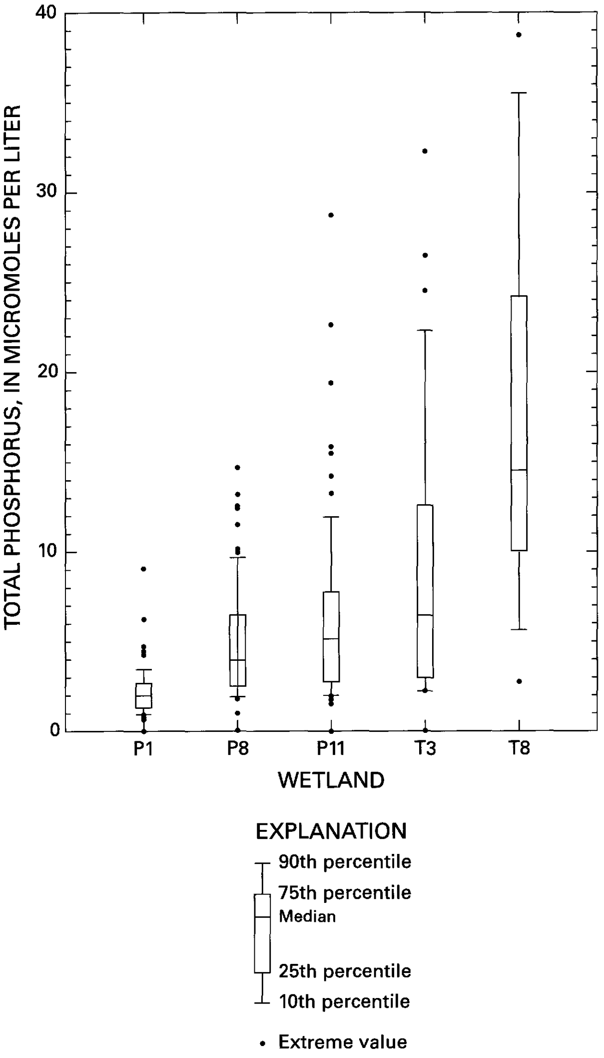


Figure 38. Summary of total phosphorus data for five wetlands for 1984 to 1987.

The collection of water samples from three transects within each wetland provided the information needed to determine the variability of the chemical constituents in the water in each wetland. One measure of this variability was the coefficient of variation, which was determined by dividing the standard deviation by the sample mean. Data from the transects enabled calculation of the coefficient of variation for each date on which the samples were collected during 1984 to 1987; these data are summarized in table 3. The coefficients of variation for dissolved iron and manganese were generally larger than those for major ions, perhaps reflecting variation in oxidizing and reducing conditions brought about by mixing or resuspension of sediments along the different transects during the time of sample collection. Generally, the coefficients of variation for phosphorus and nitrogen also were larger than those for major ions. This indicates chemicals such as phosphorus and nitrogen, which are more directly affected by uptake or loss from the biota, varied more spatially in the water in a wetland on any date of sample collection than did major ions. The coefficients of variation for chlorophyll *a* also were larger than those for major ions.

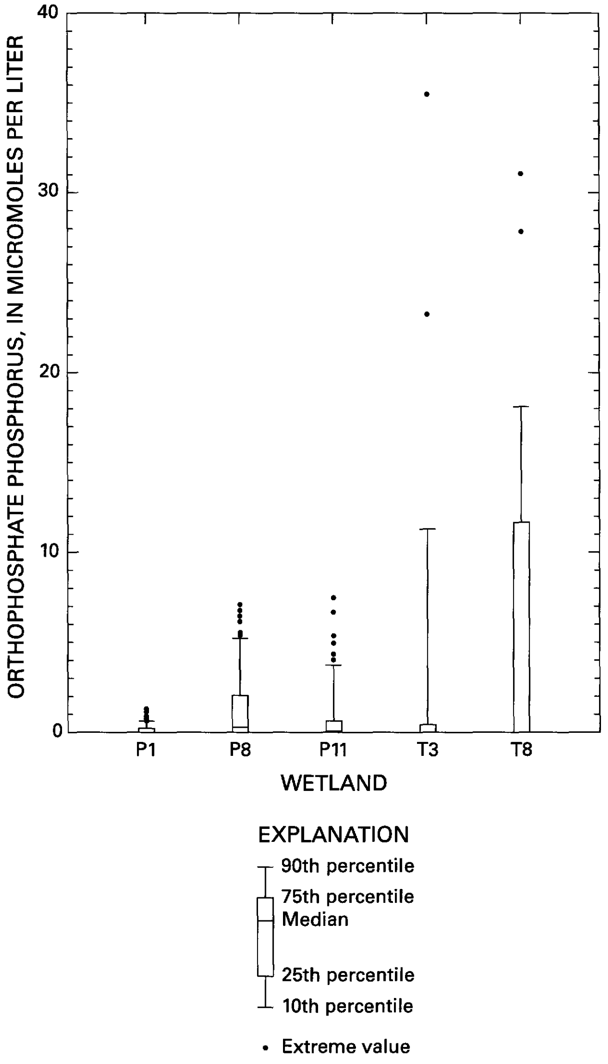


Figure 39. Summary of orthophosphate phosphorus data for five wetlands for 1984 to 1987.

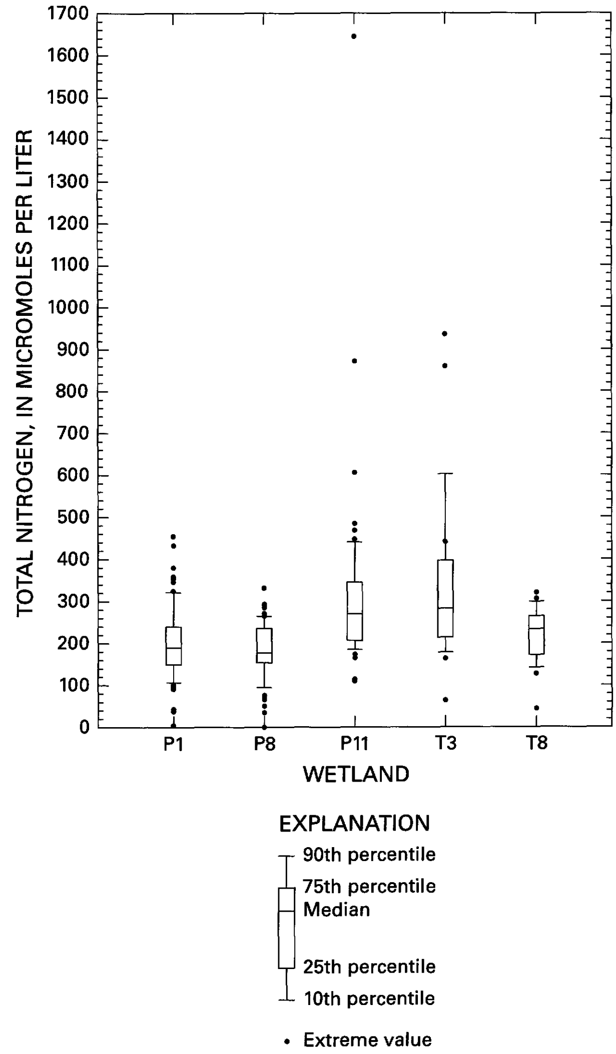


Figure 40. Summary of total nitrogen data for five wetlands for 1984 to 1987.

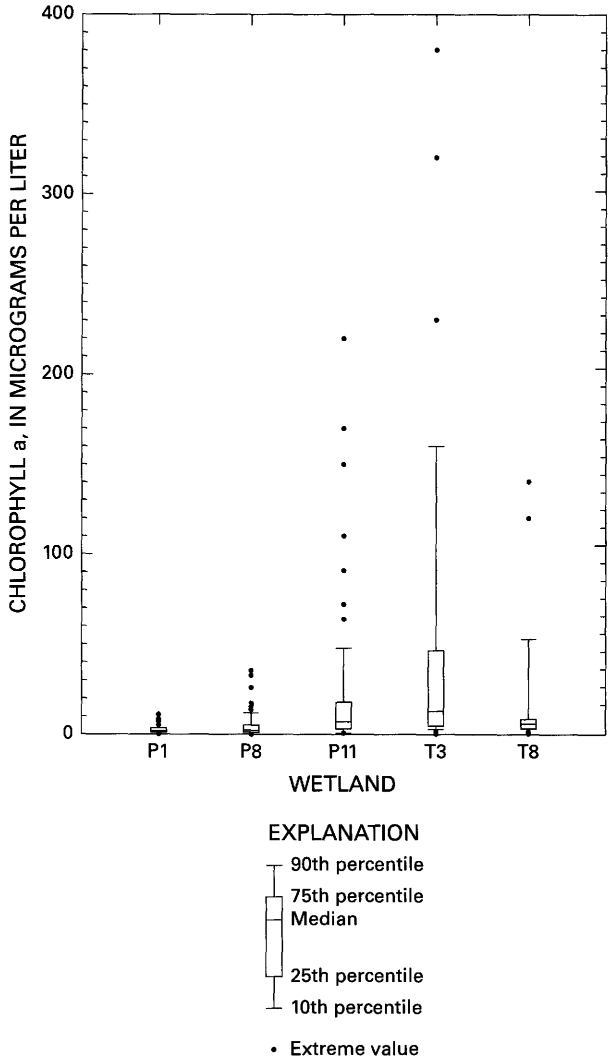


Figure 41. Summary of chlorophyll *a* data for five wetlands for 1984 to 1987.

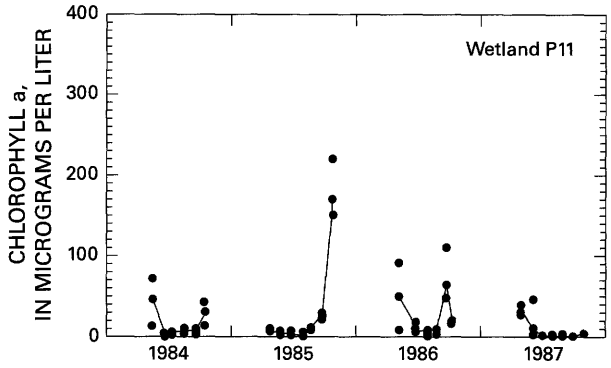


Figure 42. Chlorophyll *a* concentrations for Wetland P11 for the months when the wetland was ice free during 1984 to 1987. Gaps between lines are periods when the wetlands were ice covered. Lines connect median values. Points represent data from each of the three transects from which water samples were collected for chemical analysis. Some points overlie one another for individual dates.

BIOLOGICAL CHARACTERISTICS OF WETLANDS

Numerous algal species were found in the water in the wetlands during 1984 to 1987. Some information on the algal species is presented in LaBaugh and Swanson (1988). A large variety of algae were present in the water because the size and depth of the wetlands enabled mixing of communities from open-water areas, sediments, and vegetation zones. Biovolume data obtained for 1985 to 1987 provided information on the relative abundance of major taxa within each wetland. The taxa that were the most abundant differed among the wetlands (fig. 43). Cryptophytes and diatoms commonly were the most abundant taxa for Wetlands P1 and P8, and diatoms and chlorophytes usually were the most abundant taxa for Wetland P11. Chrysophytes were relatively more abundant in the seasonal wetlands than in the semipermanent wetlands. Chlorophytes dominated the algal community of Wetland T8, but no taxon was distinctly the major part of the community of Wetland T3.

The composition of the algal community of each wetland varied over time. Biovolume data for Wetland P1 for 1986 show the seasonal changes in the relative abundance of different taxa in the algal community of the open-water zone along each of three transects in the wetland (fig. 44). Note that the June peak in diatoms in samples collected along transects A and C was not present in the sample collected along transect E. Also, the August peak in diatoms in samples collected along transects C and E was not present in the sample collected along transect A. Thus, because of the spatial variation within the wetland, more than one sample from a single point in the wetland was needed to characterize the seasonal changes in the communities. Algal community data from all of the wetlands also indicate differences in the composition of the algal community in different parts of each wetland--in the open-water zones of the semipermanent wetlands and in the shallow-marsh zones of the seasonal wetlands.

Table 3. Median value of the coefficient of variation for each date on which water samples were collected for chemical characteristics of five wetlands in the Cottonwood Lake area, 1984-87.

Chemical Characteristic	Wetland P1	 P8	 P11	 T3	 T8
	Median value of the coefficient of variation				
Calcium	3.5	1.9	5.0	6.9	14
Magnesium	1.9	1.2	1.7	8.9	10
Sodium	2.0	1.2	1.9	8.9	34
Potassium	2.8	2.1	3.3	6.4	5.8
Alkalinity	0.8	0.5	1.3	5.7	8.3
Sulfate	2.4	3.5	3.1	9.9	4.9
Chloride	4.9	3.4	3.7	12	9.2
Silica	5.6	6.6	27	6.1	5.5
Total nitrogen	6.4	10	7.6	5.1	6.2
Nitrate plus nitrite nitrogen	50	40	32	28	27
Ammonia	18	15	16	8.2	37
Ortho phosphorus	44	12	38	64	12
Total phosphorus	17	15	20	27	8.9
Iron	15	18	12	19	19
Manganese	26	24	40	45	45
Chlorophyll *a*	38	30	46	40	42

The microinvertebrate communities of the wetlands included some species that were common to all five wetlands and some that were unique to individual wetlands (table 4). The main difference among the wetlands was the fact that no calanoid copepods (Diaptomus species in table 4), organisms often associated with open-water zones, were found in the seasonal wetlands. The total number of microinvertebrates was larger for the seasonal wetlands than for the semipermanent wetlands (fig. 45), but no distinct seasonal trend was evident for the seasonal wetlands. However, in 1987, one of the few years in which the seasonal wetlands contained water into midsummer, the number of microinvertebrates in Wetland T8 increased from the spring until the wetland became dry in August (fig. 46). The amount of algae also increased from the spring to the summer that year and chlorophyll *a* concentrations exceeded 100 g/L, coincident with the maximum abundance of microinvertebrates.

Copepods commonly were the most abundant organisms in the microinvertebrate communities of the wetlands. Data for Wetland P1 for 1986 show the seasonal changes in the relative abundance of copepods in the microinvertebrate community of that wetland (fig. 47). The relative importance of the copepods was due mainly to the relatively large number of juvenile copepods in the samples. Rotifers commonly constituted the smallest percentage of the microinvertebrate community of the wetlands. Because of the spatial variation in the distribution of organisms within the wetlands, more than one sample was needed to characterize the community of each wetland.

Other microinvertebrate and macroinvertebrate organisms also were found in samples collected along each transect. Ostracods (seed shrimps), which are crustaceans like the cladocerans and copepods, often were found but were not identified further. Hydracarina (water mites) were infrequent members of the invertebrate community of the wetland water column. Larvae of flies, such as midges, phantom midges, and mosquitoes, were occasionally caught in the process of sample collection. Other taxa, including representatives of Trichoptera (caddisflies), Gastropoda (snails), Ephemeroptera (mayflies), and Hemiptera (bugs), were infrequently captured, but were not identified to the species level.

Table 4. Crustacean microinvertebrate species found in the water column of selected wetlands in the Cottonwood Lake area, 1984-87.

Wetland				
P1	**P8**	**P11**	**T3**	**T8**
Cladocera				
Alona guttata				*Alona guttata*
Bosmina species	*Bosmina* species			
Chydorid species	*Chydorid* species		*Chydorid* species	
Chydorus sphaericus	*Chydorus sphaericus*			*Chydorus sphaericus*
Ceriodaphnia species	*Ceriodaphnia* species	*Ceriodaphnia* species	*Ceriodaphnia* species	*Ceriodaphnia* species
Ceriodaphnia laticaudata				
Ceriodaphnia quadrangula	*Ceriodaphnia quadrangula*	*Ceriodaphnia quadrangula*	*Ceriodaphnia quadrangula*	
Ceriodaphnia reticulata	*Ceriodaphnia reticulata*	*Ceriodaphnia reticulata*	*Ceriodaphnia reticulata*	*Ceriodaphnia reticulata*
Daphnia galeatae	*Daphnia galeatae*			
Mendotae	*Mendotae*			
Daphnia pulex	*Daphnia pulex*	*Daphnia pulex*	*Daphnia pulex*	*Daphnia pulex*
Daphnia rosea				
Daphnia similis	*Daphnia similis*			
		Diaphanosoma		
		Luectenbergianum		
			Kurzia latissima	
	Lantonopsis occidentalis			
	Moina macrocopa			
			Pleuroxis denticulatus	
Pleuroxis procurvatus				
			Scapholoberius species	
Scapholoberius aurita		*Scapholoberius aurita*	*Scapholoberius aurita*	
		Scapholoberius mucronata	*Scapholoberius mucronata*	
		Simocephalus species	*Simocephalus* species	
Simocephalus vetulus	*Simocephalus vetulus*		*Simocephalus vetulus*	*Simocephalus vetulus*
Copepoda				
Acanthocyclops vernalis	*Acanthocyclops vernalis*		*Acanthocyclops vernalis*	
Cyclops crassicaudis				

Table 4. Crustacean microinvertebrate species found in the water column in selected wetlands in the Cottonwood Lake area, 1984-87 (continued).

Wetland				
P1	**P8**	**P11**	**T3**	**T8**
Diacyclops icuspidatus thomasi	*Diacyclops bicuspidatus thomasi*	*Diacyclops bicuspidatus thomasi*	*Diacyclops bicuspidatus thomasi*	*Diacyclops icuspidatus thomasi*
Ectocyclops phaleratus	*Ectocyclops phaleratus*			
Eucyclops agilis	*Eucyclops agilis*			
Microcyclops varicans		*Microcyclops varicans*		*Microcyclops varicans*
Orthocyclops modestus				
Paracyclops fimbriatus poppei	*Paracyclops fimbriatus poppei*		*Paracyclops fimbriatus poppei*	
Diaptomus breweri		*Diaptomus breweri*		
Diaptomus clavipes	*Diaptomus clavipes*			
Diaptomus franciscanus		*Diaptomus franciscanus*		
Diaptomus hesperus				
Diaptomus immunis	*Diaptomus immunis*			
Diaptomus sicilis	*Diaptomus sicilis*	*Diaptomus sicilis*		
Harpacticoida				
				Canthocamptus species
Unidentified species	Unidentified species		Unidentified species	Unidentified species

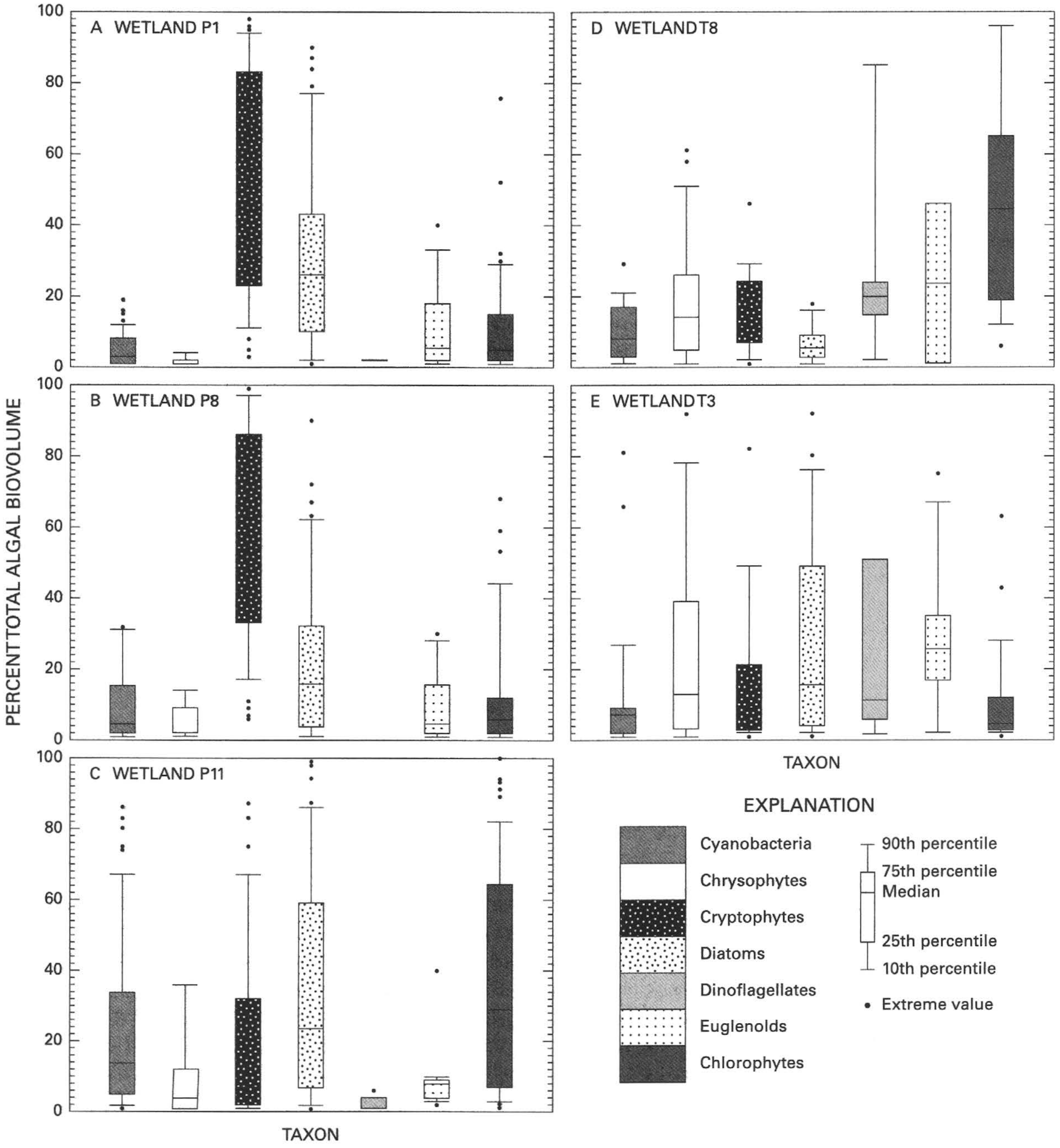


Figure 43. Summary, based on biovolume data from 1985 to 1987, of the relative abundance of taxa in the algal communities of Wetland P1 (A), Wetland P8 (B), Wetland P11 (C), Wetland T8 (D) and Wetland T3 (E).

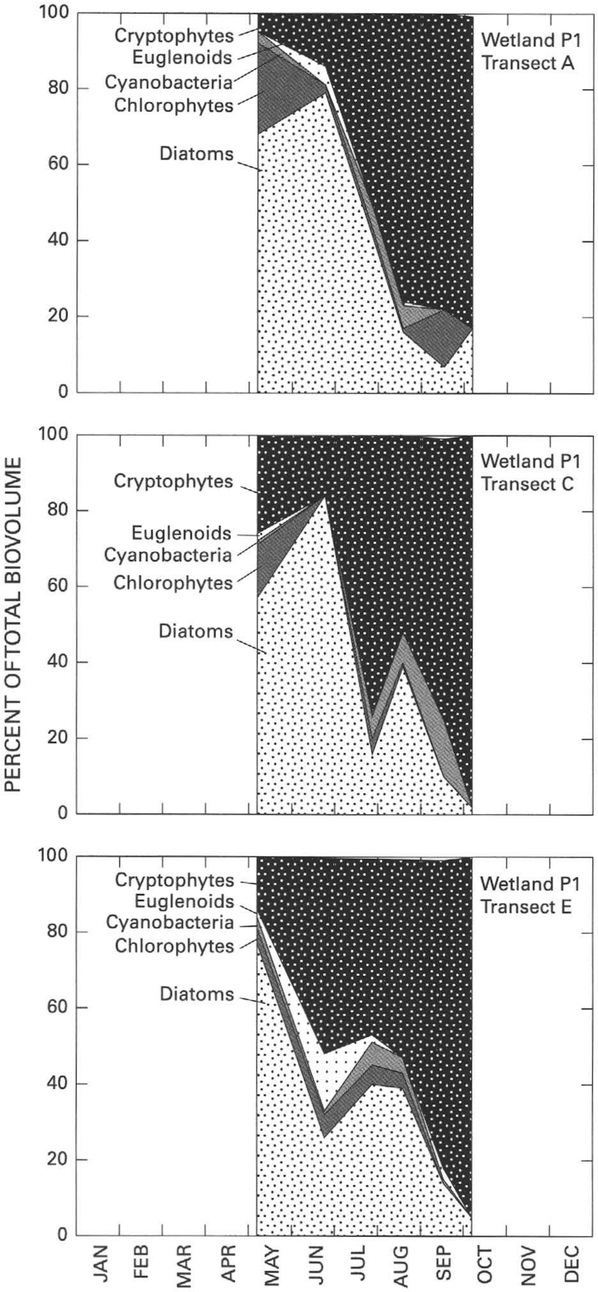


Figure 44. Seasonal changes in the relative abundance of taxa in the algal community of the open-water zone of Wetland P1 during 1986.

DISCUSSION

The variety in the abundance of major ions in the five selected wetlands in the Cottonwood Lake area is similar to the variety in wetlands throughout Stutsman and Kidder Counties (Swanson and others, 1988). Furthermore, this variety in the abundance of major ions is typical of wetlands in the glaciated prairie of North America (LaBaugh, 1989). The seasonal and annual variation in major-ions concentrations in the Cottonwood Lake area prairie wetlands was a function of the seasonal and annual variation in the balance between water inputs and losses as determined by rain, snow, evapotranspiration, and interaction with ground water as described by LaBaugh and Swanson (1992), and LaBaugh and others (1996, 1998). In addition, the wetlands varied in chemical characteristics, more so for nitrogen and phosphorus than for major ions, probably due to the use and release of those nutrients by biota.

Neely and Baker (1989) provided a summary of the different processes that can affect nitrogen and phosphorus in prairie wetlands. They concluded that the role of emergent vegetation in removing nitrogen and phosphorus from the wetlands was the only process for which detailed information was available. Atmospheric exchange affects gains and losses of nitrogen in particular, but Neely and Baker (1989) found too few studies of that process were available to make generalizations about its importance. Also, few detailed studies of the water and chemical fluxes of wetlands in general are available (LaBaugh, 1986). Kadlec's (1986) field manipulation of water levels in experimental wetlands in Delta Marsh, Manitoba, included an analysis of water and chemical fluxes that indicated atmospheric inputs were important sources of nitrogen and phosphorus. More detailed analyses of the Delta Marsh wetlands have shown that changes in aquatic macrophytes in response to wet and dry conditions control the cycling of nitrogen and phosphorus in experimental wetlands (Kadlec and others, 2000), but the importance of microbial processes has not yet been adequately documented (Murkin and others, 2000)

In one of the few detailed studies of temporal variation in plant nutrients within shallow prairie lakes, Barica (1975) indicated seasonal fluctuations of total, particulate, and dissolved nitrogen and phosphorus were quite variable. Lakes having marked growth and decline in summer algal populations had the most variability in the summer. Wetlands in the Cottonwood Lake area usually were characterized by small algal populations in the summer, but the wetlands had considerable seasonal variation in total and dissolved nitrogen and phosphorus. Large populations of cyanobacteria, which characterized the summer community in the prairie lakes in Barica's study, were not evident in the wetlands in the Cottonwood Lake area during 1984 to 1987. However, in 1967, when Wetland P1 was deeper due to wetter climatic conditions and had no emergent vegetation in the deep-marsh zone, large numbers of the cyanobacteria species *Aphanizomenon* were present. Wetter conditions returned to the Cottonwood Lake area from 1993 through 1998 and Wetland P1 again was deeper. The wetland had no emergent vegetation by 1998, and cyanobacteria were present in the wetland. Thus, changes in water level in response to variability in hydrological fluxes affect the algal community as well as vascular plant communities and zonation (Kantrud and others, 1989).

Barica's (1975) study also indicated silica varied seasonally due to fluctuations in the diatom community. Diatoms were a large component of the algal communities of the wetlands in the Cottonwood Lake area, and silica was as variable seasonally and spatially as nitrogen and phosphorus. In addition, other siliceous algae, the chrysophytes, were important parts of the communities in some wetlands and likely contributed to seasonal fluctuations of silica as well. In the prairie lakes in Barica's (1975) study, silica concentrations fluctuated from less than the detection limit to 16 mg/L. In the wetlands in the Cottonwood Lake area, silica concentrations varied from less than the detection limit to greater than 20 mg/L.

Summarizing what is known about algae in prairie wetlands, Crumpton (1989) noted the variety of aquatic habitats in these wetlands would likely yield a diverse algal community. The lack of detailed studies of algae in prairie wetlands forced Crumpton to make inferences about the composition of algal communities and the relation of the communities to hydrological and chemical conditions. Robinson and others (2000) found the algal communities of experimental wetlands in Delta Marsh on the edge of Lake Manitoba to be varied; algal assemblages in the open water, attached to plants, attached to soft sediments, or beneath the submersed surface, fluctuated in response to manipulation of water levels designed to simulate wet or dry conditions typical of conditions experienced in the mid-continent prairie. Data from the Cottonwood Lake area indicate the algal community was diverse in the wetlands and that the relative composition varied seasonally within the wetlands. Different taxa dominated the community of each wetland. In the prairie lakes studied by Barica (1975), some communities consisted primarily of diatoms, chrysophytes, and cryptomonads, and were similar to the communities in some of the wetlands in the Cottonwood Lake area. One factor that had an effect on the algal communities in the wetlands was the influence of migrating waterfowl. This factor was not considered in Crumpton's analysis. The exact nature of the birds' effect is not clear, but, during feeding, sediment resuspension could result in mixing of benthic algae into the water column, thereby increasing the amount of algae in the water column. Sediment resuspension also could increase sediment water exchange of nutrients. Increased sediment water exchange, coupled with deposition of waterfowl fecal material, could provide sufficient nutrients to stimulate the production of algae, thereby increasing the amount of algae collected in the water column.

Another factor that could affect the amount of algae collected in the water column was the influence of submerged vascular vegetation in the open-water zone. After spring thaw, the open-water zones of the semipermanent wetlands contained little submerged vascular vegetation. Thus, the entire water column of the wetlands was well mixed and the only competition for nutrients and light was among algae in the water. In the summer, after the submerged vascular vegetation had grown and partly filled the open-water zone, circulation was restricted, resulting in increased competition for light and nutrients. In the fall, when the submerged vascular vegetation in the open-water zone became senescent, competition for light and nutrients from vascular plants decreased, and the entire water column of the open-water zones of the wetlands circulated freely.

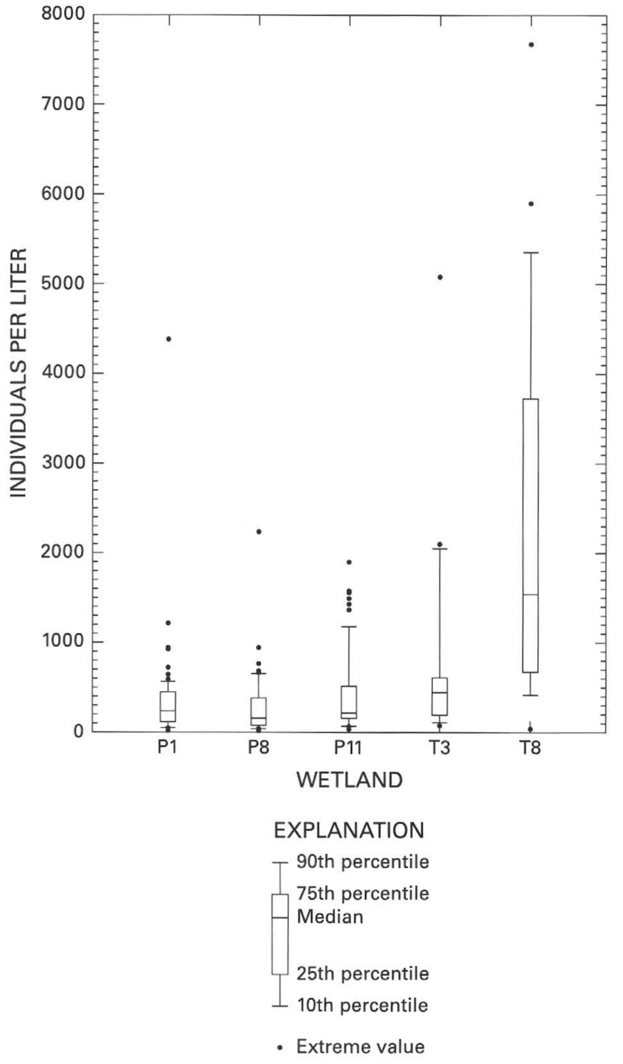


Figure 45. Summary of the abundance of microinvertebrates for five wetlands during 1984 to 1987.

Few studies have been made of the invertebrate community of prairie wetlands. Bataille and Baldassare (1993) indicated a variety of organisms occupied their three study wetlands in southwestern Manitoba. In those wetlands, crustaceans, particularly ostracods, were the most abundant taxa of the invertebrate community. Although the sampling method used in the Cottonwood Lake area was not designed to capture ostracods, data on copepod diversity and abundance were similar to the findings of Bataille and Baldassare (1993). Kantrud, Krapu, and Swanson (1989) summarized a variety of studies, including research results from the Cottonwood Lake area, and found that the invertebrate communities in prairie wetlands are diverse and highly variable. Murkin and Ross (2000) noted that variability in the invertebrate community likely is related to both the variability in the amount of time water is present in the wetlands and the spatial variability imposed by the structure of vegetation in the wetlands. Understanding the controls on invertebrate communities in the prairie wetlands is a key to understanding their use by waterfowl because, as noted by Swanson and Duebbert (1989), the invertebrate communities are an essential food resource used by waterfowl.

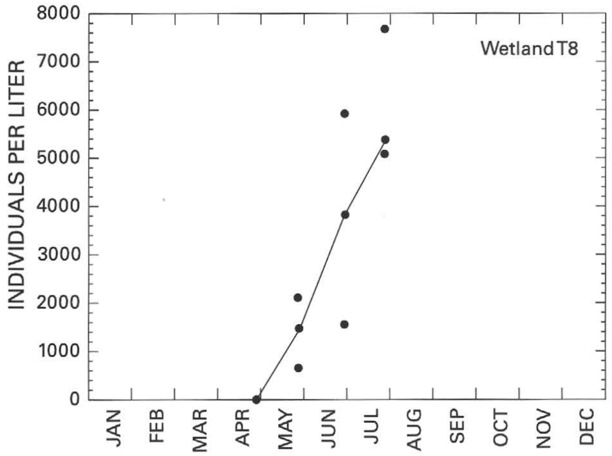


Figure 46. Seasonal changes in the abundance of microinvertebrates in Wetland T8 during the ice-free period of 1987.

In general, limnological studies of prairie wetlands are providing valuable information on spatial and temporal patterns of invertebrate community structure. Coupling these patterns with environmental factors, such as variation in hydrological conditions and related chemical characteristics, provides the framework for relating physical and chemical processes to changes in invertebrate community composition, which is important for understanding the use of the wetlands by waterfowl. Spatial variation in the algal and microinvertebrate communities of the wetlands in the Cottonwood Lake area was greater than spatial variation in the major-ion chemical characteristics. In addition, spatial variability for nitrogen and phosphorus was greater than for major ions. Thus, replicate samples are useful in any study designed to relate biological communities to hydrological or chemical characteristics of prairie wetlands.

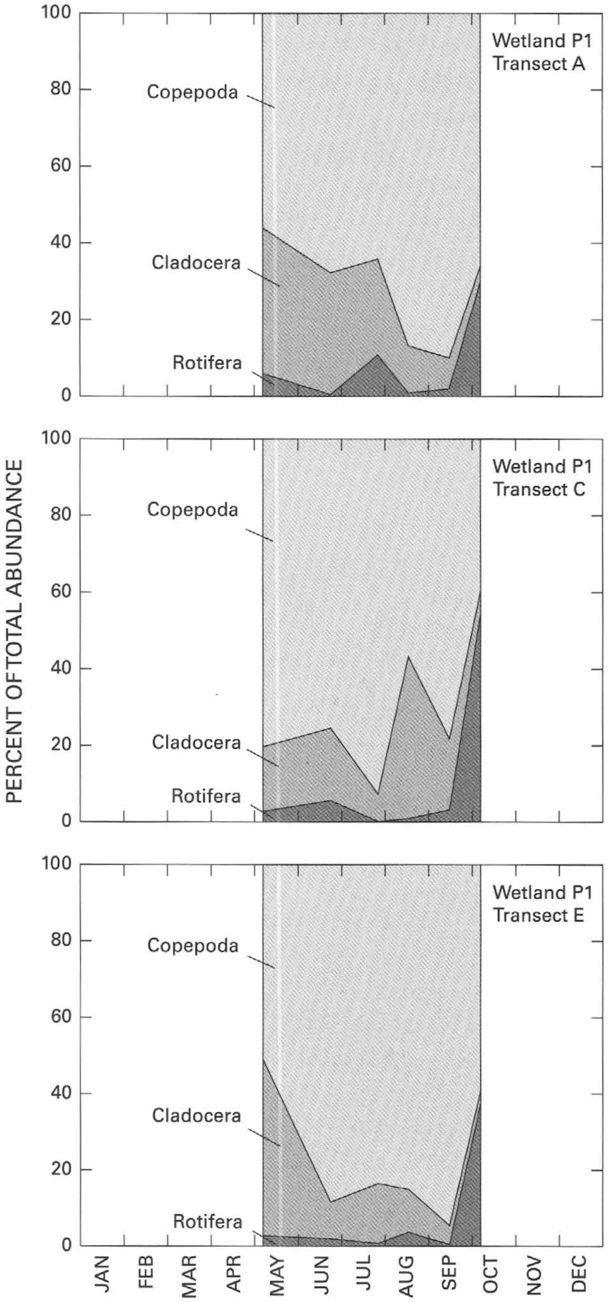


Figure 47. Seasonal changes in the relative abundance of the microinvertebrate community of Wetland P1 during the ice-free period of 1986.

REFERENCES

Arndt, J.L., and Richardson, J.L., 1993, Temporal variations in the salinity of shallow ground water from the periphery of some North Dakota wetlands (USA): Journal of Hydrology, v. 141, p. 75-105.

Barica, J., 1975, Geochemistry and nutrient regime of saline eutrophic lakes in the Erickson-Elphinstone district, southwestern Manitoba: Environment Canada Fisheries and Marine Service Technical Report 511, 82 p.

Bataille, K.J., and Baldassare, G.A., 1993, Distribution and abundance of aquatic macroinvertebrates following drought in three prairie pothole wetlands: Wetlands, v. 13, p. 260-269.

Britton, L.J., and Greeson, P.E., eds., 1988, Methods for collection and analysis of aquatic biological and microbiological samples: U.S. Geological Survey Techniques of Water-Resources Investigations, book 5, chap. A4. 686 p.

Crumpton, W.G., 1989, Algae in northern prairie wetlands, in van der Valk, A.G., ed., Northern Prairie Wetlands: Ames, Iowa, Iowa State University Press, p. 188-203.

Kadlec, J.A., 1986, Input-output nutrient budgets for small diked marshes: Canadian Journal of Fisheries and Aquatic Sciences, v. 43, p. 2009-2016.

Kadlec, J.A., van der Valk, A.G., and Murkin, H.R., 2000, The MERP nutrient budgets, in Murkin, H.R., van der Valk, A.G., and Clark, W.R., eds., Prairie Wetland Ecology: The contribution of the Marsh Ecology Research Program: Ames, Iowa, Iowa State University Press, p. 37-54.

Kantrud, H.A., Krapu, G.L., and Swanson, G.A., 1989, Prairie basin wetlands of the Dakotas: a community profile: U.S. Fish and Wildlife Service Biological Report 85(7.28), 111 p.

Kantrud, H.A., Millar, J.B., and van der Valk, A.G., 1989, Vegetation of wetlands of the prairie pothole region, in van der Valk, A.G., ed., Northern Prairie Wetlands: Ames, Iowa, Iowa State University Press, p. 132-187.

Kling, H., 1975, Phytoplankton successions and species distribution in prairie ponds of the Erickson-Elphinstone district, southwestern Manitoba: Environment Canada Fisheries and Marine Service Technical Report 512, 31 p.

LaBaugh, J.W., 1986, Wetland ecosystem studies from a hydrologic perspective: Water Resources Bulletin, v. 22, p. 1-10.

_____1989, Chemical characteristics of water in northern prairie wetlands, in van der Valk, A.G., ed., Northern Prairie Wetlands: Ames, Iowa, Iowa State University Press, p. 56-90.

LaBaugh, J.W., and Swanson, G.A., 1988, Algae and invertebrates in the water column of selected prairie wetlands in the Cottonwood Lake area, Stutsman County, North Dakota, 1984: U.S. Geological Survey Open-File Report 88-451, 96 p.

_____1992, Changes in chemical characteristics of water in selected wetlands in the Cottonwood Lake area, North Dakota, U.S.A., 1967-1989, in Robarts, R.D., and Bothwell, M.L., eds., Aquatic Ecosystems in Semi-Arid Regions: Implications for Resource Management: Saskatoon, Saskatchewan, Environment Canada, National Hydrology Research Institute Symposium Series Number 7, p. 149-162.

LaBaugh, J.W., Winter, T.C., Adomaitis, V.A., and Swanson, G.A., 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, 26 p.

LaBaugh, J.W., Winter, T.C., and Rosenberry, D.O., 1998, Hydrologic functions of prairie wetlands: Great Plains Research, v. 8, p. 17-37.

LaBaugh, J.W., Winter, T.C., Swanson, G.A., Rosenberry, D.O., Nelson, R.D., and Euliss, N.H. Jr., 1996, Changes in atmospheric circulation patterns affect midcontinent wetlands sensitive to climate: Limnology and Oceanography, v. 41, no. 5, p 864-870.

Murkin, H.R., and Ross, L.C.M., 2000, Invertebrates in prairie wetlands, in Murkin, H.R., van der Valk, A.G., and Clark, W.R., eds., Prairie Wetland Ecology: The contribution of the Marsh Ecology Research Program: Ames, Iowa, Iowa State University Press, p. 201-247.

Murkin, H.R., van der Valk, A.G., and Kadlec, J.A., 2000, Nutrient budgets and the wet-dry cycle of prairie wetlands, in Murkin, H.R., van der Valk, A.G., and Clark, W.R., eds., Prairie Wetland Ecology: The contribution of the Marsh Ecology Research Program: Ames, Iowa, Iowa State University Press, p. 99-121.

Neely, R.K., and Baker, J.L., 1989, Nitrogen and phosphorus dynamics and the fate of agricultural runoff, in van der Valk, A.G., ed., Northern Prairie Wetlands: Ames, Iowa, Iowa State University Press, p. 92 -131.

Robinson, G.G.C., Gurney, S.E., and Goldsborough, L.G., 2000, Algae in prairie wetlands, in Murkin, H.R., van der Valk, A.G., and Clark, W.R., eds., Prairie Wetland Ecology: The contribution of the Marsh Ecology Research Program: Ames, Iowa, Iowa State University Press, p. 163-199.

Sloan, C.E., 1972, Ground-water hydrology of prairie potholes in North Dakota: U.S. Geological Survey Professional Paper 585-C, 28 p.

Stewart, R.E., and Kantrud, H.A., 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, 36 p.

Swanson, G.A., 1978, A water column sampler for invertebrates in shallow wetlands: Journal of Wildlife Management, v. 42, p. 670-671.

Swanson, G.A., and Duebbert, H.F., 1989, Wetland habitats of waterfowl in the prairie pothole region, in van der Valk, A.G., ed., Northern Prairie Wetlands: Ames, Iowa, Iowa State University Press, p. 228-267.

Swanson, G.A., Winter, T.C., Adomaitis, V.A., and LaBaugh, J.W., 1988, Chemical characteristics of prairie lakes in south-central North Dakota - their potential for influencing use by fish and wildlife: U.S. Fish and Wildlife Service Technical Report 18, 44 p.

van der Valk, A.G., 1981, Succession in wetlands: A Gleasonian approach: Ecology, v. 62, p. 688-696.

_____ed., 1989, Northern Prairie Wetlands: Ames, Iowa, Iowa State University Press, 400 p.

Vollenweider, R.A., 1974, A manual on methods for measuring primary production in aquatic environments, International Biological Programme Handbook Number 12 (2nd ed.): London, Blackwell Scientific Publications, 225 p.

CHAPTER 4

DYNAMICS OF A PRAIRIE POTHOLE WETLAND COMPLEX: IMPLICATIONS FOR WETLAND MANAGEMENT

George A. Swanson[1], Ned H. Euliss, Jr.[2], Bruce A. Hanson[2], and David M. Mushet[2]

[1] U.S. Fish and Wildlife Service (Retired), Jamestown, North Dakota

[2]U.S. Geological Survey, Northern Prairie Wildlife Research Center,

Jamestown, North Dakota

ABSTRACT

Biotic communities of wetlands in the Cottonwood Lake area were influenced by the position each wetland occupied within the topographic and hydrologic landscape gradients. These gradients, together with climate, determined the hydrologic functions of the wetlands and, subsequently, the dissolved salt concentrations. The biotic communities were maintained and altered by natural fluctuations in the water levels and dissolved salt concentrations that established vegetative zones and their species structure. Variation in seasonal and annual precipitation in this semiarid area was associated with the abundance of seasonal wetlands and the dynamic characteristics of semipermanent wetlands. Long-term trends in climate conditions cycled the semipermanent wetlands between extremes of flooding and desiccation. The resulting variability in the water levels and the degree of water permanence, together with their interaction with ground water, was reflected in the variability of salinity in the wetlands. Because the biodiversity and productivity of prairie pothole wetland complexes is maintained by an abundance of temporary and seasonal wetlands and dynamic semipermanent wetlands, implications for creating, restoring, and preserving the wetland complexes in the prairie pothole region need to be based on an understanding of the response of wetland biotic communities to chemical and hydrologic gradients in the prairie wetlands.

INTRODUCTION

The semiarid climate of the prairie pothole region of North America, and the associated moisture deficits, affects the hydrological, chemical, and biological characteristics of prairie wetlands. The climate interacts with a glaciated landscape comprised of an abundance of heterogeneous, depressional wetlands, and causes the hydrogeochemical and biological characteristics in the dynamic wetland complexes to be repeatedly altered over time. Knowledge of the physical factors that determine the productivity and biological diversity of natural wetland complexes is a prerequisite to understanding biodiversity in the prairie pothole region (Swanson, 1992). Management guidelines that do not consider the dynamics of the natural wetland complexes probably will have limited success in maintaining the productivity and biological diversity of the prairie pothole region (Euliss and others, 1999).

A study to investigate the relation between waterfowl and prairie wetlands was initiated in the Cottonwood Lake area by U.S. Fish and Wildlife Service biologists in 1967 (fig. 48). An expansion of the study was initiated by U.S. Geological Survey hydrologists in 1979 to define the hydrologic characteristics of the wetlands (Winter and Carr; 1980, LaBaugh and others, 1987). Results of the now interdisciplinary study of the Cottonwood Lake area have led to an increased understanding of how the hydrologic setting affects wetland chemical characteristics and how interaction between hydrological and chemical characteristics affects wetland plant and animal communities (Winter and Carr, 1980; LaBaugh and others, 1987; Swanson and others, 1988). Although biological studies were initiated in 1967, information from the interdisciplinary study and information from a previous study of the hydrology and plant-community structure of wetlands in the vicinity of the Cottonwood Lake area (Eisenlohr and others, 1972; Stewart and Kantrud, 1971, 1972), could be used to describe long-term hydrologic trends and the response of wetland communities to climatic extremes that occurred during 1961-98. In addition, to relate the Cottonwood Lake area wetland complex to lakes and wetlands in the drift prairie, Missouri Coteau, and glacial outwash plain, a study of the chemical characteristics of lakes and wetlands in Stutsman and Kidder Counties, North Dakota, was completed by Swanson and others (1988).

Figure 48. Areal view of the Cottonwood Lake area looking west on July 1, 1981. The tip of the cultivated right triangle in the lower left side of the photograph intersects the south end of Wetland P7. The east-west road bends around the north side of Wetland P11 located in the background.

The Cottonwood Lake area was purchased by the U.S. Fish and Wildlife Service on August 6, 1963, to be managed as a Waterfowl Production Area. The 91.8-ha area contains 75.1 ha of uplands and 16.7 ha of wetlands. Eighteen percent of the land was cultivated at the time of purchase, and this land, which consisted of two fields, was seeded to non-native perennial grasses and legumes after Federal acquisition. The remaining upland is in native prairie and previously was exposed to grazing and prescribed burning.

The Cottonwood Lake area is bordered on the east and west by pasture, on the north by planted hayland, and on the south by cultivated land that was converted to grassland in 1990 under the U.S. Department of Agriculture's Conservation Reserve Program. Uplands in the wetland complex were grazed until the area was purchased in 1963. The area initially was managed by the U.S. Fish and Wildlife Service by controlled burning that was terminated to accommodate this study.

During periods of average water levels, the deep-marsh emergent zones of the semipermanent wetlands that occupy the Cottonwood Lake area, with the exception of Wetland P11, were dominated by hardstem bulrush (*Scirpus acutus*) and broadleaf and narrowleaf cattail (*T. latifolia, Typha angustifolia*) and their hybrid (*T.* x *glauca*). Wetland P11 typically was dominated by salt-tolerant plants such as prairie bulrush (*Scirpus maritimus*) and sago pondweed (*Potamogeton pectinatus*). Seasonal wetlands that functioned as ground-water recharge areas were dominated by swamp smartweed (*Polygonum amphibium*) and slough sedge (*Carex atherodes*) (LaBaugh and others, 1987). Seasonal wetlands that functioned as ground-water flow-through systems, were dominated by slough sedge and sprangletop (*Scolochloa festucacea*).

METHODS

Wetland water conditions and the response of emergent vegetation to hydrologic and chemical conditions were documented using ground and aerial photographs and 0.25-m^2 plots of emergent vegetation located along randomly selected transects. Annual trends in wetland cover (open water/emergent vegetation ratio) and zonation were documented using vertical, low-altitude, 35-mm color photographs. Plant species within zones were identified in the field, and upland vegetation at the Cottonwood Lake area was described in July 1989. The species were identified and the canopy cover was estimated (Daubenmire, 1959) from 130 quadrats (tables 5 through 10). Five 20- x 50-cm quadrats, 8.75 m apart along four transects, were used. The transects were established at random on mesic and xeric sites and on sites with east, west, north, and south aspect slopes. Upland vegetation at the study site also was mapped (fig. 49) by vegetative community (Kruse and Bowen, 1996). Dry conditions in 1989 reduced mesic areas, and most mesic transects entered basin wet-meadow zones. The brush shown in figure 49 consists mostly of western snowberry (*Symphoricarpos occidentalis*) and the brome-alfalfa portions are areas that were cultivated prior to U.S. Fish and Wildlife Service ownership of the area. Because of the intensity of the work required to relate climate-induced variations in hydrology and chemistry to wetland biota, work was concentrated on five wetlands (T3, T8, P1, P8, and P11). However, a broad overview of the response of wetlands in and near the Cottonwood Lake area to climate variability is presented first as a framework for discussion of the five wetlands.

RESPONSE OF WETLANDS IN AND NEAR THE COTTONWOOD LAKE AREA TO CLIMATE VARIABILITY FROM 1961 TO 1998

During 1961-98, the Cottonwood Lake area experienced the second worst drought (1988-92) and the greatest deluge (1993-98) in more than a century (Winter and Rosenberry, 1998; Rosenberry, Chapter 2 of this report). The climate extremes were unique in that a historic deluge terminated a historic drought. The back-to-back climate events provided a unique opportunity to document the response of a prairie pothole wetland complex to climate extremes that occurred over a short timeframe (1988-98).

A wet period following a drought also occurred from 1962 to 1966 (Eisenlohr and others, 1972) but that wet period was shorter in duration and magnitude than the wet period from 1993 through 1998. However, 4 of the 5 years that followed the drought of

1961 described by Eisenlohr and others (1972) resulted in rises in water levels. The rises in water levels in 1962 and 1964 were caused by midsummer precipitation, and the rises in water levels in 1965 and 1966 were caused by heavy runoff during spring snowmelt. During the wet conditions of 1962-66, dissolved salt concentrations were greatly reduced and emergent vegetation was drowned and eliminated in closed basins. In contrast, the dry conditions that occurred in 1973-74, 1976-77, and 1988-92 eventually caused even the most persistent semipermanent wetlands in the Cottonwood Lake area to become dry, and the wetland basins became dominated by dense, monotypic stands of emergent vegetation, primarily cattail, by the end of 1992.

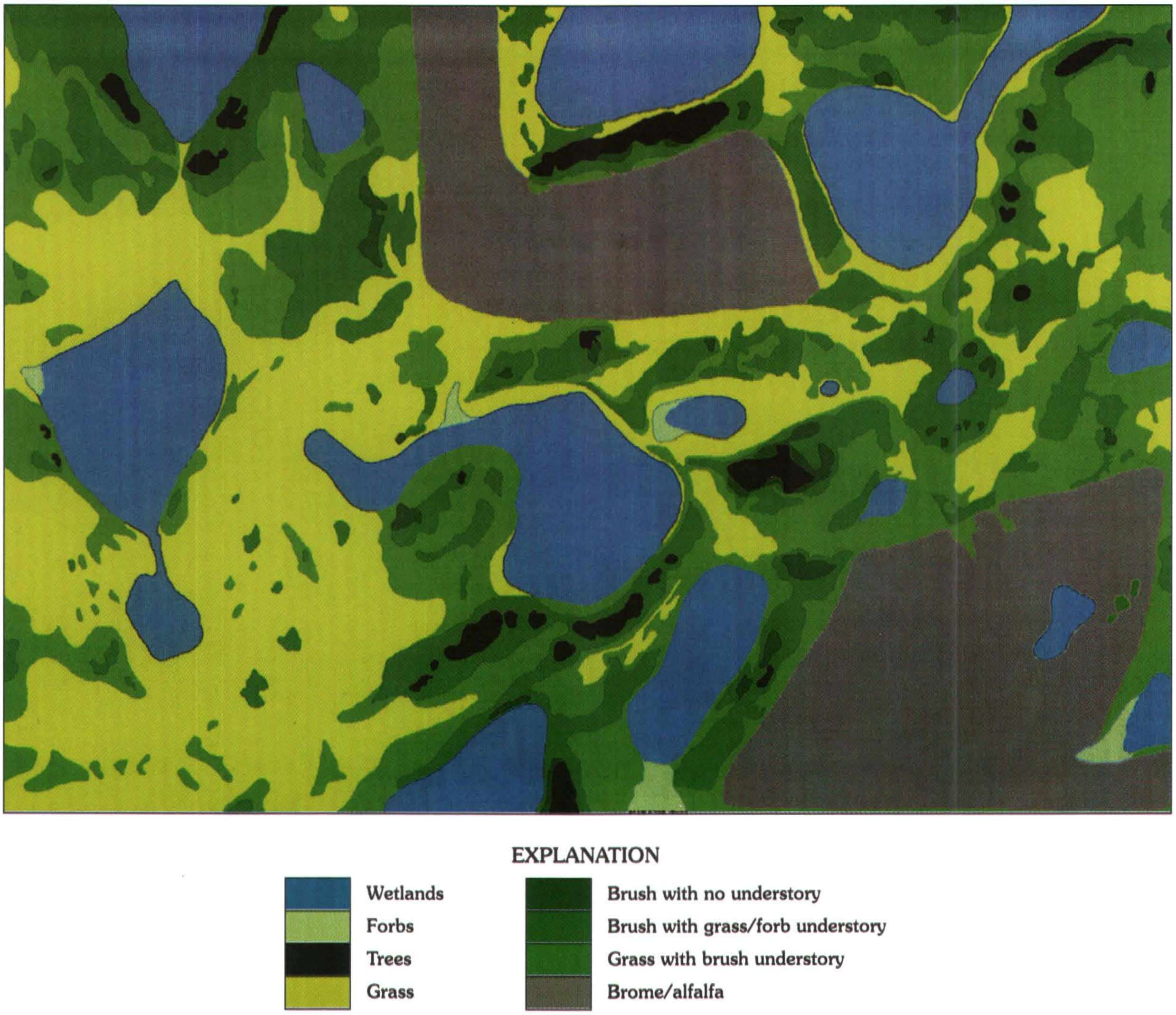


Figure 49. Upland vegetation in the Cottonwood Lake area, 1989.

The water budget of each wetland, and the subsequent chemical environment and biotic community, was determined by the dominant flow pattern that contributed water to and removed water from the wetlands. Among the semipermanent wetlands, the dominant hydrologic feature that determined the dissolved salt concentration and the biotic community structure was whether or not the basin functioned as a closed system or an open integrated system with respect to surface flow. Among closed basins, the differences in salinity were related to the magnitude of seepage losses to ground water, which exports dissolved salts. Water loss to evapotranspiration concentrated dissolved salts and peaked during midsummer when plant respiration and temperatures were high, relative humidity was low, and warm winds blew persistently. The annual hydrologic response to gains and losses of water was usually a rapid rise in water levels during spring snowmelt and drawdown (declines in water levels) in late summer (Winter and Rosenberry, 1995; LaBaugh and others, 1996; Poiani and others, 1996). Hydroperiods (the periods when wetlands contain surface water) driven by annual moisture deficits facilitated the development of concentric bands of emergent vegetation dominated by wet-meadow, shallow-marsh, and deep-marsh species (Stewart and Kantrud 1972).

Seasonal wetlands in the Cottonwood Lake area were dry by midsummer in most years and the centers of the basins were dominated by shallow-marsh plant species. In wet years, however, some seasonal wetlands held water until freezeup and the basins were dominated by deep-marsh plant species. In contrast, during dry years when the snowpack was low, the seasonal wetlands remained dry and the central zone was dominated by low-prairie and wet-meadow species.

Closed (isolated) semipermanent wetlands in the area were the most dynamic in response to climate trends (fig. 50, A-B). The lack of an outlet caused water levels in the closed basins to rise rapidly in response to major precipitation events that flooded emergent vegetation and, on occasion, upland vegetation (fig. 50C). In contrast, complete drawdown (a loss of all wetland water) of the semipermanent wetlands by evapotranspiration during periods of drought resulted in exposed mudflats, seed germination, and the subsequent dominance of mudflats by emergent vegetation. The sequence in the response of individual wetlands to drought conditions and the magnitude of change that occurred in a given year was determined by the volume of water stored in each basin and by the persistence of ground-water discharge to the basin. Trends in dissolved salt concentrations followed water-level changes that responded to precipitation and evapotranspiration (LaBaugh and others, 1996).

Trends in climate conditions resulted in the semipermanent wetlands being cycled between extremes of complete drawdown (1961, 1973-74, 1976-77, and 1988-92), which initiated seed germination, and flooding (1962-66 and 1993-98), which drowned emergent vegetation that had become established during previous drawdowns. High water levels occurred in the closed semipermanent wetlands southeast of the Cottonwood Lake area during 1962-66 (fig. 51) (Eisenlohr and others, 1972). The high water levels, once established, persisted and caused the closed semipermanent wetlands in the Cottonwood Lake area to be dominated by open water during 1967-72 (Poiani and others, 1996) and 1993 to the present (2002) (fig. 50B-C). During periods of high water levels, the closed semipermanent wetlands flooded into the surrounding prairie, eliminating emergent aquatic vegetation.

All wetlands in the Cottonwood Lake area were dry during the drought of 1961 as reported by Eisenlohr and others (1972). The period that followed the drought of 1961 (1962-1966) was one of increasing water levels that peaked in 1966 following a major March blizzard. During the next 6 years (1967-72), water stored in the closed semipermanent wetlands during 1962-66 persisted and hydrologic conditions in the wetlands remained relatively stable. The wetlands were dominated by open water and planktonic algae. The open-water zone, following the initial flooding, was characteristically surrounded by a narrow fringe of deep-marsh vegetation, primarily hardstem bulrush and cattail. Once the closed wetlands received a major contribution of water, the wetlands persisted because evapotranspiration was the dominant pathway for water loss (Eisenlohr and others, 1972). During this study, drought caused some of the semipermanent wetlands to dry up during the growing season, as in the dry periods of 1973-74 and 1976-77. However, all of the semipermanent wetlands were completely dry and dominated by emergent vegetation during the drought of 1988-92.

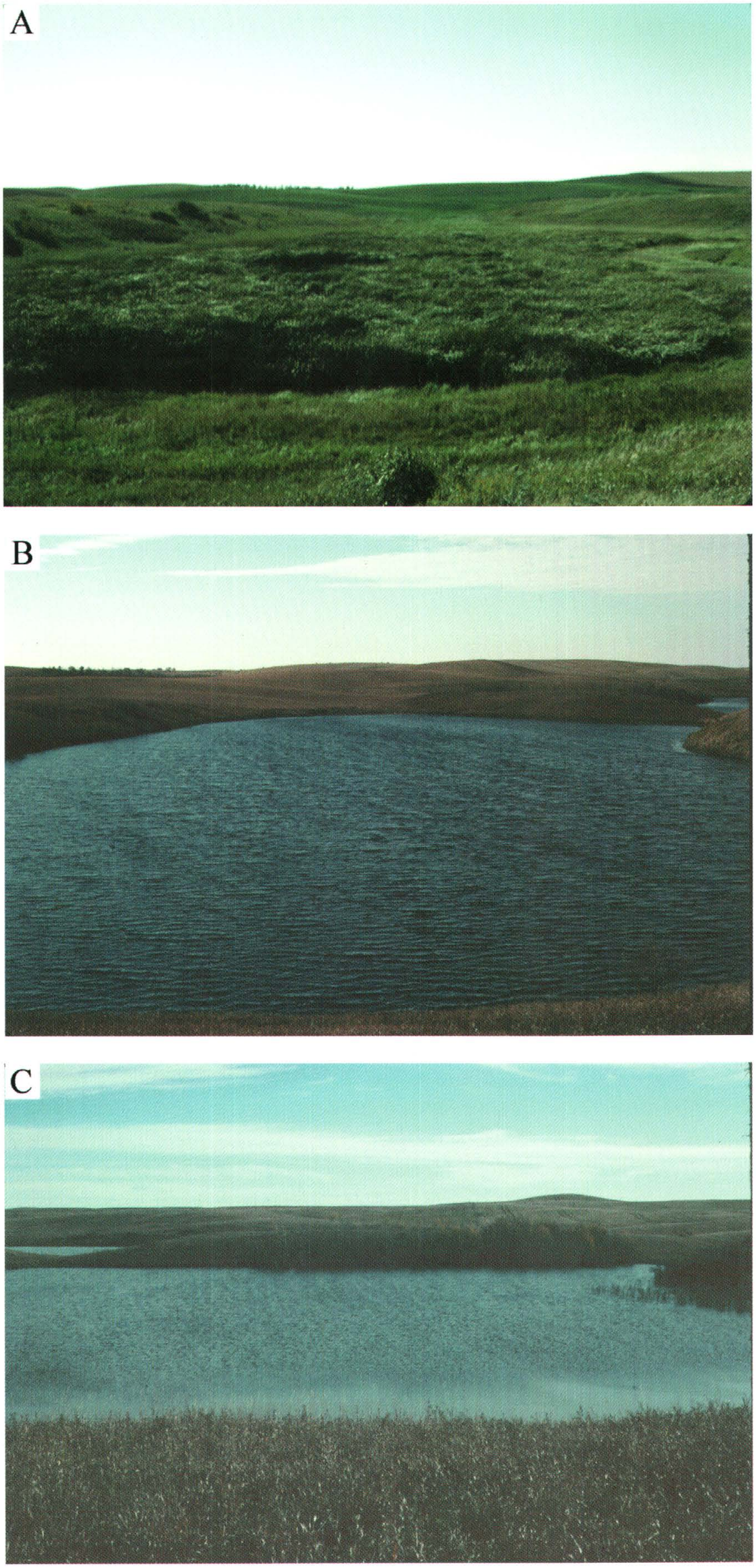


Figure 50. Wetland P6 on October 1, 1983, dominated by deep-marsh vegetation established during the drought of 1976-77 (A); Wetland P6 on October 28, 1997, dominated by open water following the deluge of 1993-98 (B); Wetland P7 on October 5, 1996, dominated by open water that flooded a 33-year old aspen stand located on the east side of the wetland (C).

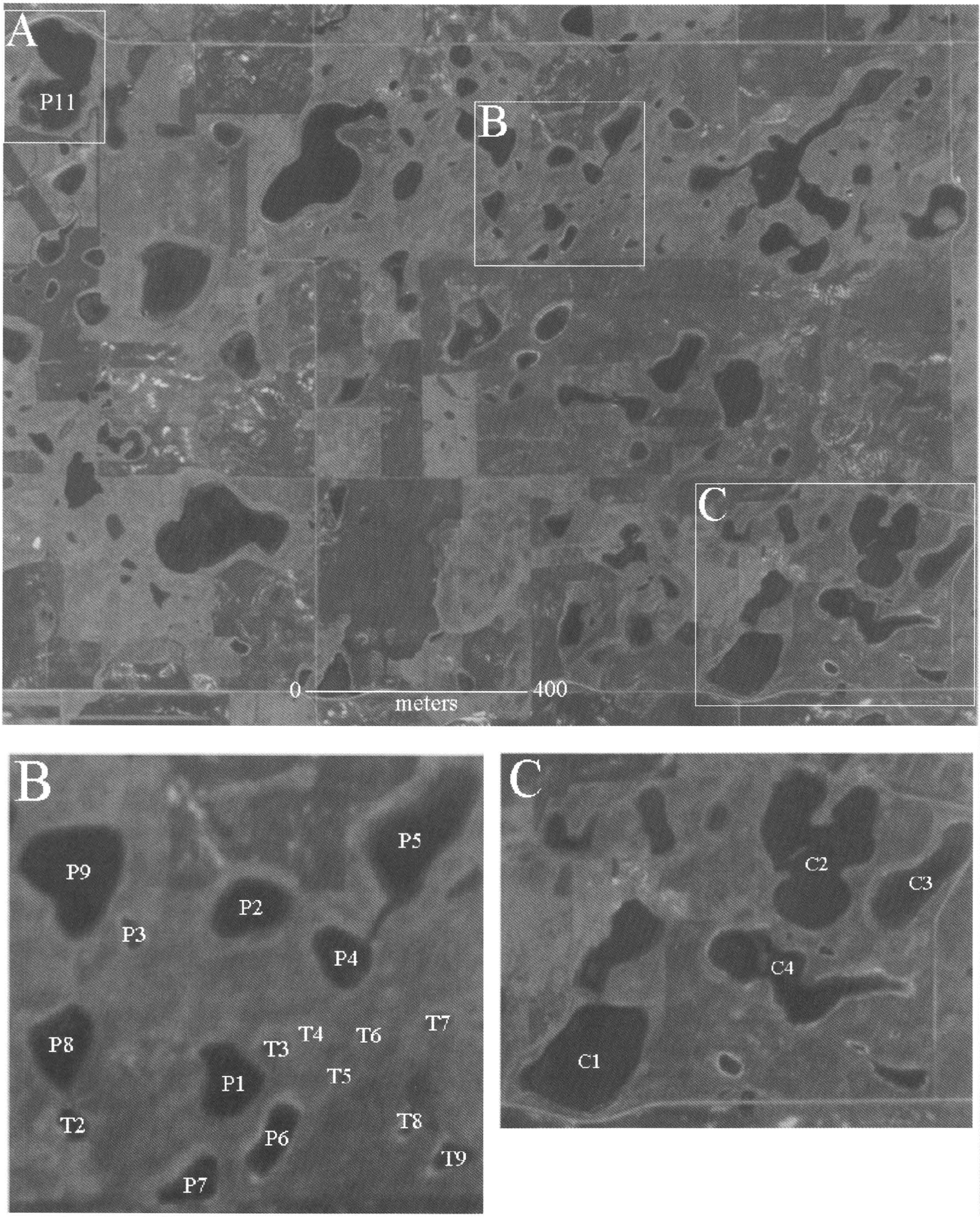


Figure 51. Aerial view during May, 1970, of Wetland P11 (A), wetlands in the Cottonwood Lake area (B) and wetlands studied by Eisenlohr and others (1972) (C).

As water levels declined from 1973 to 1992, basin substrates were exposed in the semipermanent wetlands in a sequence determined by the volume of water stored in each basin during 1962-66. Drawdown and an increase in dissolved salts caused seed germination of typical drawdown species (Stewart and Kantrud, 1971; Weller, 1978; van der Valk, 1981) when mudflats were exposed during the growing season. Annual plants dominated basin substrates during the first summer if drawdown occurred during the growing season. Annual plant dominance was succeeded by perennial plant dominance in subsequent years as water levels increased and stabilized.

All of the closed semipermanent wetlands in the Cottonwood Lake area that were open-water basins prior to 1973 eventually were converted to dense, monotypic stands of emergent vegetation dominated by cattail. Wetlands P3 and P4 were the first semipermanent wetlands to dry up and be converted after 1967. Wetland P4 contained three circular stands of hybrid cattail, one located in the center of the basin, that survived flooding during 1962-66. During the first year of drawdown, 1973, Wetland P4 was dominated by a dense stand of alkali blight (*Chenopodium rubrum*) (fig. 52A). During the second year, 1974, golden dock (*Rumex maritimus*) dominated this basin along with recently germinated *Carex* spp, sprangletop, hardstem bulrush and cattail (fig. 52B). In 1975, a year of rising water levels, wet-meadow and shallow-marsh plant species were eliminated from the central zone of the basin and cattail dominated the basin (fig. 52C). The cattail persisted as a dense monotypic stand for 18 years. The deluge of 1993-98 reversed the trend in climate conditions and converted Wetland P4 to an open-water basin, flooding out emergent vegetation that germinated during the drought of 1973-74 and the hybrid cattail that survived flooding during 1962-66 (fig. 53A-C). Although cattail seedlings germinated during the first summer of desiccation in 1973, cattails did not dominate the basin until 1975. The drought of 1976-77 converted three additional semipermanent wetlands (P2, P6, and P7) from open-water basins to monotypic stands of cattail, and the drought of 1988-92 converted the central open-water zone of all remaining semipermanent wetlands (P1 and P8) to dominant stands of cattail.

Seed germination in most semipermanent wetlands in the Cottonwood Lake area during drawdown followed the pattern observed in Wetland P4. Wetlands P1 and P11, however, were exceptions because dissolved salt concentrations in those basin substrates following drawdown selectively influenced seed germination.

Rising water levels during 1993-98 flooded out emergent vegetation established during the dry periods of 1973-74, 1976-77, and 1988-92 and converted Wetlands P1, P2, P4, P5, P6, and P7 from monotypic stands of emergent vegetation to open-water basins. By 1998, the closed semipermanent wetlands in the Cottonwood Lake area were dominated by open water as previously observed in the spring of 1967; maximum water levels in 1998, however, exceeded those in 1967. By 2002, Wetlands P2, P4, and P5 integrated and formed a single wetland, and Wetland P1 flooded into Wetland T3, causing Wetland T3 to temporarily be an extension of Wetland P1. Water levels in closed basins in the study area are controlled primarily by precipitation and evapotranspiration, which produce dynamic hydroperiods compared to those in open basins where water levels do not rise much higher than the elevations of their outlets.

Surface outflow was not a component of the water budget of most semipermanent wetlands (P1, P2, P4, P5, P6, P7, P9, and P11) in the Cottonwood Lake area or of seasonal Wetland T9 because the volumes of water contributed to the drainage basins were consistently less than the volumes required to fill the drainage basins to maximum storage capacity. The wetlands, with the exception of Wetland T9, routinely accumulated sufficient volumes of water from the drainage basins and ground-water discharge to persist for extended periods as semipermanent wetlands. Wetland T9 is located on a topographic high and due to the absence of ground-water input, functioned primarily as a seasonal wetland. The lack of surface outflow from semipermanent wetlands and the contribution of ground water to the water budget result in an accumulation of dissolved salts, which play a role in the chemical and biological characteristics of the wetlands.

Wetlands P3, P8, and T2, which have surface outlets, were the only semipermanent wetlands that contained a significant stand of emergent vegetation following the deluge of 1993-98. Of the three open semipermanent wetlands in the study area, Wetland P8 stored the largest volume of water. The elevations of the outlets of Wetlands T3 and P2 prevented the water level from exceeding the depth tolerance of hybrid cattail.

KEY WETLANDS

The previous discussion provided a general description of the response of the Cottonwood Lake area wetland complex to climate variability that occurred from 1961 to 1998. This section describes the unique hydrological, chemical, and biological characteristics of five key wetlands (T8, T3, P1, P8, and P11) that are located along a topographic and hydrologic gradient (Winter, Chapter 1 of this report).

WETLAND T8

Wetland T8, located near the highest part of the study area (fig. 54A), functioned as a ground-water recharge basin; ground-water gradients were away from the basin for the entire study period. Precipitation and snowmelt runoff were the primary sources of water to this wetland; therefore, the water was low in dissolved salts. The volume of water stored in the basin usually did not exceed the volume lost annually to evapotranspiration and recharge; as a result, Wetland T8 contained water in the spring and usually was dry by midsummer. Dissolved salt concentrations in the water column were consistently low and the salts were dominated by potassium and calcium bicarbonate (LaBaugh and Swanson, 1992; LaBaugh and Swanson, Chapter 3 of this report).

Plant and invertebrate species that occupied Wetland T8 reflected a seasonal water regime low in dissolved salts (Stewart and Kantrud, 1971; Kantrud, Krapu, and Swanson, 1989). Shallow-marsh vegetation dominated by slough sedge and swamp smartweed occupied the central zone of the wetland (fig. 54B) (LaBaugh and others,1987) along with a small stand of reed canarygrass (*Phalaris arundinacea*). Deep-marsh emergents (cattail and bulrush) invaded when surface water persisted late into the growing season but were eliminated during periods of drought. Terrestrial, low-prairie and wet-meadow species invaded the central zone of the basin when the wetland was dry in early spring following the melting of the snowpack and the thawing of frozen soils (fig. 54C). The invertebrate fauna was dominated by crustaceans (Anostraca, Conchostraca, Cladocera, and Copepoda), snails (*Gyraulus circumstriatus*, *Stagnicola caperata*, and *Promenetus umbilicatellus*), and insects (Culicidae, Chaoboridae, Corixidae, Coleoptera, and Odonata). During wet periods when surface water persisted into the growing season, species that require an annual hydroperiod of extended flooding, such as the snails *Stagnicola elodes* and *Helisoma trivolvis*, colonized the basin.

Amphibian communities of Wetland T8 also showed a marked temporal response to climate-driven hydrologic cycles. After the drought of 1988-92, amphibians did not reappear in the wetland until 1994 although the wetland had reflooded the previous year. The initial amphibian community was composed mostly of boreal chorus frogs (*Pseudacris triseriata maculata)*. Northern leopard frogs (*Rana pipiens*) appeared in 1995 and dominated the amphibian community through 1996. With prolonged inundation, tiger salamanders (*Ambystoma tigrinum)* greatly expanded their population and dominated the amphibian community in 1997. The tiger salamanders usually are not an important component of the amphibian community of Wetland T8 because the normal hydroperiod for that wetland involves a seasonal drawdown that interferes with the early development of salamanders. However, the current wet cycle is unusual in that conditions are much wetter than normal and Wetland T8 has not undergone a seasonal drawdown since 1993.

WETLAND T3

Wetland T3, located at an intermediate elevation in the study area, functioned as a flow-through system that receives ground-water discharge and also recharges ground water. Ground water usually flowed into Wetland T3 along the north, east, and south sides and seeped out of Wetland T3 toward Wetland P1 on the west side. Wetland T3 occasionally spilled into Wetland P1 (Rosenberry and Winter, 1997), which, during extremely high water conditions (for example, during 1993-98), merged with Wetland T3. The volume of water stored in Wetland T3 is controlled by the elevation of the spill point to Wetland P1 and typically is less than the volume lost annually to evapotranspiration and ground-water recharge; as a result, Wetland T3 has a seasonal water regime. The wetland is typical of all seasonal wetlands in the Cottonwood Lake area, with the exception of Wetland T9, that have storage capacities that are limited by overflow and that commonly become dry.

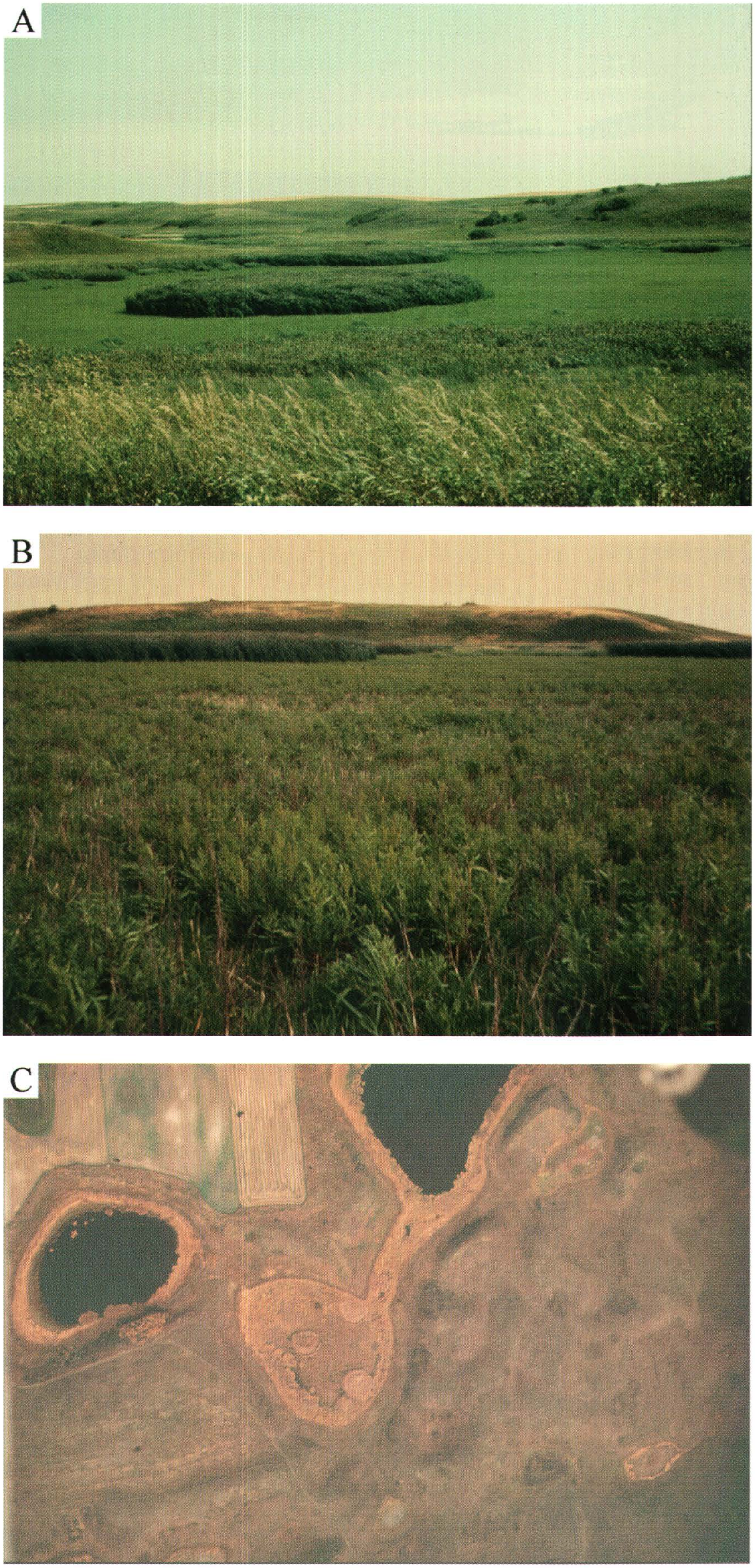


Figure 52. Wetland P4 on July 1, 1973, during a period of drawdown. A circular stand of hybrid cattail that survived flooding during 1962-66 is shown in the center (A); Wetland P4 on July 10, 1974, during a second year of drawdown (B); aerial view of Wetland P4 on October 30, 1975, showing three circular stands of hybrid cattail that survived flooding during 1962-66 and persisted as distinct units for 10 years (C).

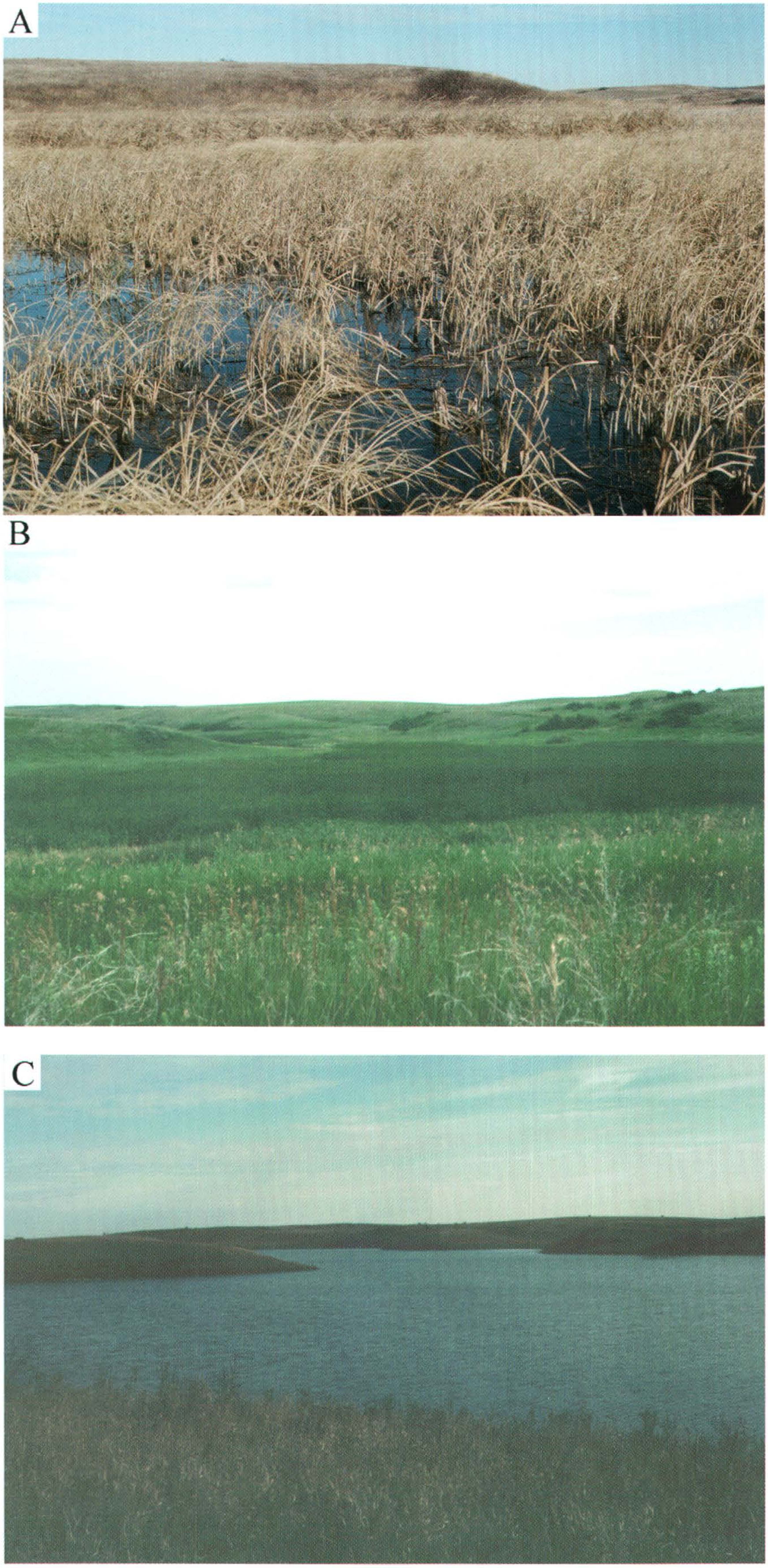


Figure 53. Wetland P4 on October 30, 1975, dominated by recently germinated cattail. (The persistent clump of hybrid cattail located in the center dominates the mixed-species stand of recently germinated cattail) (A); Wetland P4 on July 20, 1979, dominated by a monotypic stand of cattail that persisted for 18 years (B); Wetland P4 on October 28, 1997, during the deluge of 1993-98 that integrated Wetlands P2, P4, and P5 (C).

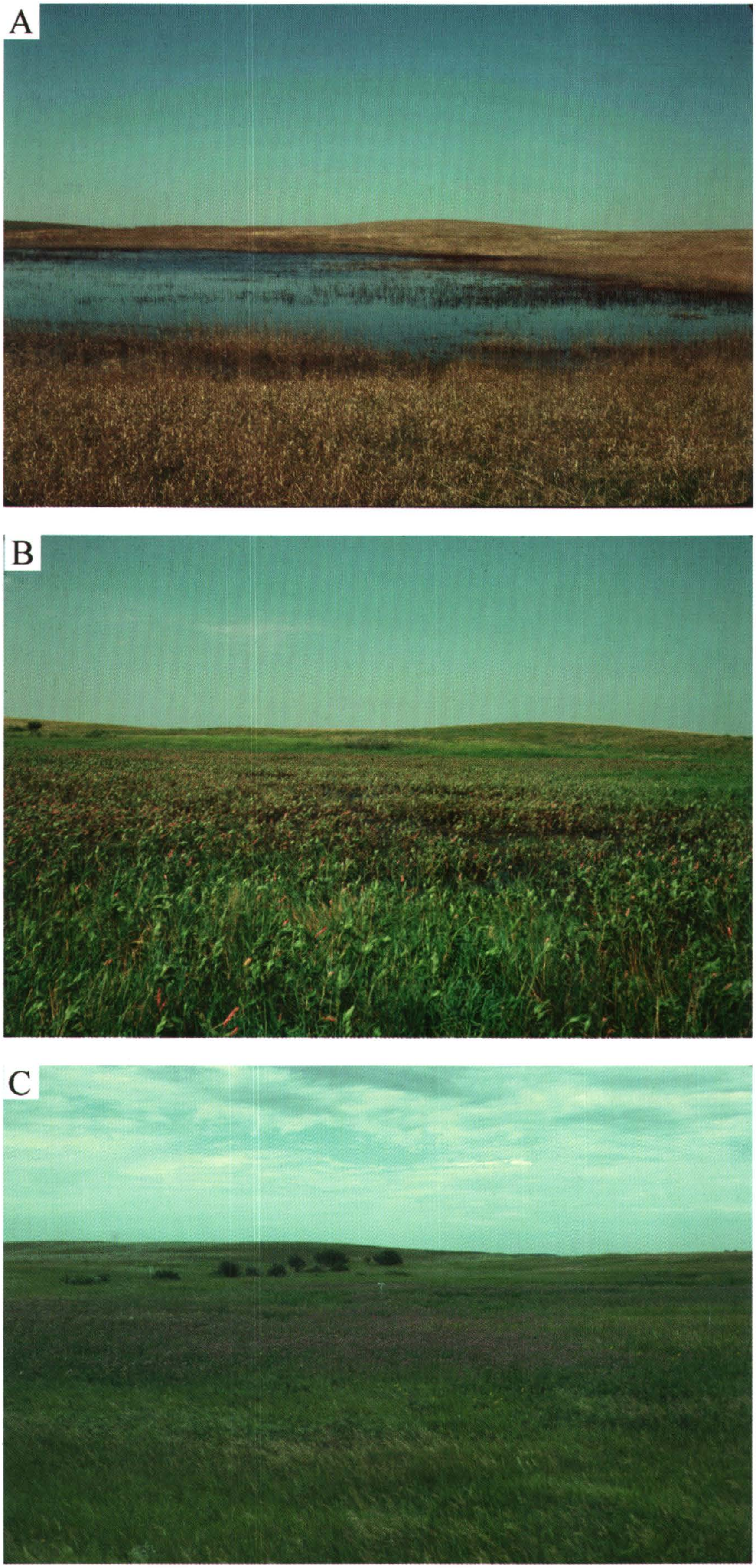


Figure 54. Wetland T8 on May 5, 1975, following flooding (A); Wetland T8 on August 1, 1975, dominated by smartweed and sloughsedge following drawdown (B); Wetland T8 on July 23, 1991, dominated by Canada thistle (*Cirsium arvense*) during the drought of 1988-92 (C).

Although Wetland T3 routinely overflowed, it consistently maintained dissolved salt concentrations that were higher than those in Wetland T8 (LaBaugh and Swanson, 1992). Dissolved salts in Wetland T3 were dominated by calcium sulfate (LaBaugh and Swanson, 1992), but the water type changed from calcium sulfate to magnesium sulfate when persistent high water drowned emergent vegetation. At times of high water levels, the water column was highly turbid and dominated by planktonic algae, which caused a decline in calcium (LaBaugh and Swanson, 1992). The differences between the dissolved salt concentrations and the major-ion water types for Wetlands T3 and T8 can be attributed to the fact that Wetland T3 receives ground-water input and Wetland T8 does not receive ground-water input. The differences in salinity are reflected in the composition of the vegetation in the wetlands; the species in Wetland T3 can tolerate a wider range in salinity than the species in Wetland T8.

The central zone of Wetland T3 was dominated by the shallow-marsh species sprangletop and slough sedge. During periods of drought, as described for Wetland T8, the plant species structure of the central zone was altered by invasions of species that normally occupy terrestrial sites, low prairie, and wet meadow (fig. 55A). Sprangletop routinely occupies seasonally-flooded zones of wetlands that receive ground-water input and that subsequently tend to have elevated salt levels (Stewart and Kantrud, 1971). For this reason, sprangletop is present in Wetland T3 but not in Wetland T8, which has no ground-water input and which has swamp smartweed as one of the dominant plants. When high water levels persisted late into the growing season in response to frequent and intense precipitation events, cattails became established in the central zone of Wetland T3 (fig. 55B).

Invertebrates inhabiting Wetland T3 were similar to those in Wetland T8 and were dominated by species that respond to seasonal water regimes. However, during periods of extremely high water levels as in 1993-98 (fig. 55C), Wetland P1 can incorporate Wetland T3; when both wetlands coalesce, the invertebrate community is more representative of a semipermanent water regime. The amphibian community of Wetland T3 likewise is similar to that of seasonal Wetland T8 except when Wetland T3 is integrated with Wetland P1.

WETLAND P1

Wetland P1 is typical of the numerous, closed, oligosaline (Cowardin and others, 1979), semipermanent wetlands (Stewart and Kantrud, 1971) that are located at intermediate elevations in the prairie pothole region. Wetland P1 functioned primarily as a ground-water discharge basin, although a limited amount of water was lost to ground water in late summer and in drier years (Winter and Rosenberry, 1995; Winter, Chapter 1 of this report). Although some water loss to seepage occurred during seasonal flow reversals in late summer, this water loss was negligible compared to water loss by evapotranspiration. On the western side of the wetland, the ground-water gradient occasionally was away from the wetland toward Wetland P8, allowing Wetland P1 to lose water and solutes through the ground-water system (Winter and Rosenberry, 1995). During the drought of 1988-92, water levels declined to well below the bottom of the wetland, except on the side toward Wetland P6.

The water type in Wetland P1 was predominately magnesium sulfate, except in 1967 and 1993-94 when emergent vegetation was flooded and the water type changed to magnesium bicarbonate (LaBaugh and Swanson, 1992; LaBaugh and others, 1996). The differences in dissolved salt concentrations among prairie wetlands that do not overflow probably are determined by the relative inputs of and losses to ground water. The volume of salts brought in by ground water and the volume of salts lost by seepage to ground water appear to explain the differences in the salt concentrations among closed wetland basins and, subsequently, the difference in the biotic communities supported by the wetlands.

During wet periods, Wetland P1 stored large volumes of water (fig. 56A and C). Once the water was stored, high water levels persisted until drought conditions caused the water levels to decline (fig. 56B). The high water levels observed in the spring of 1967 persisted for 6 years until the drought of 1973-74. The water levels then declined until the wetland became dry in the fall of 1974 after the growing season. Because the wetland became dry after the growing season, seeds germinated only on the narrow band of substrate exposed during the growing season and the substrate exposed after the growing season persisted as a barren mudflat until the wetland reflooded in the spring of 1975. Thus, the plant

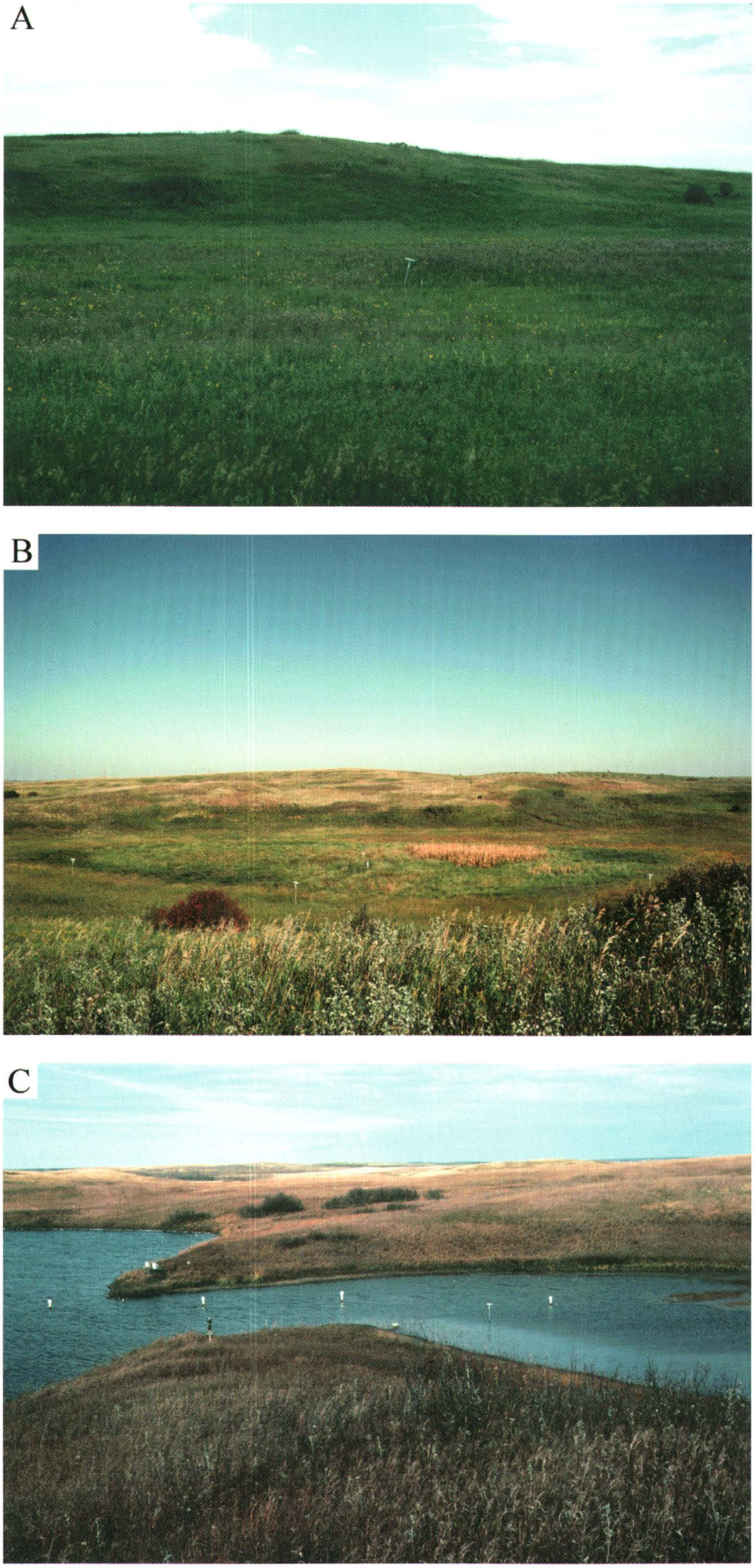


Figure 55. Wetland T3 on July 23, 1991, dominated by Canada thistle during the drought of 1988-92 (A); Wetland T3 on July 27, 1994, showing a small stand of cattail (B); Wetland T3 integrated with Wetland P1 on October 28, 1997, during the deluge of 1993-98 (C).

community of Wetland P1 remained relatively stable for 10 years until drawdown in the fall of 1976. The partial drawdown that occurred during the spring of 1976 established a narrow band of deep-marsh vegetation dominated by cattail and hardstem bulrush. The absence of a snowpack in the spring of 1977 minimized runoff to the wetland and the entire substrate was exposed during the spring and early summer of 1977. However, the drawdown during 1977 was of short duration compared to the drawdown of 1988-92. Based on water levels of nearby wetlands described by Eisenlohr and others (1972), the entire substrate was exposed for the first time since the drought of 1961.

The receding water levels during the spring of 1977 caused an increase in dissolved salt concentrations in the water column, and only salt-tolerant plant species such as prairie bulrush, foxtail barley (*Hordeum jubatum*), hardstem bulrush, and sprangletop germinated on the exposed mudflat (fig. 57A). During the spring of 1977, prior to the wetland becoming dry, specific conductance in the water column of the shallow isolated pools reached 7,700 $\mu S\ cm^{-1}$. Thus, cattail did not germinate in the summer of 1977 prior to complete drawdown. After complete drawdown, the open-water zone that dominated the center of the wetland prior to 1977 was replaced by shallow-marsh vegetation dominated by sprangletop and a few stems of hardstem bulrush (fig. 57B). The shallow-marsh emergents dominated the central vegetated zone of the wetland until 1980 when the sprangletop drowned out in response to persistent high water levels (>1 m) (fig. 57C). Sprangletop cannot tolerate persistent high water for extended periods but can dominate semipermanent wetlands for short periods following reflooding. Thus, although sprangletop in the central zone of Wetland P1 was eliminated after 3 years of high water, the shallow-marsh species continued to dominate the shallow-marsh zone along the shoreline. The central zone of Wetland P1 remained open (fig. 58A), surrounded by the wide band of deep-marsh vegetation that germinated in 1976, until the drawdown of 1988-92.

The drawdown of 1988-92, in contrast to the drawdown of 1976-77, persisted for 4 years, causing Wetland P1 to become dry and water levels to fall below the bottom of the wetland. During 1988-92, precipitation falling on the dry mudflat diluted salts. When the water level fell below the bottom of the wetland, for a short period the basin functioned as a ground-water recharge basin. This change in function reduced dissolved salt concentrations on the exposed mudflat such that specific conductance was 2,180 $\mu S\ cm^{-1}$ in spring of 1992 and allowed cattail to germinate, unlike in 1977 when only salt-tolerant species germinated. As the drought continued, the specific conductance of the water declined in response to the dilution of salts caused by subsequent precipitation (LaBaugh and others, 1996; fig. 34A in Chapter 3 of this report). Salts were not lost to deflation as was observed for some of the saline wetlands in the area that were exposed to wind action because seed germination on the exposed mudflat and the protection by emergent vegetation prevented deflation. The shift in hydrologic function thus reduced dissolved salt concentrations and altered the species structure of the biotic community of Wetland P1. During 1988-92, cattails dominated the central zone of the wetland. Thus, the response of the plant community of Wetland P1 differed between the drawdowns of 1976-77 and 1988-92 because the dynamics of the dissolved salt concentrations differed.

Wetlands P1 and P8 were the last semipermanent wetlands in the Cottonwood Lake area to be dominated by monotypic stands of cattail in the central zone during 1973-92. The cumulative effect of the abundant precipitation that fell from 1993 through 1998 reversed the trend caused by the drawdowns of 1973-74, 1976-77, and 1988-92. Cattail flooded out, and Wetland P1 currently (2002) is dominated by open water (fig. 56C). The water levels observed in 1998 exceeded the water levels observed in the spring of 1967, and Wetland P1 flooded into Wetland T3 for the first time since 1967 (figs. 58B and 55C).

The deep-marsh zone of Wetland P1 usually was dominated by hardstem bulrush and broadleaf and narrowleaf cattail and their hybrid. The shallow-marsh zone was dominated by sprangletop. A variety of annual, biannual, and perennial species germinated on the exposed mudflats during drawdown (Poiani and others, 1996). Prairie bulrush was observed only during drawdown and persisted as viable seed during extended periods of flooding. Plant communities that occupied Wetland P1 and their response to the dynamic water regimes are described by Poiani and others, (1996).

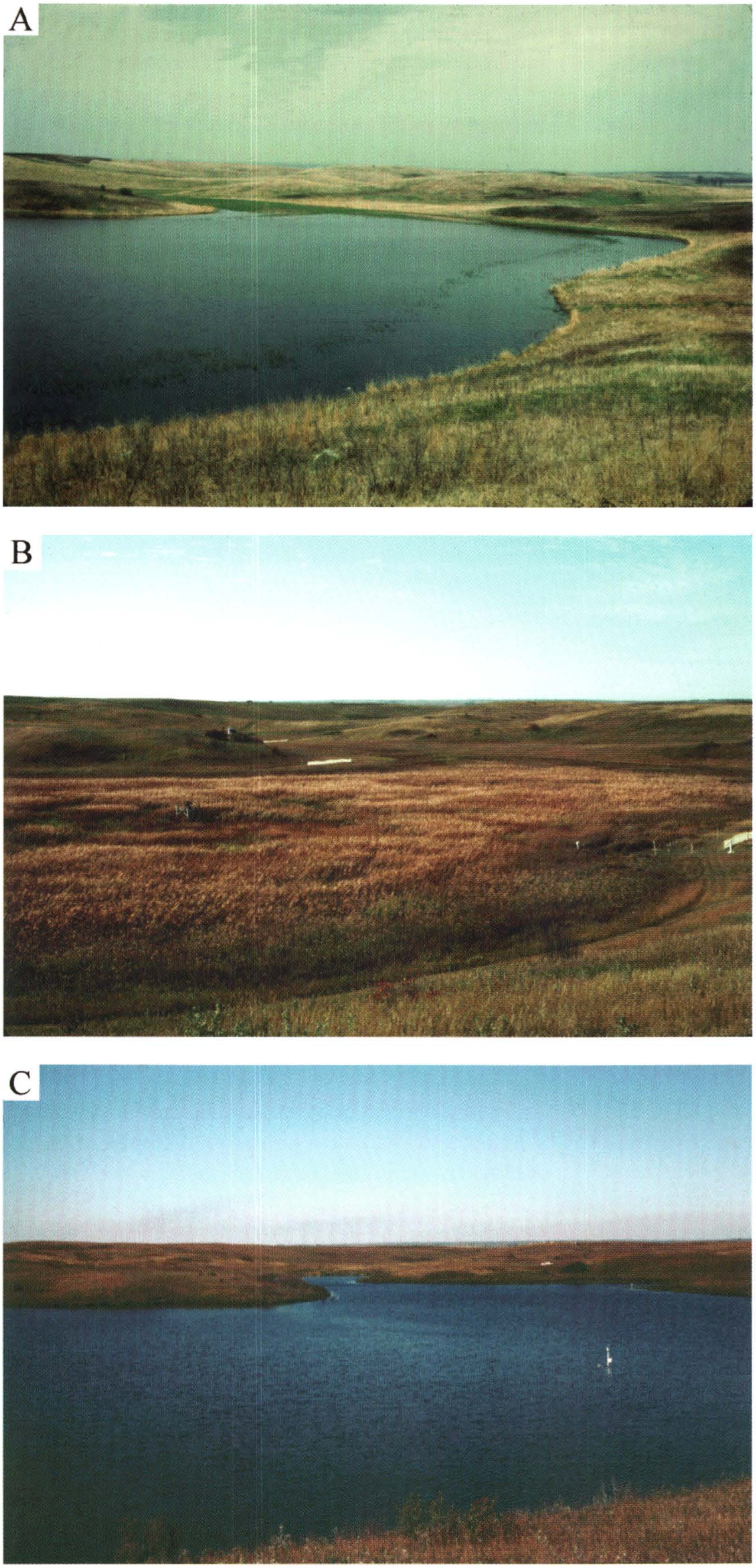


Figure 56. Wetland P1 on June 1, 1967, following a rise in water levels during 1962-1966 (A); Wetland P1 on October 29, 1992, dominated by deep-marsh vegetation following the drought of 1988-92 (B); Wetland P1 on September 25, 1999, dominated by open water following a rise in water level initiated by the deluge of 1993-98 (C).

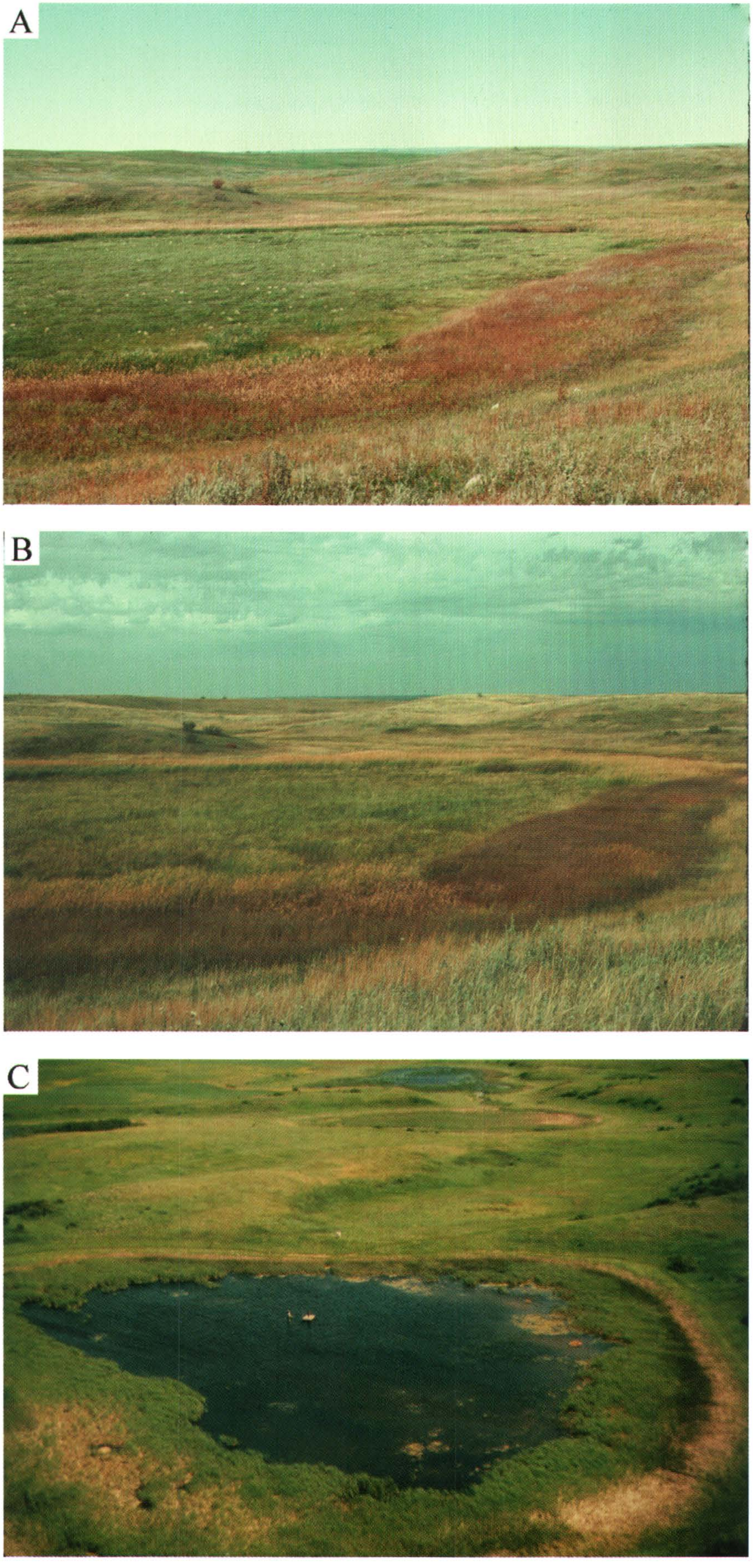


Figure 57. Wetland P1 on September 12, 1977, following drawdown (A); Wetland P1 on September 9, 1978, dominated by shallow-marsh vegetation that germinated on the mudflat inside the deep-marsh zone (B); Wetland P1 on July 1, 1984, following flooding that eliminated shallow-marsh vegetation in the center of the wetland (C). Shallow-marsh vegetation persisted in the seasonally flooded zone shown in the background.

The dominance of sprangletop in the central zone of Wetland P1 following the drought of 1976-77 facilitated the rapid return to open water in the central zone of the wetland because less water is required to drown out sprangletop than to drown out cattail. This is especially true of hybrid cattail, which can tolerate greater water depths than either broadleaf or narrowleaf cattail. Once established, hybrid cattails can develop monotypic stands that persist for extended periods as in Wetland P4 where cattails persisted for 18 years (fig. 53B). Hybrid cattail is relatively new to the prairie pothole region (Kantrud, 1992). The ability of this hybrid to dominate oligosaline wetlands, probably to the detriment of bulrush, appears to have altered aquatic communities throughout much of the prairie pothole region.

During the summer of 1978-79, following the drawdown of 1976-77 and the establishment of shallow-marsh vegetation in the central zone of Wetland P1, a large number of semipermanent wetlands in the vicinity of the Cottonwood Lake area contained a central zone of sprangletop surrounded by bands of cattail and hardstem bulrush. The presence of shallow-marsh plants in the center of semipermanent wetlands surrounded by deep marsh is not common in the prairie pothole region (Stewart and Kantrud, 1972).

Because Wetland P1 lacked a surface outlet, the wetland usually accumulated a large enough volume of water to contain water most years. The lack of a surface outlet also produced a dynamic water regime that influenced dissolved salt concentrations and initiated major changes in the plant and animal communities of the wetland. In response to climatic extremes, the wetland functioned as a ground-water discharge basin, when water persisted in the basin, and a ground-water recharge basin for short periods when the water table dropped below the bottom of the wetland during extended periods of drought (Winter and Rosenberry, 1998). Winter and Rosenberry (1998) attributed some of the water loss from Wetland P1 to transpiration of ground water along the wetland perimeter. As a result of the shift in function, although only for a relatively short period of time, dissolved salt concentrations were altered and a major change in the response of the seed bank to drawdown was initiated. The basin water budget maintained a semipermanent water regime and a biotic community that reflected the hydroperiod and the dissolved salt concentrations of the wetland.

Invertebrates that occupied Wetland P1 are typical of species that occupy oligosaline semipermanent wetlands in the prairie pothole region (Kantrud, Krapu, and Swanson, 1989). Midge larvae (Diptera: Chironomidae) are an important element in the invertebrate fauna of semipermanent prairie wetlands and to diets of waterfowl (Swanson, 1977). The maximum density of chironomid larvae, principally *Chironomus tentans* and *Glyptotendipes paripes*, in Wetland P1 exceeded 140,000 individuals m^{-2} in October 1983 (Nelson, 1989). The invertebrate community of Wetland P1 differed from the invertebrate communities of Wetlands T3 and T8 primarily by the presence of large pond snails *(Lymnaea stagnalis)* and amphipods (*Hyalella azteca* and *Gammarus lacustris)*. As noted for Wetlands T8 and T3, crustaceans (Cladocera and Copepoda) were well represented in the invertebrate community of Wetland P1 (LaBaugh and Swanson, Chapter 3 of this report). Amphipods (scuds) routinely invade wetlands during the summer by clinging to waterfowl and aquatic mammals (Swanson, 1984) but are eliminated annually when seasonal wetlands become dry and during drought in wetlands that have a more permanent water regime. The reflooding of Wetland P1 in 1993 restored the semipermanent water regime, but large numbers of *H. azteca* were not observed until 3 years later. *G. lacustris* did not appear in Wetland P1 until 1998. The large shallow-marsh zone that occupied the northwest bay of Wetland P1 was dominated by sprangletop and supported invertebrate species similar to those in Wetlands T3 and T8.

Tiger salamanders were an important component of the amphibian community of Wetland P1. Boreal chorus frogs, wood frogs (*Rana sylvatica*), and northern leopard frogs also were observed in Wetland P1, but tiger salamanders comprised the largest proportion of the population, especially during wet cycles when the wetland did not undergo significant seasonal drawdowns. Salamanders likely influenced the presence of other amphibians in Wetland P1, especially frogs, since tadpoles are an important salamander food (Lannoo and others, 1994; Lannoo, 1996).

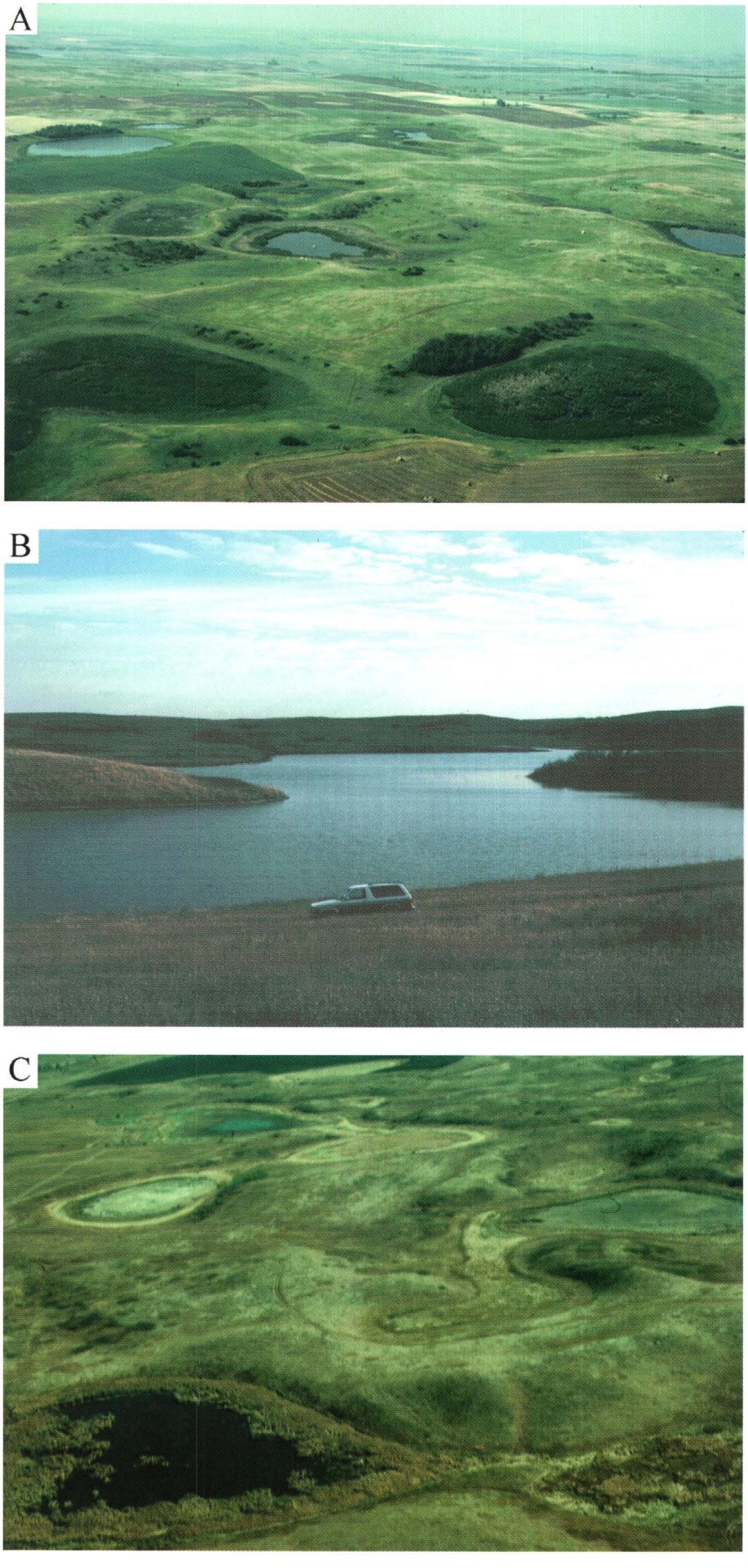


Figure 58. Aerial view looking south toward the Cottonwood Lake area on July 19, 1989, showing Wetlands P4 (lower left), P2 (lower right), and open water in the central zones of Wetlands P1 (center) and P8 (right edge) during the early stage of the drought of 1988-92 (A); Wetland T1 on October 28, 1997, looking east toward Wetland P1 into Wetland T3 located in the background (B); aerial view of the Cottonwood Lake area on October 1, 1976, showing the persistence of open water in Wetland P8 located in the lower left corner (C).

WETLAND P8

Wetland P8 (fig. 58C) differed hydrologically from Wetland P1 in that the storage capacity of the basin was fixed by the elevation of the surface outlet to Wetland P9 (fig. 59A). Runoff from the contributing drainage basin of Wetland P8 and ground-water discharge from the sand deposit in the southern part of the Cottonwood Lake area (Winter, Chapter 1 of this report) exceeded the storage capacity of the basin in most years, causing a high annual turnover of water and solutes in the wetland. This high turnover stabilized water levels and dissolved salt concentrations that, with the exception of extreme drought, were consistently lower than those in Wetland P1 although Wetland P8 is lower in elevation (LaBaugh and others, 1996; fig. 34B in Chapter 3 of this report).

The water levels, dissolved salt concentrations, and plant community of Wetland P8 remained relatively stable for 23 years until the drought of 1988-92 (fig. 59B). The droughts of 1973-74 and 1976-77 had very little effect on the water levels on Wetland P8. By using water levels of the wetlands studied by Eisenlohr and others (1972) as proxies for the water levels in Wetland P8 prior to 1967, the water levels in Wetland P8 probably did not decline appreciably for 27 years until the drought of 1988-92. The stable water levels in Wetland P8 and the associated low dissolved salt concentrations provided ideal conditions for establishing floating mats of cattail. A floating mat dominated the shoreline of the wetland and portions of the mat periodically broke loose and drifted across the basin due to wind action. The central zone of Wetland P8 at maximum water levels exceeded the depth tolerance of hybrid cattail, which was maintained only by the persistent floating mat connected to the shoreline.

The stable water levels and low dissolved salt concentrations of Wetland P8, along with the floating mat of cattail, resemble the hydrologic and chemical characteristics of wetland basins located east of the prairie pothole region in glaciated regions dominated by a moisture surplus. Under the influence of a moisture surplus, contributed volumes of water annually exceed basin storage capacity and water levels rise until stabilized by fixed outlets or substantial seepage to ground water. Floating cattail mats are not common in much of the prairie pothole region because water levels are generally too dynamic to permit their establishment and maintenance. The dynamic water regimes of closed basins in the prairie pothole region periodically drown out cattail that germinates on mudflats during complete drawdown.

During the drought of 1988-92 when Wetland P8 experienced complete drawdown, the cattail mat was stranded on the substrate and the plants responded by rooting in the substrate. High water that followed the deluge of 1993-98 approached the depth tolerance of hybrid cattail rooted in the center of the wetland and the plants began to flood out (fig. 59C.)

The chemical characteristics of Wetland P8 also differed from those of Wetland P1. Wetland P8 was dominated by magnesium bicarbonate water maintained by anaerobic conditions that persisted beneath the floating cattail mat allowing sulfate reduction to remove sulfur from the ground-water inputs (LaBaugh and Swanson, 1992). A major-ion change from magnesium bicarbonate to magnesium sulfate occurred when ground water entered the wetland beyond the stranded cattail mat during the drought of 1988-92.

Wetlands P8 and T3, as stated previously, are open basins having fixed outlets. However, unlike Wetland T3, which contained water only seasonally, Wetland P8 maintained a semipermanent water regime, containing water throughout the year in all but the driest years. The wetlands also differed in depth and in the volume of water stored in each basin. The volume of water stored in Wetland P8 exceeded the annual loss to evapotranspiration whereas the annual loss to evapotranspiration in Wetland T3 exceeded the volume of water stored. As a result, Wetland P8 functioned as a semipermanent wetland dominated by a central zone of deep-marsh vegetation and open water (Stewart and Kantrud, 1971).

The macroinvertebrates found in Wetland P8 were similar to those found in Wetland P1. Snails, *Lymnaea stagnalis* and *Helisoma trivolvis*, were common as were amphipods, *H. azteca* and *G. lacustris*. The *G. lacustris*, however, were more persistent in Wetland P8 than in the other semipermanent wetlands in the Cottonwood Lake area. This persistence reflected the stable water conditions and strong ground-water influence on Wetland P8. *G. lacustris* populations in the prairie pothole region are more common in wetlands having stable water levels caused by ground-water discharge. The drought of 1988-92 eliminated amphipods in Wetland P8, but the

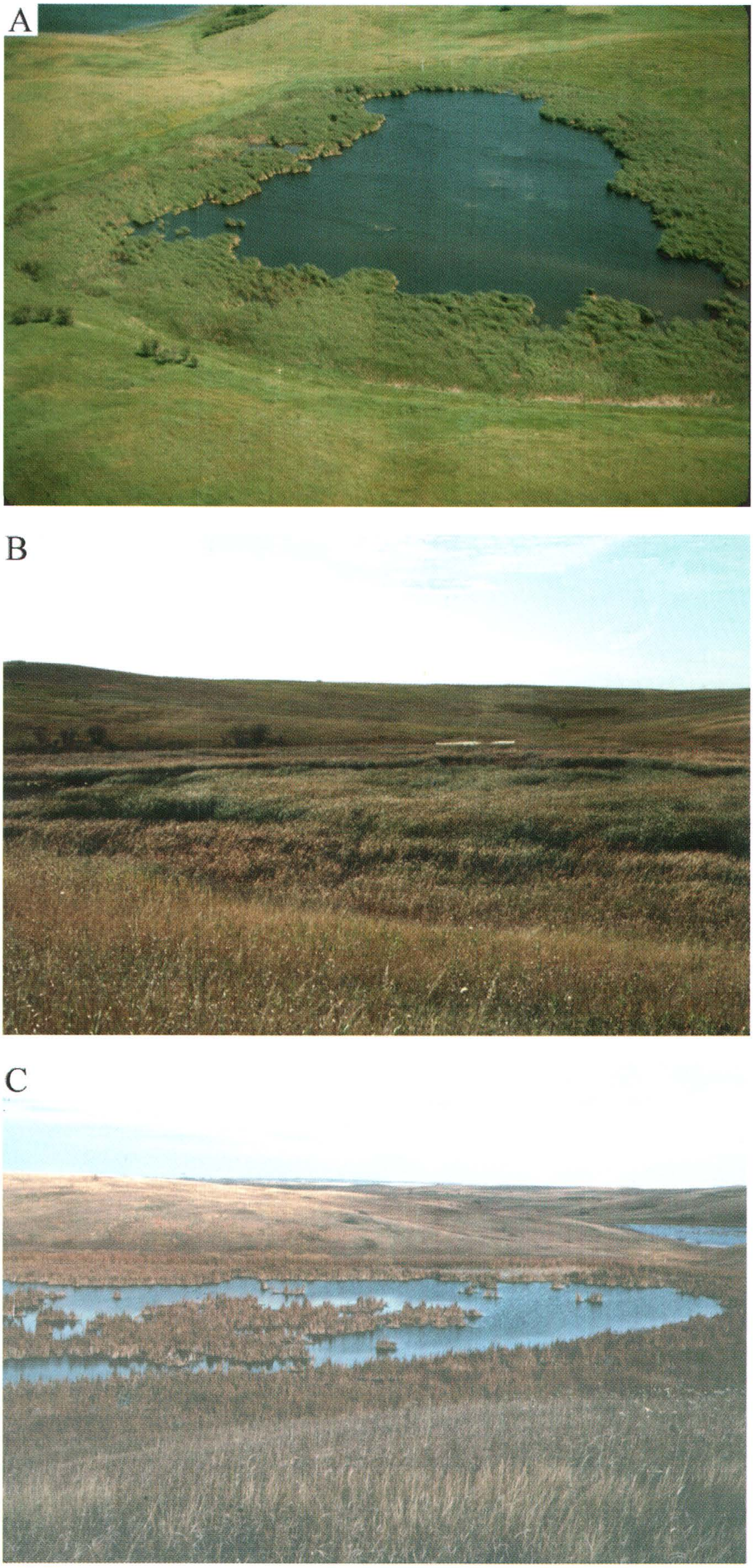


Figure 59. Wetland P8 on July 1, 1981, dominated by an open-water zone surrounded by a mat of floating cattail (A); Wetland P8 on October 29, 1992, dominated by deep-marsh vegetation following drawdown (B); Wetland P8 on October 28, 1997, dominated by deep-marsh vegetation persisting in the central zone following the deluge of 1993-98 (C).

wet period beginning in 1993 fostered the reestablishment of *H. azteca* populations by 1995. *G. lacustris* were not observed through 1997. Future long-term monitoring should provide insight into the recovery period for the *G. lacustris*.

The amphibian community of Wetland P8 also was similar to that of Wetland P1. Tiger salamanders dominated the amphibians captured after 1992 although chorus, wood, and leopard frogs also were present. As mentioned previously, tiger salamanders are effective aquatic predators and likely exert considerable influence on frogs through predation on tadpoles.

WETLAND P11

Wetland P11 (fig. 60A-C) functioned as a ground-water discharge basin and supported plants and invertebrates that tolerate elevated salt concentrations. Based on hydrologic modeling (Winter and Carr, 1980), Wetland P11 probably does not lose water to ground water because the wetland is a discharge area for local and regional ground-water flow systems. The large ratio of surface area to water volume for Wetland P11 results in evapotranspiration being large relative to the volume of water stored in the wetland. Similar hydrologic conditions cause wetlands in the prairie pothole region to have high concentrations of dissolved salts dominated by sodium sulfate (Swanson and others, 1988). Water levels in Wetland P11 remained relatively stable until the drought of 1988-92 when the wetland became dry. With the return of water in 1993-98, the basin was dominated by an open-water pool that flooded into the adjacent upland. Dissolved salt concentrations were greatly reduced by dilution and by the removal of salts by deflation during the drawdown of 1988-92 (LaBaugh and others, 1996; fig. 34C in Chapter 3 of this report).

The central zone of Wetland P11 was never dominated by emergent vegetation. Emergent vegetation that did occupy Wetland P11 was dominated by prairie bulrush that established along the shoreline where salt concentrations were favorable and the water depth did not exceed the depth tolerance for bulrush. Spring seeps in topographically low, highly saline hydrologic sumps such as Wetland P11 are consistently lower in dissolved salts than in the lake water (Swanson and others, 1988). Seeps along the shoreline of Wetland P11 supported cattail, hardstem bulrush, and common reed (*Phragmites australis*), plants that could not tolerate the salt concentrations in the lake proper. Clumps of hardstem bulrush and cattail have been observed in the center of saline lakes where ground-water discharge lower in dissolved salts enters the lake proper (Swanson and others, 1988). Broadleaf cattail is less tolerant of elevated salt concentrations than narrowleaf cattail or their hybrid (Stewart and Kantrud 1972).

When Wetland P11 was dry during 1988-92, exposed salt crystals (fig. 60B) that concentrated in the dry basin were removed by wind action and deposited in the upland (fig. 60C). A portion of the windblown salt, however, appeared to have blown beyond the drainage basin of Wetland P11. The flooded open-water zone was dominated by sago pondweed, a submerged vascular plant that can tolerate elevated salt levels. When the wetland was dry, it remained free of plants with the exception of saltwort (*Salicornia rubra*), a salt-tolerant species that invades exposed salt flats.

Invertebrates that inhabited Wetland P11 were dominated by microcrustacea and fairy shrimp common in wetlands of intermediate salt content (5 to 15,000 $\mu S\ cm^{-1}$). During 1967-87, the salinity of Wetland P11 was consistently greater than the salinity of other semipermanent wetlands located higher in the landscape, and Wetland P11 was the only wetland in which sodium was the most abundant cation. Sago pondweed that dominated the open water of Wetland P11 was attractive to fall migrating canvasbacks (*Aythya valisineria*) and tundra swans (*Cygnus columbianus*) (fig. 60A), which were never observed on other semipermanent wetlands in the Cottonwood Lake area.

An interesting pattern in the composition of the invertebrate community of Wetland P11 was observed when the basin refilled following the 1988-92 drought. Prior to the flood of 1993, nearly 80 percent of the invertebrate fauna was represented by fairy shrimp. When the wetland flooded, the community shifted to one dominated by other crustaceans (Cladocera and Copepoda) and then gradually shifted to one dominated by the amphipod *H. azteca*. In 1997, the amphipod *G. lacustris* was observed in Wetland P11 for the first time following the 1993 flood, and future increases in this species are anticipated as the wetland increases in permanence.

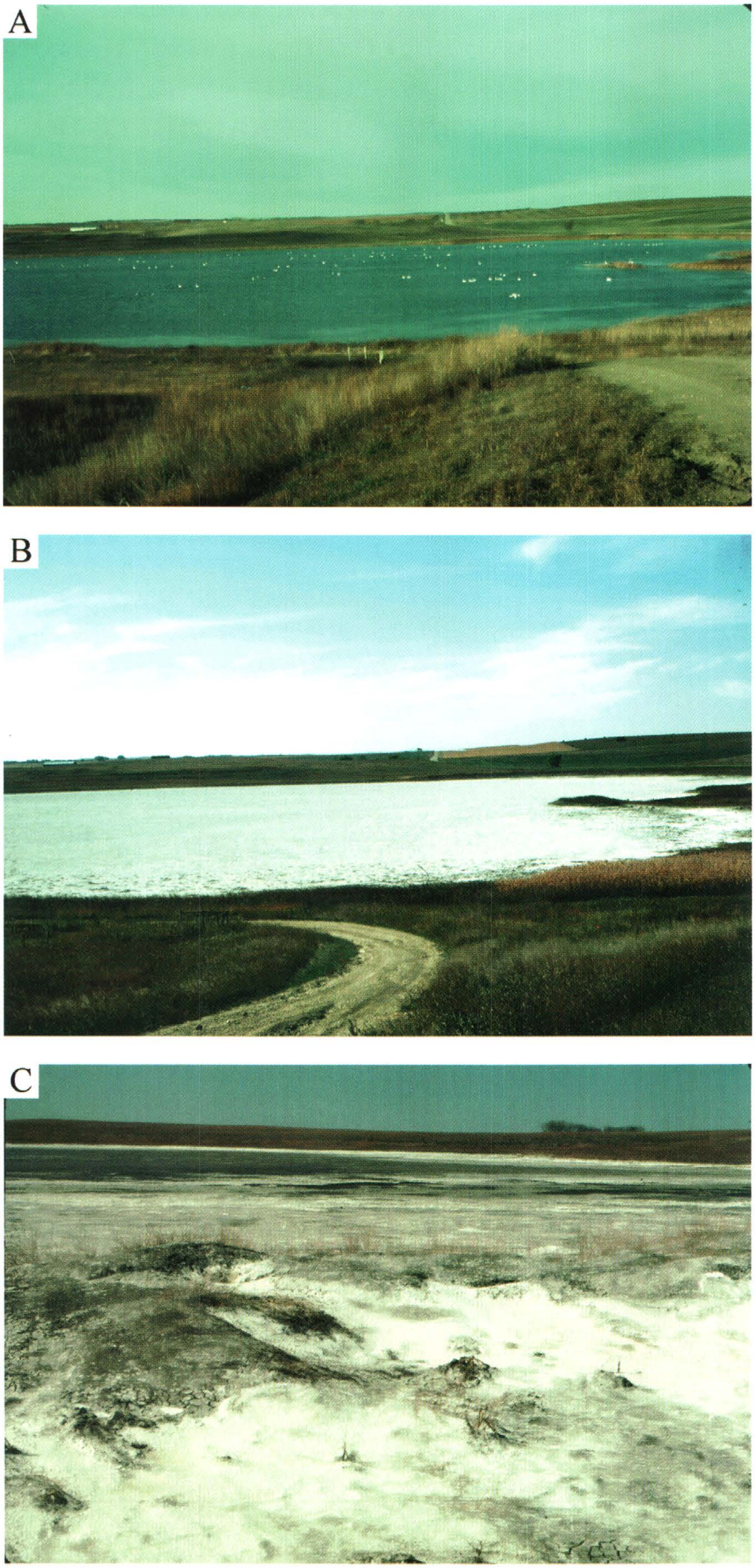


Figure 60. Wetland P11 on October 11, 1985, visited by tundra swan that feed on sago pondweed tubers (A); Wetland P11 on October 1, 1990, during drawdown that exposed salt crystals (B); Wetland P11 on June 10, 1991, during drawdown (C). Windrows of salt crystals that were blown from the basin and deposited in the upland southeast of the basin are shown.

The amphibian community of Wetland P11 also reflected the influence of wetland function on dissolved salt concentrations. In 1992, an amphibian community was not detected in Wetland P11; in fact, no amphibians were found in the wetland despite an intensive effort to document their presence prior to the 1993 flood. When Wetland P11 flooded, the reduced salt concentrations resulted in the solute concentration changing to one fiftieth of what it had been just prior to the wetland becoming completely dry in 1992, and amphibians recolonized the wetland. In contrast to the other wetlands in the Cottonwood Lake area, however, Wetland P11 was immediately recolonized by tiger salamanders and animals were found in 1993 immediately after the wetland flooded. The tiger salamander population exploded in subsequent years and reached a major peak in 1996. Interestingly, though, most of the animals captured from 1994 through 1996 were large larvae (neonates) that did not metamorphose into their terrestrial form. The large invertebrate community of Wetland P11 may have affected the physiological response of the tiger salamander and caused the animal to remain in the neonate form. In 1997, the salamander population in Wetland P11 declined substantially, the total number of trapped animals decreased more than 83 percent; at the same time, invertebrate abundance decreased by about 72 percent. The decline in invertebrates and in tiger salamanders in Wetland P11 may be related to the reduced availability of vegetative litter, which provides important substrates for production of algae that provides a forage base for invertebrates (Euliss and others, 1999). With the exception of chorus frogs, all other amphibians found in wetlands in the Cottonwood Lake area were also found in Wetland P11. Chorus frogs were abundant in Wetland P11 only in 1996 following several years of very high water levels that coincided with relatively low specific conductance.

HYDROLOGICAL, CHEMICAL, AND BIOLOGICAL INTERACTIONS IN A WETLAND COMPLEX AND THE BROADER PRAIRIE POTHOLE REGION

SPATIAL RELATIONS

Biodiversity within the Cottonwood Lake area, and within the prairie pothole region in general, can be attributed to differences in basin topographic settings and to wetland basin interaction with ground water, which determines the general salinity of the wetlands. Chemical gradients across the wetland complex of the Cottonwood Lake area tracked hydraulic gradients forming the framework for biological diversity. Wetlands located in topographically high areas were seasonally flooded. Some of these wetlands received discharge from local ground-water flow systems, while others functioned as ground-water recharge basins, and contained surface water low in dissolved salts dominated by potassium and calcium bicarbonate. Wetlands located at intermediate altitudes in the landscape were seasonally or semipermanently flooded. Some of these wetlands received discharge from local ground-water flow systems and others functioned as ground-water flow-through systems. Wetlands of this type contained moderate levels of dissolved salts dominated by magnesium bicarbonate and magnesium sulfate. Wetlands located in topographically low areas were semipermanently flooded and functioned as ground-water discharge basins, losing water primarily to the atmosphere. Ground-water discharge basins contained elevated levels of dissolved salts dominated by sodium sulfate. Although salt gradients that occur among closed basins within a wetland complex reflect landscape features, open basins that discharge surface water are exceptions.

As dissolved salt concentrations increase or decrease in response to hydrologic setting, the composition of the plant and animal communities that occupy each basin shifts. As salt concentrations increase, they may exceed the tolerance of salt-resistant emergent species such as prairie bulrush; such basins often are dominated by barren shorelines and open water with submerged vascular plants such as widgeon grass (*Ruppia maritima*) (Stewart and Kantrud, 1971). Brine shrimp (*Artemia salina*) and widgeon grass occupy basins in which specific conductance approaches 35,000 µS cm^{-1} in south-central North Dakota (Swanson and others, 1988). The differences in major-ion structure and dissolved salt concentrations for the wetlands accounted for the trends in plant communities observed in Minnesota by Moyle (1945) and in North Dakota by Stewart and Kantrud (1972). Stewart and Kantrud (1971) used specific conductance to develop subclasses in their classification of prairie wetlands and demonstrated that plant-species structure in prairie wetlands is a function of specific conductance, which is an index of dissolved salt concentration.

Biodiversity within a wetland complex also is influenced by variations in the hydroperiod (water permanence), which was used by Stewart and Kantrud (1971) to classify prairie wetlands. The hydroperiod structure (the ratio of temporary, seasonal, and semipermanent wetlands within a glacial landform) of basins that comprise a wetland complex differs between the drift prairie, which has a preponderance of temporary and seasonal wetlands; the Missouri Coteau, which has a greater number of semipermanent wetlands; and glacial outwash plains, which have a large number of shallow saline wetlands. The composition of wetland classes has a major influence on the distribution of waterfowl during the breeding season, which changes seasonally and annually in response to changing climatic conditions that fill or desiccate temporary and seasonal wetlands.

TEMPORAL RELATIONS -- RESPONSE TO CLIMATE EXTREMES

The dynamics of the aquatic communities that occupied wetland basins in the Cottonwood Lake area during the study period were driven by climate events that initiated partial or complete drawdown and subsequent flooding of the wetland basins. As the climate cycled between drought and deluge, several climate events contributed to rapid rises in water levels and subsequent changes in plant-community structures in closed basins in the study area. The record snowpacks during March 1966 and during the winter of 1996-97 and the deluge of July 1993 caused rapid rises in water levels in response to surface runoff. Periods of rising water (1962-66 and 1993-98) in the Cottonwood Lake area caused closed-basin semipermanent wetlands to drown emergent vegetation and to shift the plant community to one dominated by submerged vascular plants and planktonic algae. Eventually, a narrow, concentric band of deep-marsh and shallow-marsh species dominated the newly established shorelines.

Partial or complete drawdown during periods of drought exposed basin substrates during the growing season. The plant-community composition on the newly exposed substrates reflected the species structure of the seed bank of each substrate (Stewart and Kantrud, 1971; Weller, 1978; van der Valk, 1981; Weller, 1981; Kantrud, Krapu, and Swanson, 1989; Kantrud, Millar, and van der Valk, 1989; Poiani and Johnson, 1989; Poiani and others, 1996). Annuals dominated during the first year of drawdown, with species structure determined by the salt content of the substrate (Stewart and Kantrud, 1971). Perennials eventually dominated the substrates, usually in 2 to 3 years following the initial exposure of the mudflats. The emergent species structure was determined by the timeframe of the drawdown, which influenced salinity, and the water depth that prevailed following reflooding of the basin.

The plant-community response to the impact of drought on basin interaction with ground water varied with the duration of the drought. Droughts of short duration concentrated salts and allowed salt-tolerant plants to germinate and eventually dominate the plant community; seeds of salt-tolerant species germinated in oligosaline wetlands during drawdown, when specific conductance in the water column approached 7,700 µS cm^{-1}. In contrast, extended periods of drought caused the water levels to fall below the bottoms of the wetlands (Winter and Rosenberry, 1998), and permitted seasonal precipitation to dilute salts (LaBaugh and others, 1996) that accumulated in the basins during drawdown. When the water levels dropped below the bottoms of semipermanent wetlands, the functions of the basins shifted from a ground-water flow-through or ground-water discharge to ground-water recharge. The reduction in salt concentration altered the dominant emergent plant community and, subsequently, the water depth and time required to drown out emergent vegetation and reopen the wetlands. Once the central zone of the closed semipermanent wetlands was dominated by cattail, the cattail persisted until rising water during the deluge of 1993-98 exceeded the depth tolerance of hybrid cattail, the most persistent of the cattail species. When the central zone was dominated by sprangletop, a shallow-marsh species, wetlands reopened in 4 years at a depth that would not have drowned out hybrid cattail. The frequency of change in wetland function, in response to trends in water levels initiated by climate extremes, appears to account for most of the variation in the major-ion structure and dissolved salt concentrations among the closed wetland basins. Sloan (1972) reported that the salt concentrations in the wetlands are a function of the net loss of water to surface and ground water. The dissolved salt concentrations were altered by (1) precipitation that fell on dry exposed substrates, moving the salts into the substrate; (2) deflation when dry basins were exposed to wind action that blew salts out of the basin; and (3) deluge, which diluted the salts.

The extreme change in climate that occurred between the dry period of 1988-92 and the wet period of 1993-98 also caused a major shift in the limnological characteristics of eusaline, polysaline and mesosaline wetlands. This major shift, in turn, caused major changes in the flora and fauna in the wetlands. Closed basins previously dominated by sago pondweed, widgeon grass, and brine shrimp (Swanson and others, 1988) decreased in salinity in response to increases in the volume of water and became dominated by fresher-water flora and fauna. Some of the closed saline lakes that were less than 1 m deep or dry in 1992 currently (2002) contain 5-7 m of water and support fish. The loss of salt-tolerant species caused migrating waterfowl that normally concentrate on saline wetlands during fall migration to avoid the wetlands because the abundant, highly preferred foods these wetlands produce during drier periods were no longer present or abundantly available. The impact of the loss of preferred foods on the physiological condition of waterfowl during migration is unknown. Some of the closed wetlands shifted to open systems in response to the deluge of 1993-98 and subsequently exported previously stored dissolved salts.

Ground water that enters wetland basins contributes dissolved salts to closed basins and ground water that leaves wetland basins by surface flow or ground-water recharge removes dissolved salts from the basins. Precipitation that falls directly on a wetland basin contributes fewer salts per unit volume than runoff from surface flow or ground-water discharge. Water that travels through glacial till contributes more dissolved salts per unit volume than water from other sources. Surface outflow is more efficient than ground-water recharge in transporting dissolved salts because the clay content of glacial till reduces permeability and retards flow (Swanson, 1990). Sand deposits and fractures in the till, however, can expedite the flow of water and the movement of the dissolved salts (Winter, Chapter 1 of this report).

The large volume of water lost to evapotranspiration also affects major-ion concentrations within the water column of wetlands. Salts that are least soluble precipitate as dissolved salt concentrations increase, leaving the most soluble salts to dominate the water column. Wetlands in the prairie pothole region of south-central North Dakota that retain the highest dissolved salt concentrations usually are dominated by sodium sulfate (Swanson and others, 1988). Large shallow basins that are high in dissolved salt concentrations ($> 30,000\ \mu S\ cm^{-1}$) generally do not support emergent vegetation and subsequently lose salts by wind deflation when substrates are exposed during drought (Swanson and others, 1988).

The response of open semipermanent wetlands in the Cottonwood Lake area to climate extremes differed from that of closed basins in the area. The storage capacity of the open basins was limited because the basins spilled when the water level rose above the elevation of the surface outlet. The surface outflows reduced the variability in water level, lowered the dissolved salt concentrations, and promoted the growth of floating cattail mats in the semipermanent wetlands. The floating cattail mats were affected only when extreme drought stranded the mats on the bottoms of the wetlands and allowed the mats to root into the dry substrate; subsequent reflooding drowned the stranded cattail mats rooted in the substrate and reopened the vegetation canopy as described for the closed basins. The dynamic water regimes of the prairie pothole region prevent the dominance of wetlands by floating mats of vegetation common to areas of moisture surplus where wetland water levels are relatively stable and dissolved salts are diluted. Hence, flooding that drowned emergent vegetation in the closed basins had less impact in the open basins.

Open wetland basins that periodically overflow (for example, Wetland P8) export salts. The salt content varies as a function of the time required to replace the volume of water stored in the basin with an equal volume of precipitation, runoff, and ground-water discharge (turnover rate). As turnover rates increase, the dissolved salt concentration in the water column can be expected to approach the concentration of the dominant contributing water source. The dominant water source will vary, however, with climatic conditions that alter the ratio of runoff to ground-water discharge.

Wetlands in the Cottonwood Lake area that stored less water than lost by seepage and evapotranspiration dried up each summer and functioned as seasonal wetlands. Seasonal wetlands that functioned as ground-water flow-through basins had higher dissolved salt concentrations and were dominated by different salt and plant species than wetlands that functioned primarily as ground-water recharge basins. The biological communities of the seasonal wetlands reflected salt concentrations that varied in relation to each wetland's position in the ground-water flow system and its exchange with atmospheric water.

Some seasonal wetlands in the prairie pothole region were not affected by a fixed outlet. These wetlands (for example, Wetland T9) occupied closed basins and routinely stored a volume of water that was greater than what was lost to evapotranspiration and ground-water recharge. Wetlands of this type are highly dynamic compared to seasonal wetlands maintained by a fixed outlet and, during periods of above-average precipitation, may shift to a water regime often resembling that of semipermanent wetlands. When this occurs, the central zone of the wetland shifts from having a dominance of shallow-marsh species to having a dominance of deep-marsh species, and the wetland classification changes from seasonal to semipermanent. Other seasonal wetlands that were maintained by fixed outlets, but that held water longer into the summer and fall during wet periods, were dominated by deep-marsh species such as bulrush and cattail. During periods of drought when the seasonal wetlands were dry during the growing season, the trend reversed with plants normally occupying low-prairie and wet-meadow zones (Stewart and Kantrud, 1971) colonizing the wetlands.

The dynamic nature of wetlands in the Cottonwood Lake area excludes species of vertebrates and invertebrates that cannot tolerate periodic desiccation. Wetland aquatic invertebrates that are periodically eliminated from the wetlands during extended periods of drought use a number of methods to recolonize following seasonal or annual drawdowns induced by droughts. However, the recolonization of the wetlands by flying insects capable of rapidly recolonizing temporary and seasonal wetlands following normal seasonal drawdowns may be much slower following extended periods of drought because fewer flooded wetlands are available to provide refugia for the recolonizing stocks (Swanson, 1984). A few permanent lakes in and near the Cottonwood Lake area retain water during periods of severe drought but most have high dissolved salt concentrations and support a fauna that is salt tolerant and may not be physiologically capable of colonizing freshwater habitat (Swanson and others, 1984). George Lake (Salt Lake), located northwest of Streeter, North Dakota, in Kidder County, exceeds 33 m in depth and its water has a conductivity of 20,000 $\mu S\ cm^{-1}$ (Swanson and others, 1988). This lake supports Copepoda, Odonates, and Coleoptera but is devoid of fish and most freshwater invertebrates.

Flightless invertebrates face even greater challenges when recolonizing freshly flooded wetlands. Common recolonization mechanisms include eggs and cysts resistant to drying and freezing, diapause, aestivation, waterproof secretions, epiphragms (snails), burrowing, and passive dispersal. Passive dispersal mechanisms include wind (Pennak, 1989), the digestive tracts of birds (Proctor, 1964, Proctor and others, 1967), and clinging to more mobile fauna (Swanson, 1984). Ostracods and clams have been observed clinging to migrating Hemiptera and Coleoptera (Fryer, 1974), and amphipods can be carried in the feathers of waterfowl (Segerstråle, 1954; Rosine, 1956; Swanson, 1984). Peck (1975) observed *H. azteca* and *G. lacustris* on the fur of muskrat (*Ondatra zibethicus*) and beaver (*Castor canadensis*). However, the drainage of wetlands increases the distance between wetlands that contain water and may disrupt transporting mechanisms or delay introductions.

Fish and decapods were never found in wetlands in the Cottonwood Lake area, but leopard frogs, chorus frogs, wood frogs, and tiger salamanders were abundant, especially during periods of high water. Although several species of toads were found in the area (Wheeler and Wheeler, 1966), toads were not seen from 1967 through 1991 or from 1992 through 1997 despite an intensive trapping program for amphibians on each wetland in the area. Only one western painted turtle (*Chrysemys picta belli*), approximately 15 cm in length, was found during 32 years of observations in the area. The turtle was observed north of Wetland P1 during July 1985 and was moving toward Wetland P2. Although absent from the Cottonwood Lake area, fish, decapods, and turtles were commonly found in the Pipestem Creek area, located 12.9 km to the east of the study area.

Muskrats were common in the Cottonwood Lake area during periods of high water but were absent during extreme drought when all basins in the area were dry. During the drought of 1988-92, all wetlands in the vicinity of the Cottonwood Lake area were dry most of the time, but muskrats likely survived the drought in a few permanent lakes located in the Missouri Coteau and in the James River and Pipestem Creek located east of the Missouri Coteau. When water returned to the wetlands during 1993-98, muskrats repopulated the Cottonwood Lake area, but the high water eventually removed most of the deep-marsh vegetation that is attractive to muskrats and their populations are currently declining. Due to the lack of emergent vegetation in semipermanent wetlands during periods of high water (1962-67 and 1993-98), winter denning by muskrats was restricted primarily to bank burrows. During 1974-87, the Cottonwood Lake area was attractive to muskrats because cattail dominated during drawdown and some of the basins contained sufficient water depth to support a wintering population. Mink (*Mustela vison*), in general, followed the pattern of use described for muskrats but were less dependent on water depth for winter survival.

With the exception of the ubiquitous tiger salamander, aquatic predators (for example, fish) were absent from wetlands in the Cottonwood Lake area. The area is a habitat for breeding waterfowl, and abundant invertebrate populations in the shallow waters are readily available for waterfowl food. Breeding pairs and hens with broods have been observed to concentrate on wetlands that support an abundant invertebrate population and will feed at night to take advantage of this food source (Swanson and Sargeant, 1972).

IMPLICATIONS FOR WETLAND MANAGEMENT

BIODIVERSITY AND PRODUCTIVITY

Wetlands can be managed through water-level manipulations, preservation policies that maintain wetland-complex integrity, and restoration technology. Wetland vegetation also has been manipulated by chemical and mechanical methods and through grazing and burning designed to open wetlands dominated by dense stands of emergent vegetation. Dense monotypic stands of cattail, for example, discourage use of a wetland by waterfowl and encourage use by roosting blackbirds that depredate sunflowers (Weller, 1981; Kantrud, 1986). Knowledge of the physical factors that determine biodiversity and productivity in wetland complexes is needed to develop wetland-management strategies. Landscape features, together with prevailing climate conditions, determine the biotic communities that occupy a prairie pothole wetland complex. Landscape position and climate determine the hydrologic functions of the individual wetlands within a complex, including their hydroperiods, their water chemistry, and the composition of wetland classes and subclasses within the complex. A wide variety of wetland types, in turn, determines the spectrum of aquatic plant and invertebrate communities that are available to attract and support a variety of wildlife species.

The moisture deficit characteristic of the climate in the prairie pothole region in North Dakota maintains an abundance of temporary and seasonal wetlands and nonintegrated (closed) semipermanent wetlands and lakes. The wet-meadow and shallow-marsh species that dominate the temporary and seasonal wetlands and the dynamic species structure of the semipermanent wetlands, which is related to salt gradients, provide the basic framework for the biodiversity and productivity of wetland complexes in the prairie pothole region. Preserving and restoring wetland complexes that are capable of maximizing biodiversity in the prairie pothole region requires knowledge of the landscape ecology and the response of biotic communities to the hydrologic and chemical gradients that are related to the landscape features.

Glaciated landscapes, dominated by abundant, heterogeneous depressions, set the stage for dynamic wetland complexes that are biologically diverse and highly productive under the influence of a semiarid climate. Wetlands that have seasonal flooding of emergent vegetation (wet-meadow, shallow-marsh, and occasionally terrestrial vegetation) each spring produce abundant invertebrate populations that respond to the shallow, warm water rich in decomposing organic matter. Semipermanent wetlands cycle between periods of flooding and desiccation in response to climate extremes and periodically produce abundant invertebrate populations that respond to flooded, decomposing, emergent vegetation. The decomposing vegetation and subsequent release of nutrients in the wetlands attracts and supports invertebrates for years following inundation. Wetland complexes composed of a balance of temporary, seasonal, and semipermanent wetlands (Stewart and Kantrud, 1971) provide ideal habitats for breeding waterfowl because the temporary and seasonal wetlands provide pair habitat and the semipermanent wetlands provide renesting and brood rearing habitat. Temporarily and seasonally flooded zones in the semipermanent wetlands provide plant and animal communities similar to those provided by the temporary and seasonal wetlands, but the zones in the semipermanent wetlands are very transient and they respond to the dynamic water levels caused by climate variations.

The dynamic water regimes characteristic of midcontinent climate cycles routinely recycle wetland communities from drawdown to prolonged flooding; such regimes produce biological communities that are highly productive and similar to those of newly flooded reservoirs (Euliss and others, 1999). Prolonged inundation decreases the availability of plant nutrients, whereas oxidative processes that accompany drawdowns facilitate nutrient release and ultimately foster the development of plant communities that make significant contributions to the nutrient and detritus pool upon reflooding. The sharp increase in wetland productivity when wetlands reflood following a dry phase is the basis for artificially flooding and draining wetlands to enhance waterfowl populations (Cook and Powers, 1958; Kadlec and Smith, 1992) and for the modern-day practice of moist soil management (Fredrickson and Taylor 1982). The basic underpinnings of the water regimes of prairie wetlands relate to nutrient releases from the aerobic decomposition of accumulated macrophyte litter by terrestrial hyphomycetes (Bärlocher and others, 1978). The water regimes of prairie wetlands differ from those of reservoirs, however, in that the climate-driven cycles for the wetlands are routinely repeated, rather than being a single event such as the initial filling of reservoirs (Jenkins, 1961).

WETLAND PRESERVATION AND RESTORATION

The most effective management approach for maintaining biodiversity in the prairie pothole region is to preserve and restore wetland complexes that have been degraded or drained. Wetland-preservation strategies should consider wetland complexes as a whole and need to focus on the important wetlands that cannot be created because of their complex hydrology. Wetland-preservation strategies need to also consider processes that degrade wetlands and have the potential to eliminate wetland basins. Wetland-complex degradation can take many forms, some of which are subtle and disguised by extended timeframes. Deposition of wind borne and water borne silt in wetlands, for example, is a subtle accumulative process that is disguised each spring as vegetative growth resumes. Selective removal of wetland types that comprise a wetland complex, such as the removal (draining) of seasonal wetlands, will alter the hydrology of a complex by removing groundwater recharge basins from the complex. Diverted water then will concentrate in the remaining basins in the watershed and potentially influence biodiversity by converting the closed basins to integrated open systems as the basins respond to increases in the volume of water stored. This process has the potential for converting closed basins that cycle between open water and drawdown to open basins that stabilize water levels, trapping waterborne silt and subsequently promoting a dominance of hybrid cattail that responds to silted basins of decreased depth. As depth decreases in response to silt deposition, the hybrid cattail can no longer be eliminated by flooding if the maximum pool elevation is fixed by a surface outlet. Cattail-dominated wetlands are common in the drift prairie where open basins have been exposed to silt deposition for extended periods (Swanson, 1992). In wetlands that have lost storage capacity from silt deposition, cattail can only be eliminated naturally for short periods during severe drought. The relatively recent appearance of hybrid cattail in the prairie pothole region (Kantrud, 1992) has tempered the impact that a rise in water levels can have on dense monotypic stands of emergent vegetation dominated by cattail; the hybrid cattail tolerates greater depths and salt concentrations than the broadleaf cattail (Stewart and Kantrud, 1971).

To maintain biodiversity in the prairie pothole region, wetland-restoration programs are essential for wetland complexes that have been degraded or drained. Ground-water flow-through basins that are drained, for example, continue to receive ground-water discharge that subsequently evaporates and deposits salts. These drained flow-through basins are prime candidates for restoration because they are not productive of agricultural crops due to saturated soils and high dissolved salt concentrations. Drained ground-water recharge basins, however, are productive of agricultural crops, and special incentives will be required to restore those wetlands. When restored, both types of wetlands provide prime wildlife habitat; thus, their restoration is essential to the goal of targeting wetland complexes with restoration programs.

Management techniques that are capable of manipulating water levels and dissolved salt concentrations have great potential for restoring prairie wetlands. Through water-level manipulations, natural drawdown and flooding cycles that make prairie wetlands so productive can be duplicated. By installing control structures in restored wetlands, water can be cycled between extremes in a short timeframe, with less dependence on prevailing climate conditions, providing adequate water supplies are available. Drawdown and reflooding (for example, moist soil management; Fredrickson and Taylor, 1982) can be used to expose mudflats to germinate prolific seed-producing plants in the wetlands.

Although controlled drawdowns have been used extensively to produce plants that are attractive to waterfowl, water-level manipulations designed to benefit invertebrate communities and increase production of aquatic invertebrates, such as midges (Chironomidae) and Cladocera, that are attractive to waterfowl (Swanson, 1977; Euliss and Grodhaus, 1987) have not been fully utilized. As water levels increase in closed seasonal wetlands during wet periods, emergent vegetation drown and populations of midges and other invertebrates increase. When precipitation declines, shorter seasonal hydroperiods return and receding water levels result in invertebrates concentrating in the shrinking pools of water. Waterfowl and shorebirds respond to the concentrated, high-protein, food resources provided by the invertebrates by foraging heavily in the shallow wetlands. Swanson (1977) observed breeding pairs and hens with broods responding to dense populations of midges produced in recently flooded wetlands, barnyard ponds, waste-stabilization ponds, and recently flooded impoundments.

Drawdown also can be used to increase the availability of benthic midge larvae to breeding and migrating waterfowl by concentrating the larvae in shallow waters (Swanson and Meyer, 1977). During emergence, midges concentrate on the water surface, and hens with broods have been observed feeding at night on the abundant, highly available, food (Swanson and Sargeant, 1972). Breeding pairs also have been observed foraging heavily at night on the emerging midges in the prairie wetlands.

A variety of wetland classes can be duplicated with restoration programs if adequate water supplies are available. However, the ability to manage dissolved salt concentrations through water manipulation, is limited because salts are routinely exported in the water discharged to achieve drawdown. Thus, to maintain the high dissolved salt concentrations required by plant and animal species, such as widgeon grass and brine shrimp, that are attractive to waterfowl, (Swanson and others, 1984), restored wetlands can be allowed to draw down and concentrate salts through evapotranspiration.

If adequate water control is possible, restored wetlands have the potential for duplicating many of the aquatic communities observed to benefit waterfowl in the prairie wetlands. However, water-control structures very often have design limitations that prevent complete drawdown, and many structures are designed to deeply flood wetlands to eliminate persistent emergent deep-marsh plants. Research on the relation between waterfowl, water control, and prairie wetland ecology will provide insight into the hydrological, chemical, and biological conditions that produce optimal waterfowl habitat.

WATERFOWL

The advantage of a wetland complex to waterfowl is that each basin is unique hydrologically and chemically and the basins respond to climatic trends somewhat differently over time. Waterfowl exploit the abundant high-protein invertebrate foods that are produced in the prairie wetlands (Swanson and Duebbert, 1989), and temporary and seasonal wetlands contribute to the biological diversity of the wetland complexes and play an important role in the ecology of migrating and breeding waterfowl. Because breeding waterfowl require isolation to maximize body mass and reduce intraspecific strife, paired birds vigorously compete for optimal habitat and can expend significant body energy spacing themselves from other pairs of the same species. The lost body energy reduces the amount of energy available for egg production. During the breeding season, paired drakes routinely chase paired hens to remove competing pairs from the feeding sites and to provide ample space among breeding pairs for courtship. Breeding hens require access to readily available high-protein food resources to support egg development and have been observed to successfully complete five clutches of eggs, after previous nests have been destroyed, provided the food resources are available.

Temporary and seasonal wetlands that produce abundant invertebrate populations early in the spring provide an ideal habitat for breeding waterfowl, especially for dabbling ducks that are restricted to feeding on or near the water surface or in shallow water. Diving ducks can effectively feed in the deeper waters of semipermanent wetlands but also use seasonal wetlands during spring migration. The semipermanent wetlands provide an ideal habitat for breeding birds as the breeding season progresses and are especially valuable once the seasonal wetlands become dry and emerging insects become more available in the semipermanent wetlands. Semipermanent wetlands also provide habitat for waterfowl broods and often provide the only midseason habitat available for brood rearing. The wetlands provide the high-protein foods needed by broods during early development and by molting ducks after the breeding season to support feather development. Some waterfowl species also require high-protein foods to develop stored reserves required for fall migration. Occasionally, fall precipitation will refill the temporary and seasonal wetlands that can provide these foods and the high-energy foods required for staging and migrating waterfowl and shore birds.

During drought conditions, when temporary and seasonal wetlands are dry early in the breeding season, breeding waterfowl fly north of the prairie pothole region to reach stable water or they concentrate on large permanent prairie lakes and do not breed. When seasonal wetlands are dry during the breeding season, waterfowl production is severely impaired (Swanson and Duebbert, 1989). Thus, wetland complexes provide stability to breeding waterfowl populations except during periods of extreme drought when the wetlands are completely dry. Droughts, however, periodically reset the biological communities of the semipermanent wetlands and, thus, maintain the high productivity of prairie wetlands.

Nonintegrated (closed) prairie pothole wetland complexes provide ideal habitats for nonpiscivorous birds during the breeding season because the wetlands maintain an aquatic habitat free of most vertebrate aquatic predators that compete for invertebrate foods with laying females and their broods (Swanson and Nelson, 1970; Bouffard and Hanson, 1997; Cox and others, 1998). Open wetland complexes that eventually flow into permanent lakes and rivers that support fish are frequently colonized by fish during wet periods. Fathead minnows *(Pimephales promelas)* have been known to invade open wetlands during spring runoff and persist for several years, dominating the wetland fauna until being eliminated by winterkill or summer dessication. Tile drainage systems used in some areas of the prairie pothole region to drain wetlands also provide a corridor for fish invasions from associated drainage systems. Fish were not present in the Cottonwood Lake area during this study because the wetlands were not integrated, periodically contained elevated dissolved salt concentrations, were occasionally dry, and were anaerobic or often frozen to the bottom of the wetland during the winter months.

Saline lakes, with their unique flora and fauna, support a variety of waterfowl and shore birds that are not found in fresh-water wetland complexes located higher in the landscape. A moisture deficit, therefore, contributes to the biological diversity and productivity of the prairie pothole region by supporting flora and abundant invertebrate fauna not found in regions of moisture surplus. Stable water levels in regions having a moisture surplus tend to support fish and wetlands dominated by emergent vegetation that are less attractive to most species of breeding waterfowl and shore birds found in the prairie pothole region.

CONCLUSIONS

Biotic communities that were present in the wetlands in the Cottonwood Lake area, at any point in time, were determined by a dynamic physical environment that set boundaries on species structure. Each wetland was unique in its hydrogeochemical response to the physiographic setting and climate trends and in the biological community it produced. The synergistic effects of hydroperiods and dissolved salt concentrations established boundaries on wetland species structure and, subsequently, on biological diversity within the wetland complex. The position that each wetland occupied within the landscape with respect to topographic and hydrologic gradients determined the hydrologic function of the wetland. The hydrologic regime and the subsequent chemical environment were determined by wetland basin, climate, and ground water interactions. The semiarid conditions characteristic of the Cottonwood Lake area maintained seasonal wetlands and resulted in semipermanent wetlands cycling between extremes of flooding and desiccation. Hydroperiods determined the number and area of vegetative zones that occupied each wetland, and dissolved salt concentrations determined the species structure of the biotic communities that dominated each zone. Major-ion concentrations were determined by the hydrologic functions of the wetlands and were modified by the hydroperiods. Biological diversity within the wetland complex was maintained by a wetland class structure that reflected variations in the hydroperiods and the dissolved salt concentrations. The spectrum of wetland classes and subclasses that comprised the wetland complex determined the diversity of the plant and invertebrate communities and the avian and other vertebrate communities of the prairie wetlands.

To be reproductively successful, waterfowl require wetlands that provide isolation and abundant, highly available, high-protein food resources. Restoring and preserving wetland complexes in the prairie pothole region to maximize productivity and biodiversity requires an understanding of the landscape ecology and the response of wetland biotic communities to hydrologic and chemical gradients that are a result of landscape position. The deluge of 1993-98 that followed the severe drought of 1988-92 caused a major decline in dissolved salt concentrations in the prairie wetlands in south-central North Dakota. The shift in aquatic community structure from one that tolerated elevated salt concentrations to one that reflected a relatively fresh-water environment altered the biological community of the wetlands in a specific and predictable fashion. It would be of value to document the timeframe required to achieve the volumes of water and the dissolved salt concentrations that persisted in closed prairie wetlands prior to 1988. The timeframe required to produce the aquatic community structure that existed prior to the deluge of 1993-98 would provide additional insight into prairie wetland ecology. The time required to evaporate water during the 1993-98 wet period and to import salts lost to deflation during 1988-92 could be considerable, perhaps a decade or more.

East of the prairie pothole region in areas of moisture surplus, surface water is abundant and relatively stable but waterfowl pair densities are low. Although waterfowl species structure varies to some degree between areas of moisture extremes, the value of the dynamic prairie wetlands in maintaining North American waterfowl populations is not disputed. The future of waterfowl production in North America lies in maintaining the integrity of the sensitive prairie pothole wetland complexes to insure the availability of productive aquatic habitats. Overcoming the effects of drainage and siltation are major challenges to preserving the productivity and biodiversity of the prairie wetlands as well as to the waterfowl populations of North America.

ACKNOWLEDGMENTS

Appreciation is extended to James W. LaBaugh, Donald O. Rosenberry, and Thomas C. Winter for extensive consultation and critical review of this manuscript.

REFERENCES

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

Bouffard, S.H., and Hanson, M.A, 1997, Fish in waterfowl marshes--Waterfowl manager's perspective: Wildlife Society Bulletin, v. 25, p.146-157.

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

Cowardin, L.M., Carter, V., Golet, F.C., and LaRoe, E.T., 1979, Classification of wetlands and deepwater habitats of the United States: U.S. Fish and Wildlife Service, Biological Services Program FWS/OBS-79/31, 131 p.

Cox, R.R., Jr., Hanson, M.A., Roy, C.C., Euliss, N.H., Jr., Johnson, D.H., and Butler, M.G., 1998, Mallard duckling growth and survival in relation to aquatic invertebrates: Journal of Wildlife Management, v. 62, p. 124-133.

Daubenmire, R., 1959, A canopy-coverage method of vegetational analysis: Northwest Science, v. 33, p. 43-64.

Eisenlohr, W.S., Jr., and others, 1972, Hydrologic investigations of prairie potholes in North Dakota, 1959-68: U.S. Geological Survey Professional Paper 585-A, 102 p.

Euliss, N.H., Jr., and Grodhaus, G., 1987, Management of midges and other invertebrates for waterfowl wintering in California: California Fish and Game, v. 73, p.242-247.

Euliss, N.H., Jr., Wrubleski, D.A., and Mushet, D.M., 1999, Wetlands of the prairie pothole region: invertebrate species composition, ecology, and management, *in* Batzer, D.P., Radar, R.B., and Wissinger, S.A., eds., Invertebrates in Freshwater Wetlands of North America: Ecology and Management: John Wiley and Sons, New York, NY, USA, p. 471-514.

Fredrickson, L.H., and Taylor, T. S., 1982, Management of seasonally flooded impoundments for wildlife: U.S. Fish and Wildlife Service, Resource Publication 148, Washington, DC, USA, 29 p.

Fryer, G., 1974, Attachment of bivalve molluscs to corixid bugs: Naturalist, v. 928, p. 18.

Jenkins, R.M., 1961, Reservoir fish management, progress and challenge: Sport Fishing Institute, Washington, DC, USA, 22 p.

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

Kantrud, H.A., 1986, Effects of vegetation manipulation on breeding waterfowl in prairie wetlands: a literature review: U.S. Fish and Wildlife Service Technical Report 3, Washington, DC, USA, 15 p.

_____1992, History of cattails on the prairies: wildlife impacts, *in* Proceedings of the Cattail Management Symposium: North Dakota State University, Fargo, ND, USA, p. 9-12

Kantrud, H.A., Krapu, G.L., and Swanson, G.A., 1989, Prairie basin wetlands of the Dakotas: a community profile: U.S. Fish and Wildlife Service Biological Report 85, Washington, DC, USA, 111 p.

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

Kruse, A.D., and Bowen, B.S., 1996, Effects of grazing and burning on densities and habitats of breeding ducks in North Dakota: Journal of Wildlife Management, v. 60, p. 233-246.

LaBaugh, J.W., and Swanson, G.A., 1992, Changes in chemical characteristics of water in selected wetlands in the Cottonwood Lake area: North Dakota, USA, 1967-89, *in* Robarts, R.D. and Bothwell, M.L., eds., Aquatic ecosystems in semi-arid regions: Implications for resource management: National Hydrology Research Institute, Symposium Series 7, Environment Canada, Saskatoon, Canada, p. 149-162.

LaBaugh, J.W., Winter, T.C., Adomaitis, V.A., and Swanson, G.A. 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, 26 p.

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

Lannoo, M.J., 1996, Okoboji Wetlands: A lesson in natural history: University of Iowa Press, Iowa City, IA, USA, 190 p.

Lannoo, M.J., Lang, K., Waltz, T., and Phillips, G.S., 1994, An altered amphibian assemblage: Dickinson County, Iowa, 70 years after Frank Blanchard's survey: American Midland Naturalist, v. 131, p. 311-319.

Moyle, J.B., 1945, Some chemical factors influencing the distribution of aquatic plants in Minnesota: American Midland Naturalist, v. 34, p. 402-421.

Nelson, R.D., 1989, Seasonal abundance and life cycles of chironomids (Diptera: Chironomidae) in four prairie wetlands: Ph.D. Thesis, North Dakota State University, Fargo, ND, USA, 85 p.

Peck, S.B., 1975, Amphipod dispersal in the fur of aquatic mammals: The Canadian Field-Naturalist, v. 89, p. 181-182.

Pennak, R.W., 1989, Fresh-water invertebrates of the United States: 3rd Edition, John Wiley & Sons, New York, NY, USA, 628 p.

Poiani, K.A., and Johnson, W. C., 1989, Effect of hydroperiod on seed bank composition in semi-permanent prairie wetlands: Canadian Journal of Botany, v. 67, p. 856-864.

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

Proctor, V.W., 1964, Viability of crustacean eggs recovered from ducks: Ecology, v. 45, p. 656-658.

Proctor, V.W., Malone, C.R., and DeVlaming, V.L., 1967, Dispersal of aquatic organisms: viability of disseminules recovered from the intestinal tract of captive killdeer: Ecology, v. 48, p. 672-676.

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

Rosine, W., 1956, On the transport of the common amphipod, *Hyalella azteca*, in South Dakota by the mallard duck: Proceedings of the South Dakota Academy of Science, v. 35, p. 203.

Segerstråle, S.G., 1954, The freshwater amphipods, *Gammarus pulex* (L.) and *Gammarus lacustris* G. O. Sars, Denmark and Fennoscandia - a contribution to the late- and post-glacial immigration history of the aquatic fauna of northern Europe: Commentatiowes Biologicae Societas Scientiarum Fennica, v. 15, p. 1-91.

Sloan, C.E., 1972, Ground-water hydrology of prairie potholes in North Dakota: U.S. Geological Survey Professional Paper 585-C, 28 p.

Stewart, R.E., and Kantrud, H.A., 1971, Classification of natural ponds and lakes in the glaciated prairie region: U.S. Fish and Wildlife Service Resource Publication 92. Washington, DC, USA, 57 p.

_____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., 36 p.

Swanson, G.A., 1977, Diel food selection by Anatinae on a waste-stabilization system: Journal of Wildlife Management, v. 41, p. 226-231.

_____1984, Dissemination of amphipods by waterfowl: Journal of Wildlife Management, v. 48, p. 988-991.

_____1992, Cycles of cattails in individual wetlands: environmental influences, *in* Proceedings of the Cattail Management Symposium: North Dakota State University, Fargo, ND, USA, p. 13-17.

Swanson, G.A., Adomaitis, V.A., Lee, F.B., Serie, J.R., and Shoesmith, J.A., 1984, Limnological conditions influencing duckling use of saline lakes in south-central North Dakota: Journal of Wildlife Management, v. 48, p. 340-349.

Swanson, G.A., and Duebbert, H.F., 1989, Wetland habitats of waterfowl in the prairie pothole region, *in* A.G. van der Valk, ed., Northern prairie wetlands: Iowa State University Press, Ames, IA, USA, p. 228-257.

Swanson, G.A., and Meyer, M.I., 1977, Impact of fluctuating water levels on feeding ecology of breeding blue-winged teal: Journal of Wildlife Management, v. 41, p. 426-433.

Swanson, G.A., and Nelson, H.K., 1970, Potential influence of fish rearing programs on waterfowl breeding habitat, *in* Schneberger, E. ed., A symposium on the management of midwestern winterkill lakes: North Central Division of the American Fisheries Society Special Publication No. 1, Winnipeg, MB, Canada, p. 65-71

Swanson, G.A., and Sargeant, A.B., 1972, Observation of nighttime feeding behavior of ducks: Journal of Wildlife Management, v. 36, p. 959-961.

Swanson, G.A., Winter, T.C., Adomaitis, V.A., and LaBaugh, J.W., 1988, Chemical characteristics of prairie lakes in south-central North Dakota--their potential for influencing use by fish and wildlife: U.S. Fish and Wildlife Technical Report 18, Washington, DC, USA, 44 p.

Swanson, K.D., 1990, Chemical evolution of ground water in clay till in a prairie wetlands setting in the Cottonwood Lake area, Stutsman County, North Dakota: MS Thesis, University of Wisconsin, Madison,WI, USA, 229 p.

van der Valk, A.G., 1981, Succession in wetlands, a Gleasonian approach: Ecology, v. 62, p. 688-696.

Weller, M.W., 1978, Management of freshwater marshes for wildlife, *in* Good, R.E., Whigham, D.F., and Simpson, R.L., eds., Freshwater wetlands, ecological processes and management potential: Academic Press, New York, NY, USA, p. 267-284.

_____1981, Freshwater marshes, ecology and wildlife management: University of Minnesota Press, Minneapolis, MN, USA, 146 p.

Wheeler, G.C., and Wheeler, J., 1966, The amphibians and reptiles of North Dakota: The University of North Dakota Press, Grand Forks, ND, USA, 104 p.

Winter, T.C., and Carr, M. R., 1980, Hydrologic setting of wetlands in the Cottonwood Lake area, Stutsman County, North Dakota: U.S. Geological Survey Water-Resources Investigations 80-99, 42 p.

Winter, T.C., and Rosenberry, D.O., 1995, The interaction of groundwater with prairie pothole wetlands in the Cottonwood Lake area, east-central North Dakota, 1979-90: Wetlands, v. 15, p. 193-211.

_____1998, Hydrology of prairie pothole wetlands during drought and deluge: a 17-year study of the Cottonwood Lake wetland complex in North Dakota in the perspective of longer term measured and proxy hydrologic records: Climatic Change, v. 40, p. 189-209.

Table 5. Species composition, occurrence (percent), and average canopy cover for vegetation in mesic upland sites in the Cottonwood Lake area in July 1989. Canopy cover values range from 1 to 7; 1 = <1 percent, 2 = 1 percent - 4 percent, 3 = 5 percent - 24 percent, 4 = 25 percent - 49 percent, 5 = 50 percent - 74 percent, 6 = 75 percent - 94 percent, and 7 = 95 percent - 100 percent.

	Occurrence (percent)	Canopy cover
Achillea millefolium L.	7	2
Agropyron caninum L.	10	2
Agropyron repens (L.) Beauv.	47	2
Ambrosia psilostachya DC.	17	2
Andropogon gerardii Vitman	10	3
Anemone canadensis L.	43	2
Apocynum cannabinum L.	23	3
Artemisia ludoviciana Nutt.	3	2
Asclepias ovalifolia Dene.	3	2
Aster simplex Willd.	68	2
Bromus inermis Leyss.	33	2
Calamagrostis stricta (Timm.) Koel.	13	2
Carex L.	83	3
Cirsium arvense (L.) Scop.	13	3
Elaeagnus commutata Bernh.	10	3
Fragaria virginiana Duchn.	3	2
Galium boreale L.	17	3
Gentiana andrewsii Griseb.	3	3
Glycyrrhiza lepidota Pursh	30	3
Helianthus maximilianii Schrad.	20	3
Heuchera richardsonii R. Br.	10	3
Hordeum jubatum L.	3	3
Liatris ligulistylis (A. Nels.) K. Schum	20	1
Liatris punctata Hook.	3	2
Lilium philadelphicum L.	3	3
Mentha arvensis L.	7	2
Muhlenbergia richardsonis (Trin.) Rydberg	3	1
Onosmodium molle Michx.	3	3
Panicum virgatum L.	10	2
Poa pratensis L.	70	3
Populus tremuloides Michx.	3	4
Potentilla anserina L.	50	3
Rumex crispus L.	3	3
Solidago canadensis L.	27	3
Solidago mollis Bartl.	10	3
Solidago rigida L.	3	3
Sonchus arvensis L.	63	2
Spartina pectinata Link	23	3
Stachys palustris L.	17	2
Symphoricarpos occidentalis Hook.	20	3

Table 6. Species composition, occurrence (percent), and average canopy cover for vegetation in xeric upland sites in the Cottonwood Lake area in July 1989. Canopy cover values range from 1 to 7; 1 = <1 percent, 2 = 1 percent - 4 percent, 3 = 5 percent - 24 percent, 4 = 25 percent - 49 percent, 5 = 50 percent - 74 percent, 6 = 75 percent - 94 percent, and 7 = 95 percent - 100 percent.

	Occurrence (percent)	Canopy cover
Achillea millefolium L.	35	2
Agropyron caninum L.	40	2
Agropyron cristatum (L.) Gaertn.	5	3
Agropyron smithii Rydb.	15	2
Ambrosia psilostachya DC.	20	2
Amorpha canescens Pursh	5	2
Anemone patens L.	20	3
Artemesia frigida Willd.	40	2
Artemesia ludoviciana Nutt.	25	3
Aster falcatus Lindl.	50	2
Astragalus crassicarpus Nutt.	5	2
Astragalus flexuosus (Hook.) G. Don.	15	2
Bouteloua gracilis (H.B.K.) Lag. Ex Griffiths	25	3
Bromus inermis Leyss.	35	3
Carex L.	95	2
Cerastium arvense L.	15	2
Chenopodium album L.	10	1
Chrysopsis villosa (Pursh) Nutt.	25	3
Cirsium floodmanii (Rydb.) Arthur	10	3
Comandra umbellata (L.) Nutt.	5	2
Echinacea angustifolia DC.	5	3
Erysimum asperum (Nutt.) DC.	5	2
Gallium boreale L.	10	2
Grindelia squarrosa (Pursh) Dun.	10	3
Hedeoma hispidum Pursh	5	2
Koeeleria pyramidata (Lam.) Beauv.	25	3
Liatris punctata Hook.	25	2
Phlox hoodii Rich.	20	3
Poa pratensis L.	55	3
Potentilla norvegica L.	5	2
Psoralea argophylla Pursh	5	2
Psoralea esculenta Pursh	10	3
Ratibida columifera (Nutt.) Woot & Standl	15	2
Rudbeckia hirta L.	5	3
Senecio integerrimus Nutt.	5	2
Solidago missouriensis Nutt.	10	3
Stipa comata Trin. & Rupr.	50	3
Stipa spartea Trin.	15	3
Stipa viridula Trin.	35	3
Vicia americana Muhl. Ex Willd.	5	1
Viola pedatifida G. Don	5	2

Table 7. Species composition, occurrence (percent), and average canopy cover for vegetation in north aspect upland sites in the Cottonwood Lake area in July 1989. Canopy cover values range from 1 to 7; 1 = <1 percent, 2 = 1 percent - 4 percent, 3 = 5 percent - 24 percent, 4 = 25 percent - 49 percent, 5 = 50 percent - 74 percent, 6 = 75 percent - 94 percent, and 7 = 95 percent - 100 percent.

	Occurrence (percent)	Canopy cover
Achilla millefolium L.	20	2
Agropyron caninum L.	5	1
Agropyron repens (L.) Beauv.	25	2
Amalanchier alnifolia Nutt.	20	3
Ambrosia psilostachya DC.	5	1
Anemone canadensis L.	10	3
Andropogon gerardii Vitman	10	3
Apocynum cannabinum L.	10	3
Artemesia ludoviciana Nutt.	25	2
Aster falcatus Lindl.	10	2
Bromus inermis Leyss.	75	2
Carex L.	45	2
Cirsium arvense (L.) Scop.	30	2
Crataegus rotundifolia Moench.	5	3
Elaeagnus commutata Bernh.	5	3
Gallium boreale L.	35	3
Geum triflorum Pursh	5	2
Lithospermum canescens (Michx) Lehm.	5	2
Parthenocissus vitacea (Knerr.) Hitchc.	5	2
Poa pratensis L.	50	3
Populus tremuloides Michx.	30	4
Prunus virginiana L.	5	6
Ratibida columnifera (Nutt.) Woot. & Standl.	10	2
Salix exigua Nutt.	10	3
Solidago canadensis L.	20	3
Solidago mollis Bartl.	10	3
Solidago rigida L.	15	3
Stipa spartea Trin.	5	2
Symphoricarpos occidentalis Hook.	65	4
Toxicodendron rydbergii (small) Greene	5	2
Urtica dioica L.	15	2

Table 8. Species composition, occurrence (percent), and average canopy cover for vegetation in south aspect upland sites in the Cottonwood Lake area in July 1989. Canopy cover values range from 1 to 7; 1 = <1 percent, 2 = 1 percent - 4 percent, 3 = 5 percent - 24 percent, 4 = 25 percent - 49 percent, 5 = 50 percent - 74 percent, 6 = 75 percent - 94 percent, and 7 = 95 percent - 100 percent.

	Occurrence (percent)	Canopy cover
Achillea millefolium L.	45	2
Agropyron caninum L.	35	2
Allium textile A. Nels. & Macbr.	5	1
Ambrosia psilostachya DC.	25	1
Amorpha canescens Pursh	10	3
Andropogon gerardii Vitman	5	1
Andropogon scoparius Michx.	10	4
Anemone cylindrica A. Gray	20	2
Anomone patens L.	20	3
Artemesia ludoviciana Nutt.	55	3
Aster falcatus Lindl.	25	2
Carex L.	40	2
Cirsium floodmanii (Rydb.) Arthur	20	2
Echinacea angustifolia DC.	10	2
Elaeagnus commutata Bernh.	5	3
Galium boreale L.	15	2
Helictotrichon hookeri (Scribn.) Henr.	15	2
Lactuca oblongifolia Nutt.	20	2
Poa pratensis L.	100	4
Rosa arkansana Porter	20	2
Senecio integerrimus Nutt.	10	3
Solidago rigida L.	20	2
Sphaeralcea coccinea (Pursh) Rydb.	5	2
Stipa comata Trin. & Rupr.	15	3
Stipa viridula Trin.	15	3
Trogopogon dubius Scop.	5	1
Vicia americana Muhl & Willd.	15	2
Viola pedatifida G. Don	10	2

Table 9. Species composition, occurrence (percent), and average canopy cover for vegetation in east aspect upland sites in the Cottonwood Lake area in July 1989. Canopy cover values range from 1 to 7; 1 = <1 percent, 2 = 1 percent - 4 percent, 3 = 5 percent - 24 percent, 4 = 25 percent - 49 percent, 5 = 50 percent - 74 percent, 6 = 75 percent - 94 percent, and 7 = 95 percent - 100 percent.

	Occurrence (percent)	Canopy cover
Agropyron caninum L.	15	1
Agropyron repens (L.) Beauv.	55	3
Amorpha canescens Pursh	10	3
Apocynum cannabinum L.	5	1
Artemesia ludoviciana Nutt.	60	2
Aster falcatus Lindl.	20	1
Bromus inermis Leyss.	25	2
Carex L.	45	1
Crataegus rotundifolia Moench.	15	3
Dichanthelium leibergii (Vasey) Freckmann	10	2
Echinacea angustifolia DC.	10	2
Elaeagnus commutata Bernh.	5	3
Galium boreale L.	75	3
Helianthus rigidus (Cass.) Desf.	10	4
Lactuca oblongifolia Nutt.	40	1
Linum perenne L.	10	2
Linum rigidum Pursh	5	1
Onosmodium molle Michx.	5	3
Poa pratensis L.	100	4
Prunus virginiana L.	10	3
Rosa arkansana Porter	20	2
Solidago missouriensis Nutt.	25	2
Sphaeralcea coccinea (Pursh) Rydb.	5	3
Symphoricarpos occidentalis Hook.	25	3

Table 10. Species composition, occurrence (percent), and average canopy cover for vegetation in west aspect upland sites in the Cottonwood Lake area in July 1989. Canopy cover values range from 1 to 7; 1 = <1 percent, 2 = 1 percent - 4 percent, 3 = 5 percent - 24 percent, 4 = 25 percent - 49 percent, 5 = 50 percent - 74 percent, 6 = 75 percent - 94 percent, and 7 = 95 percent - 100 percent.

	Canopy cover	Occurrence (percent)
Agropyron caninum L.	50	2
Agropyron cristatum (L.) Gaertn.	5	3
Agropyron repens (L.) Beauv.	10	2
Agropyron smithii Rydb.	15	2
Andropogon scoparius Michx.	15	3
Anemone cylindrica A. Gray	10	2
Amorpha canescens Pursh	5	3
Artemesia frigida Willd.	25	2
Artemesia ludoviciana Nutt.	10	2
Asclepias viridiflora Raf.	5	2
Aster falcatus Lindl.	60	2
Bouteloua gracilis (H.B.K.) Lag ex Griffiths	25	2
Bromus inermis Leyss.	15	3
Calamovilfa longifolia (Hook.) Scribn.	45	2
Calylophus serrulatus (Nutt.) Raven	5	2
Campanula rotundifolia L.	10	2
Carex L.	95	3
Echinacea angustifolia DC.	20	2
Elaeagnus commutata Bernh.	10	2
Helianthus rigidus (Cass.) Desf.	50	2
Koelaria pyrimidata (Lam.) Beauv.	10	3
Lactuca oblongifolia Nutt.	15	2
Liatrus punctata Hook.	15	2
Linum rigidum Pursh	5	2
Melilotus officinalis (L.) Pall.	5	1
Mirabilis hirsuta (Pursh) MacM.	5	2
Oxytropis lambertii Pursh	5	3
Physalis virginiana P. Mill.	5	3
Poa pratensis L.	65	3
Potentilla arguta Pursh	5	3
Potentilla pennsylvanica L.	5	2
Ratibida columifera (Nutt.) Woot & Standl.	10	3
Rosa arkansana Porter	35	2
Solidago mollis Bartl.	10	3
Stipa spartea Trin.	35	3
Symphoricarpos occidentalis Hook.	10	3
Solidago rigida L.	25	3
Sphaeralcea coccinea (Pursh) Rydb.	10	2
Stipa comata Trin. & Rupr.	55	2

CHAPTER 5

SIMULATION OF HYDROLOGY AND VEGETATION DYNAMICS OF PRAIRIE WETLANDS IN THE COTTONWOOD LAKE AREA

Karen A. Poiani, The Nature Conservancy of Hawaii, Honolulu, Hawaii

W. Carter Johnson, South Dakota State University, Brookings, South Dakota

ABSTRACT

Several generations of spatial simulation models of water depth and of wetland vegetation have been developed on the basis of long-term data sets for the Cottonwood Lake area in North Dakota. WETSIM 1.0 and 2.0 were developed for semipermanent wetlands in the area to simulate temporal and spatial dynamics of water depth and vegetation cover. Despite the use of simple model structure and algorithms, the models accurately simulated the general characteristics of the wetland vegetation cycle. Initially, the models were used to assess the potential effects of climate change on wetland and wildlife resources, but the models have wider applicability for the management of natural and restored wetlands. The most recent model version is WETSCAPE. WETSCAPE is based on the surface-water submodel in WETSIM 2.0 but includes multiple wetland basins and a ground-water submodel necessary to simulate the hydrology of temporary and seasonal wetlands.

INTRODUCTION

The development and use of simulation models has increased the understanding of complex ecosystems (Jorgensen, 1983). Although the models necessarily simplify highly complex ecological processes and interacting components, they also help elucidate relations between the structure and function of ecosystems and are useful in exploring past and future dynamics of ecosystems. Developing simulation models usually is more practical and less expensive than conducting field experiments, particularly for large systems; however, the models must be thoroughly evaluated and tested before results are deemed reliable for use in management decisions and planning.

Various simulation models have been developed to manage freshwater and coastal wetlands (Costanza and Sklar, 1985; Mitsch and others, 1982, 1988). These models include energy- and nutrient-budget models, tree-growth or gap-dynamic models, habitat-succession or spatial ecosystem models, hydrology models, and economic models (Mitsch and others, 1982). For example, several gap-dynamic, tree-growth models have been developed for southern wetland forests (Phipps, 1979; Pearlstine and others, 1985). These models "grow" individual trees on various sized plots and incorporate the effects of flooding, depth to water table, shade tolerance, overtopping and crowding, and probability of death and reproduction (Phipps, 1979). One such gap model (FORFLO) was used to explore the potential effects of a river diversion project on the bottomland forest communities in the Santee River floodplain in South Carolina (Pearlstine and others, 1985). The model predicted a loss of as much as 97 percent of the existing bottomland forest under the new hydrologic regime. The model also showed that an alternative water release schedule could retain much of the native cypress-tupelo forest.

Several spatially-defined wetland succession models have been developed for use in wetland management and impact assessments (Browder and others, 1985; Boumans and Sklar, 1990; Costanza and others, 1990; Lee and others, 1992; Ellison and Bedford, 1995). These models simulate vegetation changes in grid cells on the basis of biotic and abiotic ecosystem processes. The models use different mathematical approaches, including probabilistic (for example, Browder and others, 1985), process-based (for example, Costanza and others, 1990), and rule-based (for example, Lee and others, 1992) calculations. The Coastal Ecological Landscape Spatial Simulation (CELSS) model is an example of a habitat-succession model used to examine both natural changes and human-induced impacts to a large marsh/estuarine complex in south Louisiana (Sklar and others, 1985; Costanza and others, 1990).

Management of northern prairie wetlands for wildlife (Swanson and Duebbert, 1989) depends on a thorough understanding of the climate-driven vegetation and hydrologic cycles that these wetlands exhibit (Kantrud and others, 1989; Swanson and others, Chapter 4 of this report). The processes underlying the cyclic patterns have been extensively described in van der Valk and Davis (1978), van der Valk (1981), and Weller (1994). The first mathematical simulation model of prairie wetland vegetation and hydrology was based on the conceptual model of van der Valk (1981) and field data from the Cottonwood Lake area. Initially, the Cottonwood Lake area model was used to assess the potential effects of human-induced climate change on wetland and wildlife resources (Poiani and Johnson 1991, 1993b, Poiani and others, 1995) but the model also has potential for wetland management. This chapter discusses the general structure and testing of the model and the work performed to date on the assessment of potential climate change and gives an example of how the model can guide the management of natural and restored wetlands.

SPATIAL SIMULATION MODEL

STRUCTURE AND DEVELOPMENT

A spatially-defined, rule-based simulation model was developed for semipermanent wetlands in the Cottonwood Lake area (Poiani and Johnson, 1993a). The Cottonwood Lake area was chosen because of its extensive, long-term data sets for water levels, air temperature, precipitation, and vegetation (Winter and Carr, 1980; LaBaugh and others,1987). The model was developed primarily using data for semipermanent Wetland Pl. A seed bank study of semipermanent Wetlands P1 and P4 also was conducted (Poiani and Johnson 1988, 1989).

The first model (WETSIM 1.0) consisted of interacting hydrologic and vegetation submodels. The hydrologic submodel calculated daily water levels during the growing season (May-October) on the basis of air temperature and precipitation. The model estimated the initial spring water level from total spring precipitation. To illustrate, the water-level change from late fall to May 1 was calculated from the following empirically-derived equation ($P < 0.001$, $R^2 = 87.7$): water-level change = 1.68 + 4.59 * sprpre, where sprpre = March and April direct precipitation + estimated snowmelt runoff (all values are in centimeters).

Data for Wetland P1 indicated that contributions from snowmelt runoff were significant only when the March maximum snow depth was greater than 30 cm. Therefore, snowmelt runoff was calculated for years when the snow depth was greater than 30 cm by determining the water equivalent for the March maximum snow depth (a 1:10 ratio of equivalent water to snow depth was assumed) and multiplying the water equivalent by 1.5 to account for drifting into the basin (Shjeflo, 1968).

Water-level changes during the growing season were calculated daily. Hydrologic inputs were from direct precipitation and estimated runoff from heavy summer or fall rains. An analysis of the daily water-level changes for Wetland P1 showed that for rainfall events greater than 2.4 cm, the water level often rose in excess of direct precipitation input. This excess rise in water level, attributed to runoff, was calculated from an empirical, nonlinear equation for precipitation events greater than 2.4 cm: $\text{runoff} = 0.164 * \text{precip}^{1.25}$ (all values are in centimeters). Outputs due to evapotranspiration were calculated using a modified version of the climatic water-budget method of Thornthwaite and Mather (1957). Calculations of evapotranspiration using this method relied on daily air temperature, latitude, day length, a heat index that was calculated from monthly mean temperature, and a vegetation scalar (Poiani and Johnson, 1993a). The vegetation scalar was an empirically-calibrated coefficient derived from comparisons of calculated evapotranspiration versus actual water loss in Wetland P1. Daily values of evapotranspiration calculated using the Thornthwaite method were increased by 25 percent to better represent actual losses.

In the hydrologic submodel, the elevation of the bottom of the wetland was set as the lower limit for the water level. Negative water levels (for example, the elevation of the water table) were restricted to upland and wetland fringe cells, and water levels in the deepest part of the basin were assumed to remain near ground level. As shown in Chapter 1 of this report, the water table under the central part of Wetland P1 fluctuated several decimeters during 5 consecutive dry years (1988-92). While ground-water processes were not considered directly in the submodel, calculations of runoff and evapotranspiration included inputs to and outputs from the local ground-water system. Improvements to ground-water components were made in subsequent versions of WETSIM 1.0.

The vegetation submodel calculated the amount and distribution of emergent vegetation and open water in a wetland. Topographic characteristics of a basin were determined from a Geographic Information System (GIS) by interpolating surveyed point elevations. Within the submodel, a wetland basin and some of the surrounding upland were represented by a grid having uniform cells. The cell size was determined according to the size of the wetland and the appropriate resolution for vegetation processes. Simulations of semipermanent Wetlands P1 and P4 in the Cottonwood Lake area had a cell size of 9.3 m^2. The topographic characteristics determined from the GIS and the water levels generated by the hydrologic submodel were provided to the vegetation component, and the water depth in each cell was calculated monthly (water depth = water level – ground-surface elevation).

An initial vegetation type was assigned to each cell and was thereafter updated monthly during the growing season. In general, the vegetation composition for each grid cell at any time, t, was a function of $COV_t = f(WD_t, WD_{t-1}, LENWD_t, LOC, COV_{t-1}, t)$, where COV = the vegetation type, WD = the water depth, LENWD = the time period at that water depth, and LOC = the cell location (for example, simulating the 'vegetative spread' of an emergent zone).

The vegetation submodel used eight vegetation types (table 11). Four of the types—upland vegetation, combined wet-meadow/shallow-marsh emergents, deep-marsh emergents, and open water—represented relatively permanent zones and corresponded to a specific range of water depths. The remaining four types—seedlings, mixed species of drawdown plants (for example, mixed plants), mixed species of shallow- and deep-marsh emergents (for example, mixed emergents), and exposed soil—represented the more transient vegetation types present during the dry phase of the vegetation cycle.

Both submodels were developed and calibrated using 1979-89 data for Wetland P1. Initial parameter estimates were based on methods and values in the literature and personal observations (Poiani and Johnson, 1993a). Simulations of the hydrology and vegetation for Wetland P1 were performed with first-cut versions of the submodels. The output was evaluated by comparison with actual data, and, based on the comparisons, several calculations and coefficients in both submodels were adjusted to produce more accurate results (Poiani and Johnson, 1993a). The simulations reported below were based on the latter version of WETSIM 1.0, unless otherwise indicated.

WETSIM 1.0 also was modified (WETSIM 2.0) to produce a 30-year simulation. Modifications (Poiani and others, 1996) included (1) seed germination restricted late in the growing season (for example, seeds germinate in 95 percent of the dry cells in May and June, 30 percent in July and August, 10 percent in September, and 0 percent in October); (2) the addition of stochastic components to kill emergents by flooding and to establish upland, wet-meadow/shallow-marsh, and deep-marsh types; (3) the use of the Blaney-Criddle method (McGuinness and Bordne, 1972) to compute evapotranspiration; and (4) the use of EPIC, a stand-alone soil-water simulation model (Sharpley and Williams, 1990), to generate surface runoff and subsurface inflow to the wetland.

Table 11. Rules for changes in vegetation submodel. COV = vegetation type, WDC = water-depth category, MON = month, LENWDC = time period in water-depth category (months), LOC = cell location. Water-depth categories: (1) <-55 cm, (2) -55 to -10 cm, (3) -9 to 3 cm, (4) 4 to 19 cm, (5) 20 to 55 cm, and (6) >55 cm. OW = open water, DM = deep-marsh emergents, MSM = wet-meadow/shallow-marsh emergents, UPL = upland vegetation, SEEDL = seedlings, MIXPLT = mixed young plants, MIXEM = mixed species of shallow- and deep-marsh emergents, EXPSOIL = exposed soil.

(1) Wetland drawdown:
If MON = MAY or JUN and COV = OW or EXPSOIL and WDC = 1 or 2 or 3 then COV = SEEDL (95 percent) or COV = EXPSOIL (5 percent)
If MON = JUL or AUG and COV = OW or EXPSOIL and WDC = 1 or 2 or 3 then COV = SEEDL (30 percent) or COV = EXPSOIL (70 percent)
If MON = SEP and COV = OW or EXPSOIL and WDC = 1 or 2 or 3 then COV = SEEDL (10 percent) or COV = EXPSOIL (90 percent)
If MON = OCT and COV = OW or EXPSOIL and WDC = 1 or 2 or 3 then COV = EXPSOIL (100 percent)
(2) Fate of drawdown:
If COV = SEEDL and WDC = 1 or 2 or 3 then COV = MIXPLT
If COV = SEEDL or EXPSOIL and WDC = 4 or 5 or 6 then COV = OW
If COV = MIXPLT and WDC = 5 or 6 then COV = OW
(3) Spring following drawdown:
If COV = MIXPLT and MON = MAY and WDC = 1 then COV = MSM
If COV = MIXPLT and MON = MAY and WDC = 2 or 3 or 4 or 5 then COV = MIXEM
If COV = MIXPLT and MON = MAY and WDC = 6 then COV = OW
(4) Flooding of mixed emergents:
If COV = MIXEM and WDC = 4 or 5 or 6 and LENWDC> 15 then COV = OW (35 percent)
(5) Spread of deep marsh[1]:
If WDC = 3 or 4 or 5 and LENWDC > 4 and LOC = next to cell with COV = DM then COV = DM (95 percent)
(6) Spread of wet meadow/shallow marsh[1]:
If WDC = 2 and LENWDC> 12 and LOC = next to cell with COV = MSM then COV = MSM (95 percent)
(7) Establishment of open water:
If WDC = 6 and LENWDC> 12 then COV = OW (85 percent)
(8) Establishment of upland:
If WDC = 1 and LENWDC> 12 then COV = UPL (95 percent)

[1] This change was permitted to occur only once per growing season (for example one cell neighborhood spread).

VALIDATION AND TESTING

WETSIM 1.0 parameters were tested using a data set for semipermanent Wetland P4, which is similar to Wetland P1. Initial conditions of the emergent vegetation, open water, and water levels were from actual data (1979). Three 11-year simulations were run for (1) the water-level changes in Wetland P4 from 1979-89, (2) the vegetation changes in Wetland P4 from 1979-89 using actual water levels, and (3) the vegetation changes in Wetland P4 from 1979-89 using water levels calculated from the hydrologic submodel. The first simulation evaluated the hydrologic submodel, the second evaluated the vegetation submodel without confounding error from hydrologic calculations, and the third evaluated the combined performance of both submodels.

To assess model performance, output from the three simulations was compared to actual historic data. Although the vegetation submodel included eight vegetation types, only six (open water, deep marsh, mixed emergents, mixed plants, seedlings, and exposed soil) could be evaluated from the historic aerial photos. The wet-meadow/shallow-marsh and upland types were not clearly discernible on the photos and, therefore, could not be quantified. Details of those model evaluations can be found in Poiani and Johnson (1993a) and are summarized below.

HYDROLOGIC SUBMODEL

The hydrologic submodel satisfactorily calculated the water-level changes in Wetland P4 for most years. Years with 'average' conditions were represented most accurately. Calculated water levels were within 5 cm of observed values 46 percent of the time and within 10 cm of observed values 75 percent of the time. However, calculations of potential evapotranspiration were underestimated late in the growing season during years when the wetland was nearly dry. The method of estimating potential evapotranspiration did not consider directly the effects of water and sediment temperatures, which increase evaporation as a wetland dries up. Calculations of spring refill also fell short of actual peaks in years after Wetland P4 was nearly dry. Therefore, adjustments to evapotranspiration calculations were made in WETSIM 2.0.

VEGETATION SUBMODEL

In general, the vegetation submodel closely simulated changes in the amount and distribution of emergent vegetation and open water in Wetland P4. Calculated values of open water ranged from 0 to 8 percent and actual values ranged from 0 to 7 percent, generally with the correct spatial distribution. However, seeds germinated on exposed mudflats too late in the growing season in the vegetation submodel. These areas in the actual wetland remained bare because a dry bed occurred late in the growing season and detritus impeded germination. Therefore, adjustments to germination seasonality were made in WETSIM 2.0. The timing of emergent growth and death (for example, conversions between deep-marsh emergents and open water) also was not always accurate although the percent and distribution were often correct. However, model stochasticity in WETSIM 2.0 improved the performance of the model.

OVERALL MODEL

In general, the model accurately represented the observed water-level and vegetation changes in Wetland P4 during the test period. The typical seasonal cycle of spring refill and summer drawdown in prairie wetlands was reproduced. The 1979-89 test period, however, did not include extremely wet climatic conditions but, rather, included a number of slightly below average rainfall years followed by several years of drought.

As previously discussed, model performance also was evaluated for a wider range of weather conditions (the complete weather cycle) by modifying the model to produce a 30-year simulation for Wetland P1. WETSIM 2.0 (Poiani and others, 1996) depicted known wet-dry periods during 1961-92 (fig. 61) and simulated the wettest period prior to 1993 (1966-70) and the moderately wet periods (1975, 1978-80, and 1983-86) accurately. However, water volumes in 1981-82 and 1987 were underestimated. The four known low-water periods (1961, 1973-74, 1976-77, and 1988-1992) were reproduced (fig. 61), and water-level declines were remarkably accurate for some of those periods. Simulated vegetation dynamics generally were realistic for low water periods except in those years when simulated water levels differed from actual water levels by more than 10 to 20 cm.

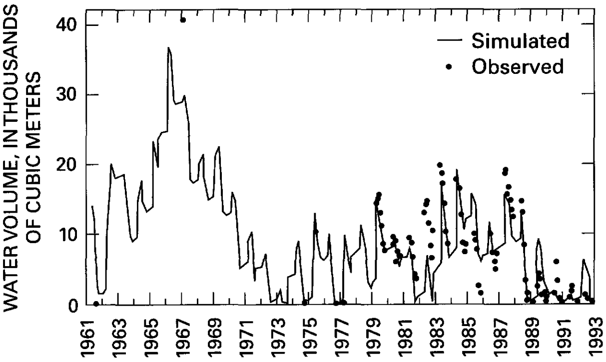


Figure 61. Observed water volume in Wetland P1 compared to calculated water volume obtained using WETSIM 2.0 model, 1961-92.

CLIMATE CHANGE STUDIES

WETSIM 1.0 also has been used in several climate impact studies (Poiani and Johnson, 1991, 1993b; Poiani and others, 1995). All simulations for this study were performed for semipermanent Wetland P1 using climate data for 1979-89 adjusted for a double-CO_2 climate. Climate adjustments included (1) projections from the Goddard Institute for Space Studies (GISS) climate model ('GISS simulation'), (2) a range of possible temperature (+2°C and +4°C) and annual precipitation (–20, –10, 0, +10, and +20 percent) changes ('sensitivity simulations'), and (3) a +2°C increase in temperature combined with a 10-percent increase or decrease in total growing season precipitation that varied by season (all months, spring, summer, and fall) ('seasonal simulations'). The simulated water-level and vegetation changes obtained using the climate adjustments were compared to the simulated water-level and vegetation changes obtained using data for 1979-89 with no adjustments ('current climate'). The same starting water level (558.54 m above sea level) and initial vegetation conditions (8,000 m^2 emergent cover and 8,300 m^2 open water) were used in all simulations.

GODDARD INSTITUTE FOR SPACE STUDIES (GISS) SIMULATION

Simulations were performed for Wetland P1 using temperature and precipitation projections from the GISS general circulation model (GCM). GCMs provide an initial, albeit limited, assessment of the sensitivity of climate to atmospheric additions of greenhouse gases (Kittel and others, 1995). Output from the large grid cells of the GISS model was interpolated by Takle and Zhong (1990) to the Jamestown station located about 40 km from the study area. Projected changes in temperature and precipitation varied by month (table 12), and daily values for each month were adjusted accordingly. Initially, simulations were run with the original version of the vegetation submodel in which seeds could germinate on exposed mudflats at any time during the growing season (Poiani and Johnson, 1993a).

Marked differences in wetland hydrology occurred between the GISS and current climate simulations (Poiani and Johnson, 1993b). The water levels in Wetland P1 were significantly lower in the greenhouse gas climate simulations, and, although the water levels rose each spring, the wetland dried up almost every year (fig. 62). Peak water levels were almost 0.5 m lower than in the current climate simulations. Differences in the ratio of vegetation to open water also occurred between the two simulations (Poiani and Johnson, 1993b). The open-water area declined slightly in the current climate simulations due to drought late in the decade (fig. 63A). In contrast, in the GISS simulations, the open-water area decreased quickly from the initial 51 percent to 0 percent by year 4 (fig. 63B).

The area of wet-meadow/shallow-marsh vegetation also declined in the GISS simulations and went from 4,600 to 2,100 m^2 (fig. 63B). The area for this vegetation type expanded almost 20 percent (from 4,600 to 5,400 m^2) in the current climate simulations (Poiani and Johnson, 1993b). The implications of the differences in the ratios of vegetation to open water to the quality of waterfowl breeding habitat in the prairie pothole region were discussed in Poiani and Johnson (1991). Other studies using statistical models suggest more droughts occurring in a future greenhouse gas climate, resulting in fewer breeding ponds and much smaller duck populations (Larson, 1994, 1995; Sorenson and others, 1998).

To illustrate the effect of seedling germination on vegetation dynamics and the use of the model in exploring related questions, the GISS simulation was rerun in WETSIM 1.0 using a modified vegetation submodel that restricted germination late in the growing season (see earlier section "Spatial Simulation Model - Structure and Development"). Wetland vegetation dynamics were significantly different in the

Table 12. Adjustments to daily temperature and precipitation data as projected by the GISS general circulation model for Jamestown, North Dakota. Data from Takle and Zhong (1990). Details in Poiani and Johnson (1993b).

Month	Temperature increase (°C)	Precipitation change (percent)
March	not used	+29
April	not used	+ 8
May	3.1	+ 7
June	3.2	+ 5
July	3.2	+ 3
August	3.3	+ 19
September	4.9	–17
October	4.3	– 4

GISS simulations when late-season seedling germination was restricted. For example, the wetland did not become vegetated with mixed emergents in the center of the basin by year 4 (fig. 64) as in the initial simulation (fig. 63B), and more than 1,300 m^2 of open water was still present in the wetland in year 8 (fig. 64). Many cells in the center of the basin did not become colonized by vegetation because either water levels in the wetland dropped too late in the season to allow germination or drawdown plants were killed by high water the following spring (fig. 62). A small area (450 m^2) of mixed emergents did become established in year 7. By the end of the simulation period, the open-water area had declined significantly and the vegetative spread of the deep-marsh zone covered most of the wetland basin (fig. 64). These results indicate that a simple parameter such as the timing of seedling germination may strongly affect the overall vegetation cycle in semipermanent prairie wetlands. The results also illustrate the use of a simulation model for exploring potential impacts to wetlands.

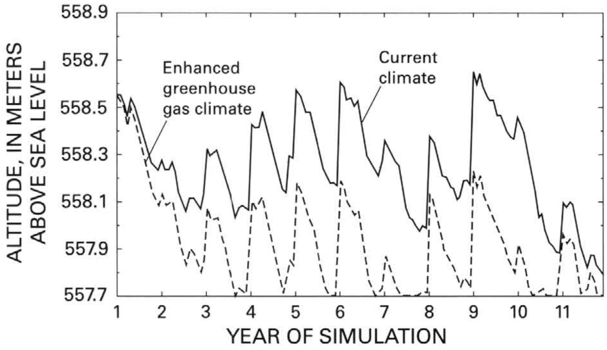


Figure 62. Model output of water-level changes in Wetland P1 for an 11-year simulation under current climate and enhanced greenhouse gas climate conditions. Temperature and precipitation adjustments for the enhanced greenhouse gas climate were from the GISS general circulation model. The entire wetland was dry at approximately 557.7 meters above sea level. (From Poiani and Johnson, 1993b).

SENSITIVITY SIMULATIONS

To supplement the results obtained on the basis of the GCM projections, 10 hypothetical climate change simulations (+2°C or $+4^0$C temperature combined with –20, –10, 0, +10, or +20 percent precipitation) were performed for Wetland P1 using WETSIM 1.0. The ranges of temperature and precipitation changes are the approximate ranges used in other climate models for the United States central grasslands (Houghton and others, 1990). The sensitivity simulations elucidated several additional important aspects of wetland behavior. The hydrologic processes were, in general, more sensitive to temperature and precipitation changes than the vegetation processes (Poiani and Johnson, 1993b). Water levels ranged from relatively high to very low in the various simulations. In contrast, nearly all (9 of the 10) GISS simulations eventually produced more frequent low-water periods and emergent plant colonization in the wetland basin than what was produced by the current climate simulations. The wetland went from a nearly balanced ratio of vegetation to open water to a completely vegetated basin.

The GISS simulations also showed that there may be a threshold temperature beyond which precipitation changes become less important to wetland hydrology. Precipitation change had much less effect on wetland water levels with a temperature increase of +4°C than with a temperature increase of +2°C (Poiani and Johnson, 1993b). Wetland hydrology was more sensitive, however, to increases versus decreases in precipitation at the more moderate temperature increase (+2°C). These results stress the need for accurate projections of climate change, particularly at the regional scale (Kittel and others, 1995).

SEASONAL SIMULATIONS

A second series of hypothetical climate change simulations performed for Wetland P1 (Poiani and others, 1995) identified several important aspects of wetland behavior. The climate change simulations were run with a temperature increase of 2°C and a total growing season precipitation increase or decrease of 10 percent. Precipitation changes were applied either evenly across all growing season months, that is, May through October (all months), or to individual seasons (spring, summer, or fall).

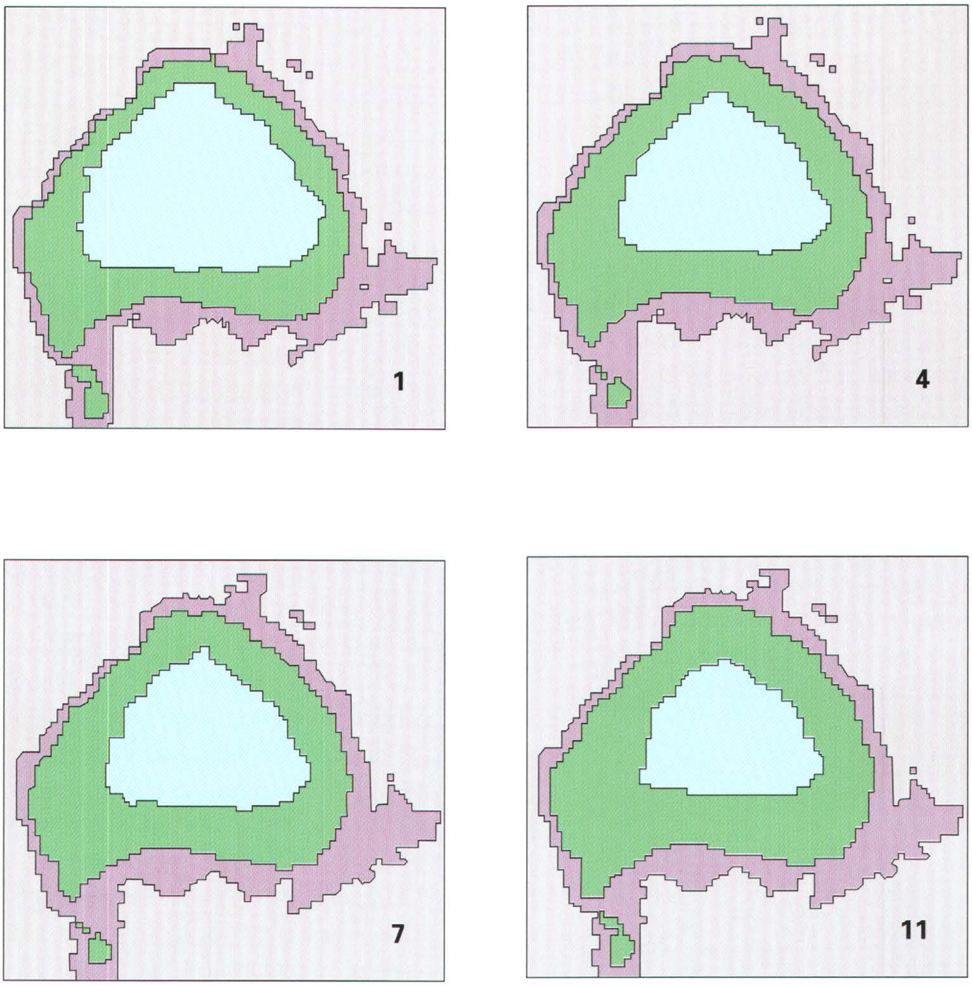


Figure 63A. Model output of emergent vegetation cover and open-water distributions for years 1, 4, 7, and 11 of an 11-year simulation for semipermanent Wetland P1 under current climate. Simulations were on August 1 of each year using unrestricted seed germination. (From Poiani and Johnson, 1991)

The response of Wetland P1 to precipitation changes was similar for all months, summer, and fall. Even a 10-percent increase in precipitation in those seasons produced lower water levels with a +2°C temperature increase than the current climate due to increased evapotranspiration (Poiani and others, 1995). Wetland hydrology was most impacted by spring precipitation changes. Thus, potential climate changes that affect spring refill, such as spring precipitation changes and snowmelt, may have the greatest impact on prairie wetland hydrology and vegetation. The vegetation response was relatively consistent across all simulations. Seven of the eight seasonal simulations produced drier conditions with no open-water areas and greater vegetation cover than did the current climate simulations (Poiani and others, 1995). Simulation results also showed that relatively small water-level changes during dry years can significantly impact the proportion of emergent vegetation in a basin. Emergent vegetation was persistent in shallow, fluctuating water.

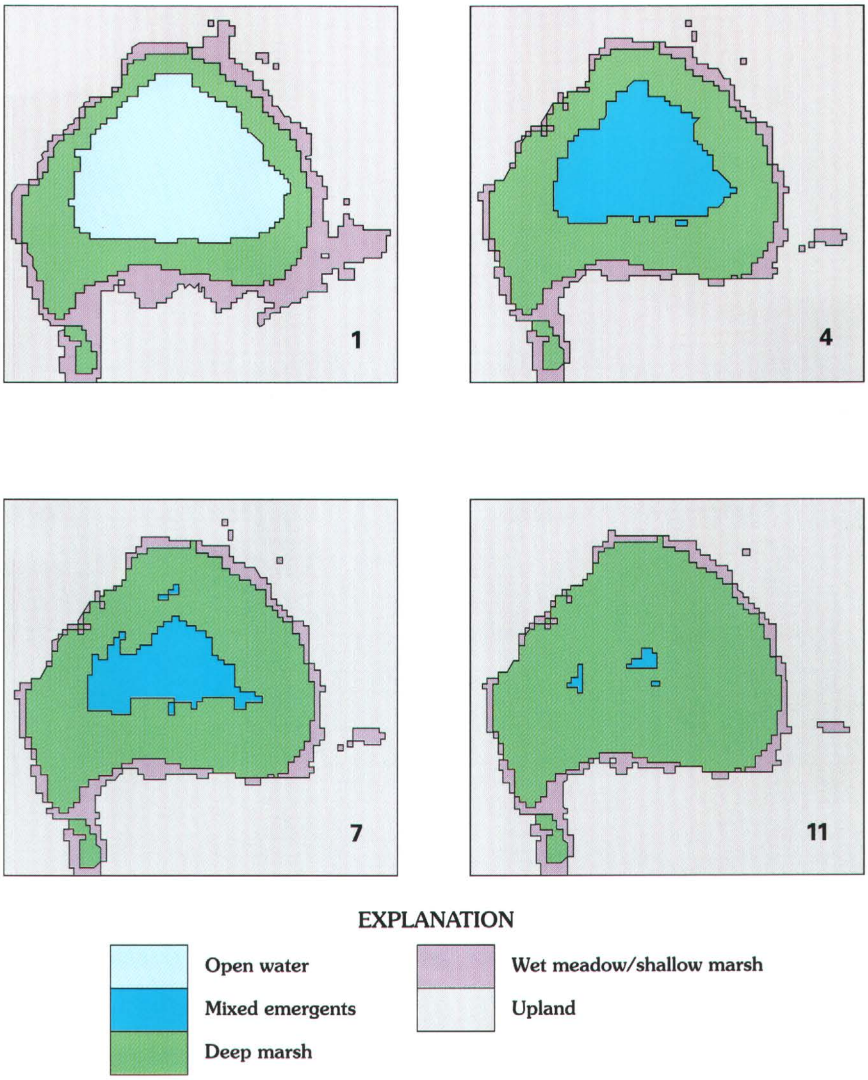


Figure 63B. Model output of emergent vegetation cover and open-water distributions for years 1, 4, 7, and 11 of an 11-year simulation for semipermanent Wetland P1 under an enhanced greenhouse gas climate as projected by the GISS general circulation model. Simulations were on August 1 of each year using unrestricted seed germination. (From Poiani and Johnson, 1991)

MANAGEMENT AND RESTORATION APPLICATIONS

A prolonged drought in central North Dakota during 1988-92 caused the quality of wetland habitat for nesting waterfowl in the Cottonwood Lake area to significantly decline (Swanson and others, Chapter 4 of this report). Many of the semipermanent wetlands in the area became covered by emergent vegetation (primarily cattail) and contained few or no open-water areas, which lead to maximum production (Weller and Spatcher, 1965, Weller and Frederickson, 1974). These were opportune conditions to illustrate the use of the wetland model in estimating the water depth and duration needed by either natural or artificial sources to restore productive habitat. Although water levels currently cannot be manipulated in the Cottonwood Lake area, the experiment shows the potential of the model as a management and restoration tool.

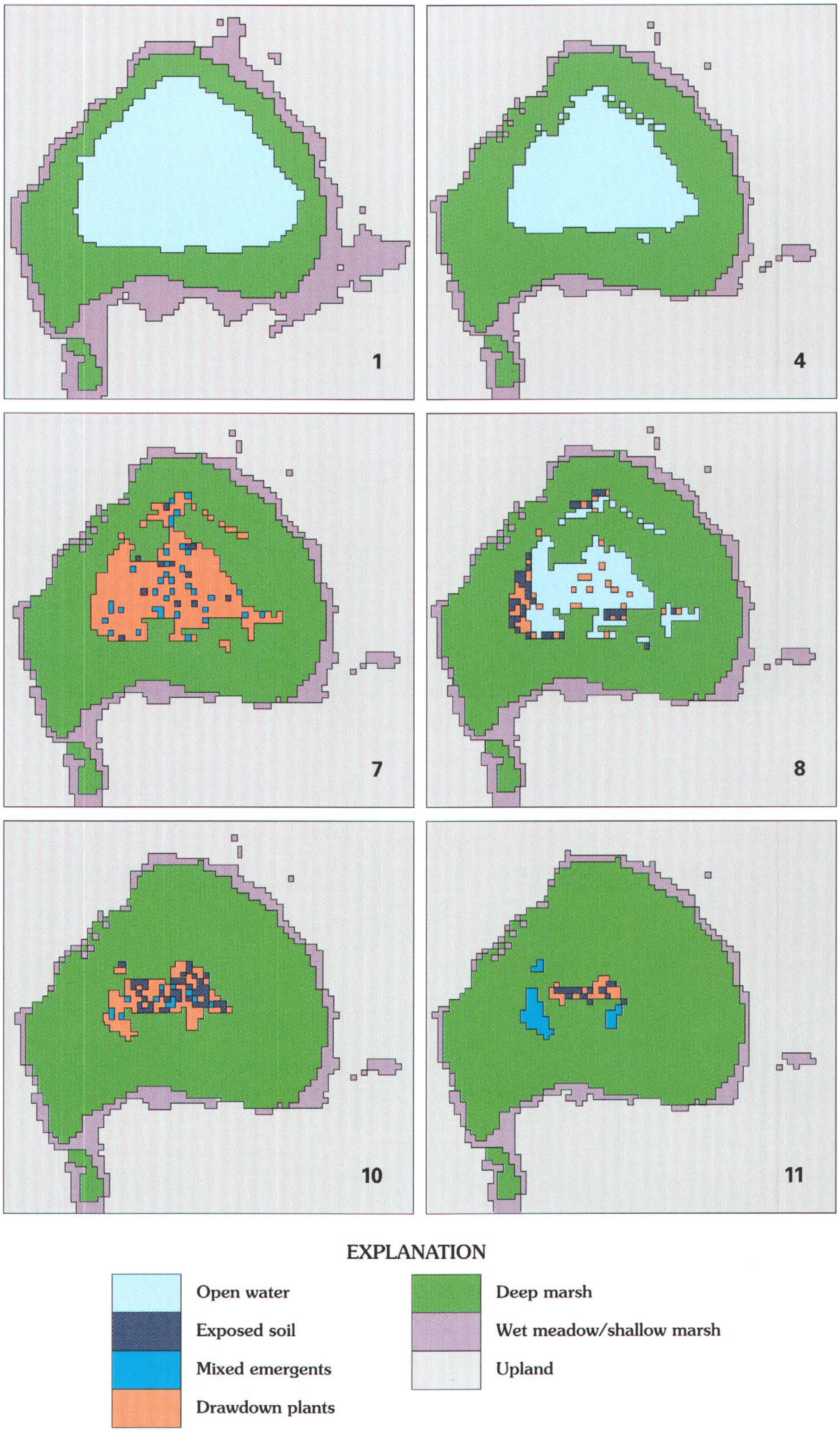


Figure 64. Model output of emergent vegetation cover and open-water distributions for years 1, 4, 7, 8, 10, and 11 of an 11-year simulation for semipermanent Wetland P1 under an enhanced greenhouse gas climate as projected by the GISS general circulation model. Simulations were on August 1 of each year. Seed germination was limited according to the timing of the drawdown.

Management simulations were performed for Wetland P4. The effects of four water depths (75, 100, 125, and 150 cm) were simulated for a 5-year period. Simulations were performed with both fluctuating and constant water-level conditions. 'Fluctuating-depth' simulations had an average water depth of 75, 100, 125, or 150 cm in the deepest part of the basin, with a range of 15 cm above or below this level over the course of the growing season. This range of fluctuations approximated the observed range of water-level changes in semipermanent wetlands. Constant water-level conditions were assigned to each of the four depths for the duration of the simulations.

As expected, the water-depth simulations produced markedly different ratios of vegetation to open water. Among the fluctuating-depth simulations, open water ranged from about 1 to 68 percent, and among the constant-depth simulations, from about 11 to 73 percent (table 13). The percentage of open water in the fluctuating-depth simulations increased most significantly between 100 cm (17 percent) and 125 cm (51 percent). In contrast, the largest increase in open water in the constant-depth simulations was between 75 cm (11 percent) and 100 cm (42 percent) (fig. 65; table 13).

There also were differences between the constant and fluctuating conditions for the same water depth (fig. 65). For example, a constant depth of 100 cm in Wetland P4 produced about 42 percent open water, but an average water depth of 100 cm produced only about 17 percent open water (table 13). The percentage of open water was always greater for a given water depth with constant conditions. The desired 50:50 ratio of vegetation to open water was best approximated by the 125-cm water depth with fluctuating conditions. A nearly balanced ratio of vegetation to open water (58:42) also occurred in the 100-cm constant-depth simulation (table 13).

The death of deep-marsh emergents and the conversion to open water occurred in all eight simulations during year 3 due to deep water conditions for greater than 12 growing season months. Previous model evaluations indicated that the timing of emergent growth and death was not represented adequately by a simple threshold function (see section “Validation and Testing”). The death of emergent vegetation from flooding is highly variable (Shay and Shay, 1986), even among species in a single genus (Grace, 1989). Thus, model-generating information on water depths needed for establishing open-water areas in Wetland P4 is more reliable than that for flooding duration given the current model limitations.

The water-depth simulations also produced differences in the wet-meadow/shallow-marsh vegetation area (table 13). In six of the simulations, the area of this vegetation type either expanded from the original 3,800 m^2 (the 75-cm fluctuating and constant depth and the 100-cm constant depth), declined slightly (the 125-cm fluctuating and constant depths), or remained the same (the 100-cm fluctuating depth) (table 13). In contrast, the area significantly declined over 5 years in the two deepest-depth simulations (the 150-cm fluctuating-depth and the 150-cm constant-depth). A large rise in water levels caused an expansion of the deep-marsh zone upslope (fig. 65), but the steep-sided basin did not allow the wet-meadow/shallow-marsh zone to migrate upslope. Results for the wet-meadow/shallow-marsh zone should be interpreted with caution, however, because few data were available to test this aspect of the model (Poiani and Johnson, 1993a).

Table 13. Percentage of deep-marsh emergents and open water and area of wet-meadow/shallow-marsh emergents. Values are for end of 5-year management scenarios for Wetland P4.

Water-depth simulation (cm)	Deep-marsh emergents	Open water (percent)	Wet-meadow/shallow-marsh emergents (m^2)
75 fluctuating	99	1	5,500
75constant	89	11	6,800
100 fluctuating	83	17	3,800
100 constant	58	42	5,200
125 fluctuating	49	51	3,700
125 constant	37	63	3,500
150 fluctuating	32	68	100
150 constant	27	73	300

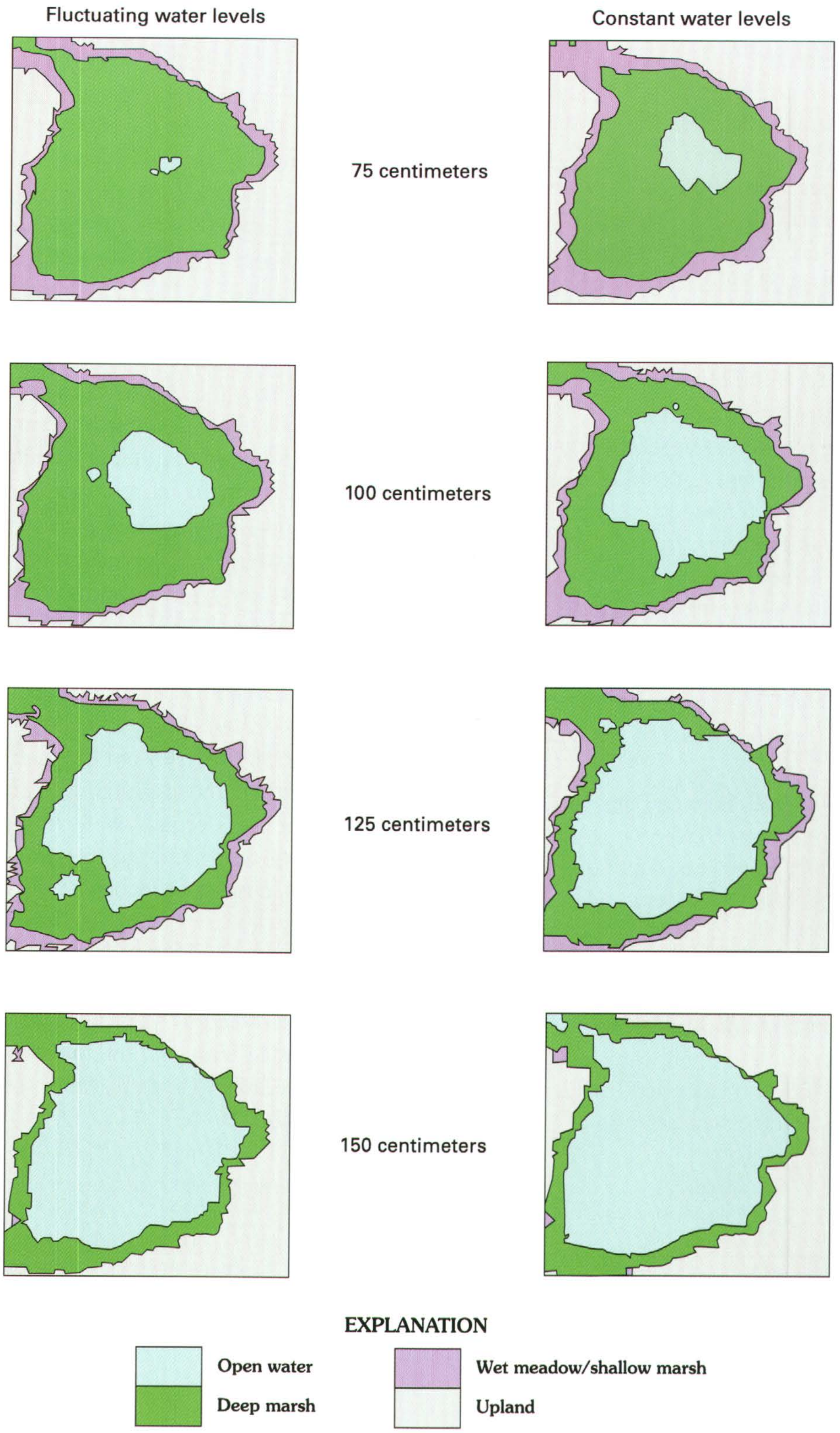


Figure 65. Model output of emergent vegetation cover and open-water distributions for eight 5-year water-depth simulations for Wetland P4. Results are shown for October of year 5.

These results indicate that a spatially-defined model that integrates hydrology, topography, and vegetation dynamics can provide target water levels for managers to reach desired habitat characteristics either for natural or restored wetlands. The simulations particularly are useful for wetlands that have controlled water levels or in designing basins for restoring and constructing wetlands. Model simulations should be less expensive to conduct than field experiments, particularly once a model is tested adequately and deemed reliable.

FUTURE NEEDS AND DIRECTIONS

The WETSIM models accurately represented wetland processes despite being based on simple algorithms and relations. The timing and magnitude of wetland drawdown and refill, and vegetation dynamics, closely followed observed values. Yet, while the models satisfactorily simulated major wetland dynamics during the test period, considerable work still is needed before the models can be used reliably to direct management or to assess more comprehensively the ramifications of human-induced impacts on prairie wetlands and waterfowl.

Several needs currently are being addressed through the development of a wetland landscape simulator (WETSCAPE). WETSCAPE expands WETSIM 2.0 to include ground-water dynamics and the hydrology of temporary and seasonal wetlands that typically occur near semipermanent wetlands in glaciated prairie landscapes. The response of these more ephemeral wetlands to climate change or management practices may differ from that of semipermanent wetlands. Shallow temporary and seasonal wetlands warm early in the spring and provide an abundant invertebrate community for migrating waterfowl and laying dabbling ducks (Swanson, 1988; Murkin and others, 1992). When these wetlands are dry in the spring or have a shortened annual hydroperiod, waterfowl production declines, even if semipermanent wetlands are in good condition (Swanson and Duebbert, 1989).

Models for all three wetland types (temporary, seasonal, and semipermanent) need to be tested beyond the Cottonwood Lake area for regional transferability. While model testing using the Cottonwood Lake data set will continue, data also are being collected from a wetland landscape in Deuel County, South Dakota (Hubbard and others, 1988). This site will enable the calibration and testing of WETSIM and WETSCAPE for a warmer and wetter portion of the prairie pothole region. The site has ground-water, surface-water, and vegetation data for 13 years, making it the site with the second longest data set for prairie wetlands in the Dakotas.

ACKNOWLEDGMENTS

We gratefully acknowledge the long-term consultation and data provided by Tom Winter and George Swanson. Both have been instrumental in model development and testing. Past funding for this work was provided by the Northern Prairie Wildlife Research Center, National Ecology Research Center, Patuxent Wildlife Research Center, and U.S. Environmental Protection Agency Global Change Program. Eugene Takle of Iowa State University provided GISS climate projections. The South Dakota Agricultural Experiment Station provided funds to interpolate GISS projections for the Dakotas. Tim Kittel provided valuable advice on various aspects of climate-impact studies.

REFERENCES

Boumans, R.M.J., and Sklar, F.H., 1990, A polygon-based spatial (PBS) model for simulating landscape change: Landscape Ecology, v. 4, p.83-97.

Browder, J.A., Bartley, H.A., and Davis, K.S., 1985, A probabilistic model of the relationship between marshland-water interface and marsh disintegration: Ecological Modeling, v. 29, p. 245-260.

Costanza, R. and Sklar, F.H., 1985, Articulation, accuracy and effectiveness of mathematical models: a review of freshwater wetland applications: Ecological Modeling, v. 27, p. 45-68.

Costanza, R., Sklar, F.H., and White M.L., 1990, Modeling coastal landscape dynamics: BioScience, v. 40, p. 91-107.

Ellison, A.M. and Bedford, B.L. 1995, Response of a wetland vascular plant community to disturbance: A simulation study: Ecological Applications, v. 5, p. 109-123.

Grace, J.B., 1989, Effects of water depth on Typha latifolia and Typha domingensis: American Journal of Botany, v. 76, p. 762-768.

Houghton, J.T., Jenkins, G.J. and Ephraums, J.J. (eds.), 1990, Climate change: The IPCC scientific assessment: Cambridge University Press, Cambridge, 404 p.

Hubbard, D.E., Millar, J.B., Nab, D.D., and Higgins, K.F., 1988, Soil-vegetation correlations in prairie potholes of Beadle and Deuel Counties, South Dakota: U. S. Fish & Wildlife Service Biological Report 88, 97 p.

Jorgensen, S.E. ed., 1983, Application of ecological modeling in environmental management, Part A: Elsevier, Amsterdam, 736 p.

Kantrud, HA., Millar, J.B. and van der Valk, A.G., 1989, Vegetation of wetlands of the prairie pothole region, *in* van der Valk, A.G., ed., Northern prairie wetlands: Iowa State University Press, Ames, p. 132-187.

Kittell, T.G.F., Sulzman, E.W., and Poiani, K.A., 1995, Modeling human climatic change: A summary for environemental managers: Environmental Management, v. 19, no. 2, p. 197-224.

LaBaugh, J.W., Winter, T.C., Adomaitis, V.A., and Swanson, G.A., 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, 26 p.

Larson, D. L., 1994, Potential effects of anthropogenic greenhouse gases on avian habitats and populations in the northern Great Plains: American Midland Naturalist, v. 131, p. 330-346.

Larson, D.L., 1995, Effects of climate on numbers of northern prairie wetlands: Climatic Change, v. 30, p.169-180.

Lee, J.K., Park, R.A., and Mausel, P.W., 1992, Application of geoprocessing and simulation modeling to estimate impacts of sea level rise on the northeast coast of Florida: Photogrammetric Engineering and Remote Sensing, v. 58, p.1579-1586.

McGuiness, J. L. and Bordne, E.F., 1972, A comparison of lysimeter-derived potential evapotranspiration with computed values: USDA Technical Bulletin 1452, 71 p.

Mitsch, W.J., Day, J.W., Taylor, J.R., and Madden, C.H., 1982, Models of North American freshwater wetlands: International Journal of Ecology and the Environment, v. 8, p.109-140.

Mitsch, W. J., Staskraba, M., and Jorgensen, S.E., 1988, Wetland modeling: Elsevier, New York, 238 p.

Murkin, E.J., Murkin, H.R., and Titman, R.D., 1992, Nektonic invertebrate abundance and distribution at the emergent vegetation-open water interface in the Delta Marsh, Manitoba, Canada: Wetlands, v. 12, p. 45-52.

Pearlstine, L., McKellar, H., and Kitchens, W., 1985, Modeling the impacts of a river diversion on bottomland forest communities in the Santee River floodplain, South Carolina: Ecological Modeling, v. 29, p. 283-302.

Phipps, R.L., 1979, Simulation of wetlands forest vegetation dynamics: Ecological Modeling, v. 7, p. 257-288.

Poiani, K.A., and Johnson, W.C., 1988, Evaluation of the emergence method in estimating seed bank composition of prairie wetlands: Aquatic Botany, v 32, p. 91-97.

_____1989, Effect of hydroperiod on seedbank composition in semipermanent prairie wetlands: Canadian Journal of Botany, v. 67, p.856-864.

_____1991. Global warming and prairie wetlands: Potential consequences for waterfowl habitat: BioScience, v. 41, p. 611-618.

_____1993a, A spatial simulation model of hydrology and vegetation dynamics in semi-permanent prairie wetlands: Ecological Applications, v. 3, p. 279-293.

_____1993b, Potential effects of climate change on prairie wetland hydrology and vegetation: Climatic Change, v. 24, p.213-232.

Poiani, K. A., Johnson, W .C., and Kittel, T.G.F., 1995, Sensitivity of a prairie wetland to increased temperature and seasonal precipitation changes: Water Resources Bulletin, v. 31, p. 283-294.

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

Sharpley, A.N. and Williams, J.R., eds., 1990, EPIC-Erosion/productivity impact calculator: 1. Model documentation: U.S. Department of Agriculture Technical Bulletin 1768, 235 p.

Shay, J.M., and Shay, C.T., 1986, Prairie marshes in western Canada, with specific reference to the ecology of five emergent macrophytes: Canadian Journal of Botany, v. 64, p.443-454.

Shjeflo, J.B., 1968, Evapotranspiration and the water budget of prairie potholes in North Dakota: U.S. Geological Survey Professional Paper 585-B, 49 p.

Sklar, F.H., Costanza, R., and Day, J.W., 1985, Dynamic spatial simulation modeling of coastal wetland habitat succession: Ecological Modeling, v. 29, p. 261-281.

Sorenson, L.G., Goldberg, R., Root, T., and Anderson, M. G., 1998, Potential effects of global warming on waterfowl populations breeding in the northern Great Plains: Climatic Change, v. 40, p.343-369.

Swanson, G.A., 1988, Aquatic habitats of breeding waterfowl, *in* Hook, D.D., ed., Ecology and management of wetlands, v. 1: Ecology of wetlands: Timber Press, Portland, Oregon. p. 195-202.

Swanson, G.A. and Duebbert, H.F., 1989, Wetland habitats of waterfowl in the prairie pothole region, *in* van der Valk, AG., ed., Northern prairie wetlands: Iowa State University Press, Ames, p. 228-267.

Takle, E.S. and Zhong, S., 1990. Dakota climate as projected by the global climate model of the Goddard Institute for Space Studies for a doubling of atmospheric carbon dioxide: Unpublished report. Iowa State University.

Thornthwaite, C.W., and Mather, J.R., 1957, Instructions and tables for computing potential evapotranspiration and the water balance: Drexel Institute of Technology, Publications in Climatology, v. 10, p.185-311.

van der Valk, A.G., 1981, Succession in wetlands: A Gleasonian approach: Ecology v. 62, p. 688-696.

van der Valk, A.G. and Davis, C.B., 1978, The role of seed banks in the vegetation dynamics of prairie glacial marshes: Ecology, v. 59, p. 322-335.

Weller, M.W., 1994, Freshwater marshes: Ecology and Wildlife Management: University of Minnesota Press, Mineapolis, 154 p.

Weller, M. W. and Frederickson, L.H., 1974, Avian ecology of a managed glacial marsh: The Living Bird, v. 12, p. 269-291.

Weller, M.W. and Spatcher, C.E., 1965, Role of habitat in the distribution and abundance of marsh birds: Iowa State University, Agricultural and Home Economics Experiment Station Special Report Number 43, 31 p.

Winter, T.C. and Carr, M.R., 1980, Hydrologic setting of wetlands in the Cottonwood Lake area, Stutsman County, North Dakota: U.S. Geological Survey Water-Resources Investigation 80-99, 42 p.

Printed on recycled paper

ISBN 0-607-89431-8

9 790607 894317