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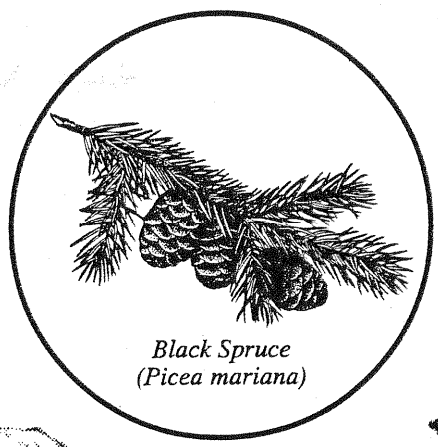
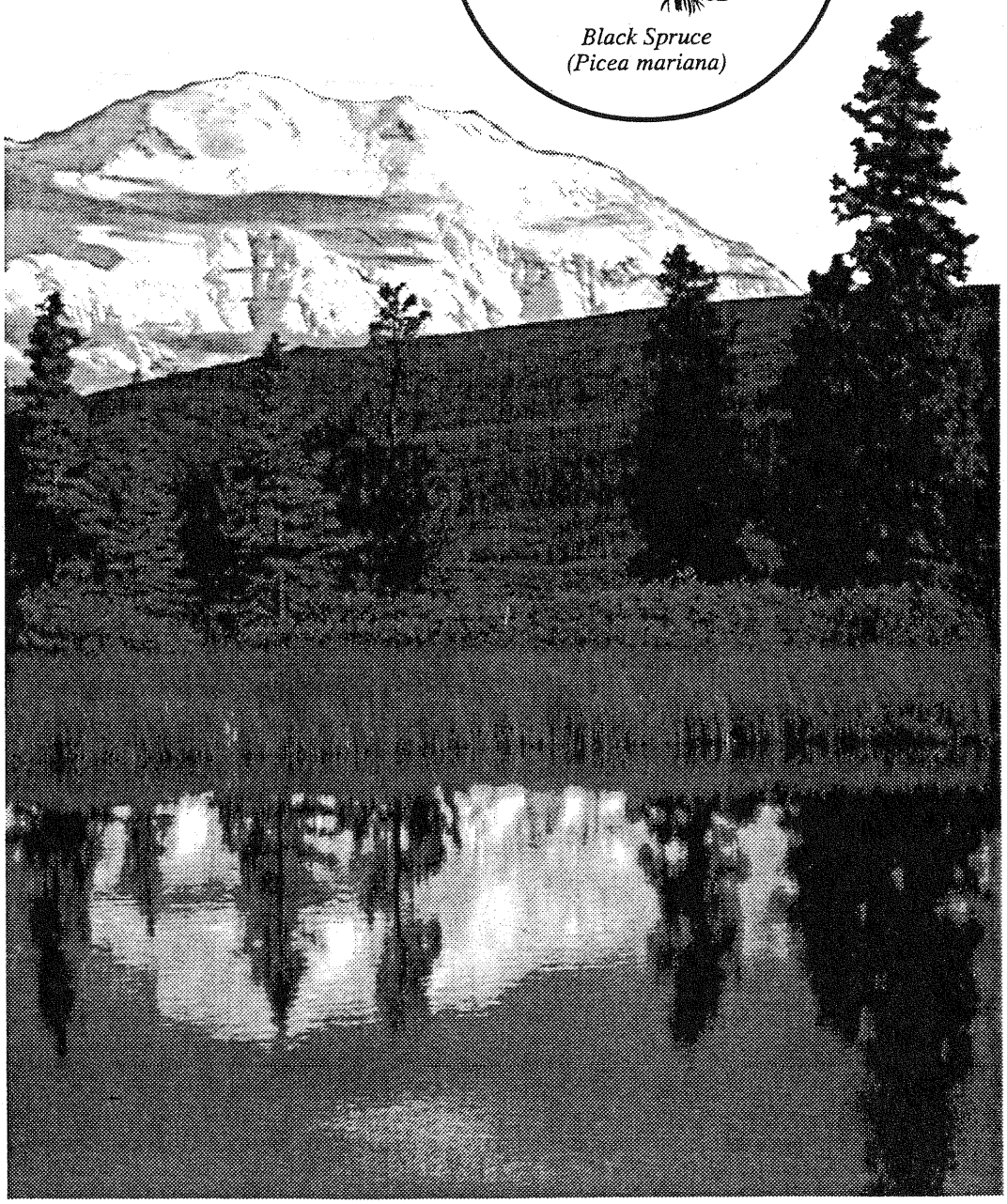


Black Spruce
(Picea mariana)



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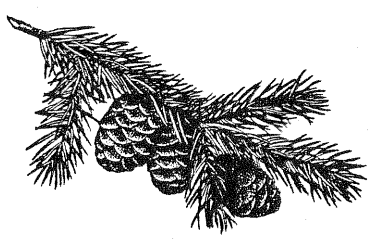
FUNCTIONAL PROFILE OF BLACK SPRUCE WETLANDS IN ALASKA

Prepared for
U.S. Environmental Protection Agency
Region 10

Prepared by
Roger A. Post
Alaska Department of Fish and Game
Fairbanks, Alaska

1996



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FUNCTIONAL PROFILE OF
BLACK SPRUCE WETLANDS IN ALASKA

by
Roger A. Post,
Alaska Department of Fish and Game

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FUNDING

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DEDICATION

This profile is dedicated to Dr. Maurice M. Alexander, Professor Emeritus, State University of New York, College of Environmental Science and Forestry at Syracuse. Dr. Alexander found room for "one more grad student" in his Department of Forest Zoology and through a teaching assistantship for his field ecology course exposed that student to the cattails of Clay Marsh, bulrushes of the inlet delta at Jamesville Reservoir, and hemlock swamps of the Heiberg Forest. Perhaps that exposure to wetlands needed a decade or two of incubation before recently surfacing in my career, but I am extremely grateful that it did, thanks in no small part to Dr. Alexander.

PREFACE

The functions and values of Alaska's wide variety of wetlands have received little study. This lack of information has posed difficulties for wetlands regulation pursuant to Section 404 of the federal Clean Water Act. The U.S. Environmental Protection Agency (EPA) and the U.S. Army Corps of Engineers (USACE) must balance the public's interest in a viable economy against the public's interest in wetland conservation and protection of water quality. Knowledge of wetland functions and values is a necessary component of such balancing in the regulatory process.

Alaska wetlands supporting black spruce are abundant and therefore commonly affected by development. These wetlands have been widely perceived as having low value, but objective documentation of their functions was lacking. Consequently, the EPA funded the Alaska Department of Fish and Game (ADF&G) to comprehensively review available literature and prepare a community profile for black spruce wetlands in Alaska. The ADF&G proposed, and EPA accepted, organizing the profile around commonly accepted wetland functions to maximize usefulness to wetland regulators and the regulated community.

Our initial expectations were that we would find little applicable literature and the profile would soon be written. Upon conducting our initial review, however, we discovered that a fair number of boreal forest studies and studies addressing treed bogs and fens existed in the literature. The ADF&G contributed substantial resources beyond the original grant matching funds to this project in order to produce a comprehensive treatment of black spruce wetlands. This process has taken more time than intended, but we believe the profile benefited from its long gestation.

The USACE, Natural Resources Conservation Service, and State of Alaska currently are developing models for use in the Hydrogeomorphic (HGM) approach to wetland assessment. Functional profiles of various wetland classes are an integral part of this approach. We hope that this profile will advance development of HGM for Alaska and benefit Alaskans for years to come.

CONTENTS

DEDICATION ii

PREFACE iii

CONTENTS iv

PHOTOGRAPHS viii

FIGURES ix

TABLES x

ACKNOWLEDGEMENTS xiii

PHOTOGRAPHS xiv

INTRODUCTION 1

BLACK SPRUCE AND THE TAIGA ENVIRONMENT 4

CLIMATE 4
Temperature and Precipitation 4
Evapotranspiration 4
Solar Radiation 6
PERMAFROST 7
Distribution 7
Formation and Degradation 7
Geomorphic Features 9
Effect on Soil Moisture 10
TAIGA ECOSYSTEMS 10
Paleoecology 10
Zones of Taiga Vegetation 10
Black Spruce Communities 12
Ecologic Succession 12
Succession-Permafrost Relationships 14
BLACK SPRUCE SPECIES CHARACTERISTICS 15
Distribution 15
Growth Forms and Densities 15
Adaptations 16
Reproduction 17

BLACK SPRUCE WETLANDS **18**

WHAT IS A WETLAND? 18
Definitions and Defining Characteristics *18*
Mires *20*
Relationship of Black Spruce Wetlands to Mires *21*
VEGETATION 22
Wetland Classes and Forms Supporting Black Spruce *22*
Wetland Potential of Representative Black Spruce Community Types in Alaska *22*
ACTIVITIES POTENTIALLY AFFECTING BLACK SPRUCE WETLANDS 24
Placement of Fill *24*
Drainage *24*
Flooding *24*
Clearing and Harvest of Woody Vegetation *25*
Disposal of Waste *25*
Mining of Peat *25*
RESEARCH 26
Forestry Studies *27*
Ecologic Studies *27*
Physical Studies *27*
Current Knowledge *27*

HYDROLOGIC FUNCTIONS **29**

GROUNDWATER DISCHARGE 29
Suprapermafrost Groundwater *29*
Subpermafrost Groundwater *30*
Groundwater Discharge in Unfrozen Terrain *30*
Functional Summary *31*
Functional Sensitivity to Impacts *31*
GROUNDWATER RECHARGE 32
Suprapermafrost Groundwater *32*
Subpermafrost Groundwater *33*
Groundwater Recharge in Unfrozen Terrain *33*
Functional Summary *33*
Functional Sensitivity to Impacts *33*
FLOW REGULATION 34
Subsurface Storage of Precipitation *34*
Detention and Depression Storage of Precipitation *35*
Release of Stored Precipitation and Effect on Streamflow *35*
Functional Summary *36*
Functional Sensitivity to Impacts *37*
EROSION CONTROL 38
Thermal Stability in Permafrost Terrain *38*
Mechanical Stability *38*
Functional Summary *38*
Functional Sensitivity to Impacts *38*
DATA GAPS 39
Groundwater Discharge *39*
Groundwater Recharge *39*
Flow Regulation *39*
Erosion Control *39*
Functional Sensitivity to Impacts *39*

WATER QUALITY FUNCTIONS **40**

SEDIMENT RETENTION 40

Suspended Solids in Wetland Runoff 40
Functional Summary 41
Functional Sensitivity to Impacts 42
NUTRIENT UPTAKE 42
Moss Layer 42
Tree, Shrub, and Herb Layers 44
Functional Summary 46
Functional Sensitivity to Impacts 46
NUTRIENT TRANSFORMATION 47
Nitrogen 47
Phosphorus 51
Functional Summary 54
Functional Sensitivity to Impacts 55
CONTAMINANT REMOVAL 55
Metal Uptake and Storage 55
Nutrient Immobilization 56
Buffering Capacity 58
Contaminant Degradation 58
Functional Summary 59
Functional Sensitivity to Impacts 59
DATA GAPS 60
Sediment Retention 60
Nutrient Uptake 60
Nutrient Transformation 60
Contaminant Removal 60
Functional Sensitivity to Impacts 60

GLOBAL BIOGEOCHEMICAL FUNCTIONS 62

CARBON CYCLING AND STORAGE 62
Primary Production 62
Decomposition 63
Functional Summary 65
Functional Sensitivity to Impacts 66
DATA GAPS 66

ECOLOGIC FUNCTIONS 67

NUTRIENT CYCLING 67
Distribution of Nutrients 67
Cycling Times and Fates of Nutrients 67
Functional Summary 69
Functional Sensitivity to Impacts 69
NUTRIENT EXPORT 69
Nitrogen 70
Phosphorus 70
Particulate and Dissolved Organic Carbon 71
Functional Summary 73
Functional Sensitivity to Impacts 73
FOOD CHAIN SUPPORT 74
Primary Production 74
Food Chains 76
Functional Summary 78
Functional Sensitivity to Impacts 79
HABITAT 79
Birds 79
Mammals 80

Amphibians *81*
Functional Summary *112*
Functional Sensitivity to Impacts *112*
DATA GAPS 113
Nutrient Cycling *113*
Nutrient Export *113*
Food Chain Support *113*
Habitat *113*
Functional Sensitivity to Impacts *114*

SOCIOECONOMIC USES 115

CONSUMPTIVE 115
Subsistence and Personal Uses *115*
Extraction of Economic Resources *116*
Use Summary *118*
Use Sensitivity to Impacts *118*
NONCONSUMPTIVE 118
Active Recreation *119*
Passive Recreation and Use of Heritage Sites *119*
Use Summary *120*
Use Sensitivity to Impacts *120*
DATA GAPS 121
Consumptive Uses *121*
Nonconsumptive Uses *121*
Use Sensitivity to Impacts *122*

SUMMARY AND CONCLUSIONS 123

BLACK SPRUCE AND THE TAIGA ENVIRONMENT 123
BLACK SPRUCE WETLANDS 124
HYDROLOGIC FUNCTIONS 125
WATER QUALITY FUNCTIONS 126
GLOBAL BIOGEOCHEMICAL FUNCTIONS 127
ECOLOGIC FUNCTIONS 128
SOCIOECONOMIC USES 129
CONCLUSIONS 130

LITERATURE CITED 131

APPENDIX A - WETLAND CLASSIFICATION 156

U.S. FISH AND WILDLIFE SERVICE SYSTEM 156
CANADIAN SYSTEM 156

APPENDIX B - SUBARCTIC AND BOREAL BOGS AND FENS IN THE CANADIAN CLASSIFICATION SYSTEM 158

APPENDIX C - PHYSICAL DESCRIPTIONS OF REPRESENTATIVE BLACK SPRUCE COMMUNITY TYPES OF ALASKA 161

APPENDIX D - INTERPRETATION OF AVIAN SURVEYS WITH RESPECT TO BLACK SPRUCE WETLAND HABITATS 163

ALASKA 163
CANADA 163
LOWER 48 STATES 163

GLOSSARY 168

PHOTOGRAPHS

Photo 1. Aerial view of black spruce/*Sphagnum* wetland, Eagle Quadrangle, eastern Interior Region viv

Photo 2. Ground-level view of black spruce/*Sphagnum* wetland, Eagle Quadrangle, eastern Interior Region xiv

Photo 3. Lowland black spruce wetland in a wetland mosaic, McGrath Quadrangle, western Interior Region xv

Photo 4. Moderately treed black spruce wetland near Aniak, southwestern Interior Region xv

Photo 5. Upland black spruce wetlands on interfluves, Yukon-Charley Rivers National Preserve, eastern Interior Region xvi

Photo 6. Black spruce/graminoid tussock wetland, Gulkana Quadrangle, southern Interior Region xvi

Photo 7. Black spruce/cotton grass wetland, Kenai Peninsula, Southern Region xvii

Photo 8. Black spruce/shrub wetland, Talkeetna Quadrangle, Southern Region xvii

FIGURES

Figure 1. Physical subdivisions of Alaska 2

Figure 2. Distribution of North American taiga 5

Figure 3. Equivalent latitudes for several forest research stands at 65 degrees N latitude 7

Figure 4. Permafrost distribution in Alaska 8

Figure 5. Nutrient uptake by green moss tissue in a permafrost black spruce stand, interior Alaska, as compared to nutrient addition by precipitation throughfall and litterfall 43

Figure 6. Comparative nutrient requirements for black spruce and other taiga trees as a group (white spruce, quaking aspen, paper birch, and balsam poplar) 44

Figure 7. Cattail and sedge biomasses at wastewater discharge and control sites, Hay River, N.W.T 46

Figure 8. Concentrations of NH_4-N and NO_3-N in incubated organic material from a mature black spruce-lichen woodland, Quebec 50

Figure 9. Net primary production for components of a northern ribbed fen in subarctic Quebec 64

Figure 10. Carbon balance for components of a northern ribbed fen in subarctic Quebec 64

Figure 11. Potassium distribution in a raised bog 68

Figure 12. Phosphorus exports from an organic-substrate cattail marsh, Ontario 71

Figure 13. Humic and fulvic acid concentrations in runoff from Minnesota mires 72

Figure 14. Soil and air temperatures at which maximum photosynthetic rates occurred in seedlings of taiga hardwoods 75

Figure 15. Annual production of taiga trees near Fairbanks, Alaska 75

Figure 16. Distribution of aboveground arthropod taxa among trophic levels in black spruce stands of interior Alaska 77

TABLES

Table 1. Representative climatic data for interior Alaska (Fairbanks) 6

Table 2. Permafrost-related geomorphic features of wetlands 9

Table 3. Paleoecologic history of black spruce in interior Alaska 11

Table 4. Paleoecologic history of black spruce in Yukon and western Northwest Territories 11

Table 5. Representative black spruce community types of interior Alaska 13

Table 6. Fire recurrence intervals for North American taiga locations 13

Table 7. Stem densities of several immature and mature black spruce stands, interior Alaska 16

Table 8. Soil pH at several black spruce sites in interior Alaska 16

Table 9. Representative wetland definitions 19

Table 10. Representative characteristics of bogs and fens 20

Table 11. Organic layer thickness and typical soils of Alaska Vegetation Classification (Level IV) classes dominated by black spruce 21

Table 12. Frequently occurring genera and species in North American bogs and fens 22

Table 13. Inferred probabilities that typical interior Alaska black spruce community types are jurisdictional wetlands based on stand descriptions from Foote (1983:28-48) 23

Table 14. Water quality variables that have shown increased levels in runoff from ditched or mined peatlands 26

Table 15. Typical concentrations of total suspended solids (TSS) in runoff from nonpermafrost peatlands 41

Table 16. Comparative N mineralization in several European and North American mires and forest stands 49

Table 17. Pools of NH_4-N and NO_3-N in wetland and nonwetland Alaska forest stands 50

Table 18. Phosphorus concentrations in several Canadian taiga mires with Fe concentrations <3.7 mg $Fe \cdot g^{-1}$ 52

Table 19. Phosphorus concentrations and pools in organic and mineral layers of several taiga black spruce stands 53

Table 20. Phosphorus-related characteristics of interior Alaska black spruce stands 53

Table 21. Periods of active peat accumulation in several North American and Asian mires 57

Table 22. Soil carbon contents of representative interior Alaska black spruce stands 63

Table 23. Combined carbon contents of aboveground tree components and forest floors of representative interior Alaska black spruce stands based on biomass 63

Table 24. Contrasting turnover times for nutrient elements in nonpermafrost black spruce stands in Ontario and largely permafrost stands in Alaska 68

Table 25. Nitrogen mineralization and fixation in a Minnesota bog and Alaska black spruce stands 69

Table 26. Nitrogen export in runoff from bogs and tundra peatland 70

Table 27. Phosphorus concentrations in runoff from northern peatlands 70

Table 28. Carbon concentrations in runoff from northern peatlands 72

Table 29. Carbon export rates for swamps and peatlands 73

Table 30. Comparative production of selected wetland communities and community components 76

Table 31. Common soil invertebrates found in European blanket bogs and Alaska tundra 78

Table 32. Use of aquatic habitats potentially associated with black spruce wetlands (BSW) by waterbirds (loons, grebes, waterfowl, gulls, and terns) in Alaska 82

Table 33. Use of black spruce wetlands (BSW) in Alaska by raptorial birds (hawks, eagles, harriers, ospreys, falcons, and owls) 86

Table 34. Use of black spruce wetlands (BSW) in Alaska by nonpasserine birds other than waterbirds and raptors (see preceding tables) 89

Table 35. Use of black spruce wetlands (BSW) in Alaska by passerine birds 94

Table 36. Frequently occurring avian species in Alaskan and Canadian black spruce forests and wetlands (all waterbirds except gulls, all raptors, and species not occurring in interior Alaska are excluded) 101

Table 37. Use of black spruce wetlands (BSW) in Alaska by insectivores, chiropterans, rodents, and lagomorphs 103

Table 38. Use of black spruce wetlands (BSW) in Alaska by carnivores 107

Table 39. Use of black spruce wetlands (BSW) in Alaska by cervid artiodactyls (moose, caribou) 110

Table 40. Mammals most characteristic of black spruce wetlands in Alaska 111

Table 41. Wood frog reproduction under ombrotrophic and minerotrophic conditions 111

Table 42. Representative subsistence harvests for several interior Alaska resources directly or indirectly related to black spruce wetlands 116

Table 43. Mean annual estimated furbearer harvests between 1986 and 1991 in Game Management Unit (GMU) 25 (northeastern Interior), GMU 24 (Koyukuk River), and GMU 21 (mid-Yukon River) 117

Table 44. Motorized forms of active recreation that occur in black spruce wetlands (BSWs) in Alaska 119

Table 45. Nonmotorized forms of active recreation that occur in black spruce wetlands (BSWs) in Alaska 119

Table D-1. Interpretation of avian surveys by Spindler and Kessel (1980) in eastern interior Alaska with respect to black spruce wetlands 164

Table D-2. Interpretation of breeding bird surveys by Cooper et al. (1991:279-280) near Tok and Gulkana, Alaska, with respect to black spruce wetlands 164

Table D-3. Interpretation of breeding bird surveys by Martin et al. (1995) in the Badger Slough watershed near Fairbanks, Alaska, with respect to black spruce wetlands 165

Table D-4. Interpretation of avian habitat studies by Spindler (1976) on the Fairbanks Wildlife Management Area with respect to black spruce wetlands 165

Table D-5. Interpretation of avian surveys by Kessel et al. (1982) near the Susitna River, Alaska, with respect to black spruce wetlands 165

Table D-6. Interpretation of avian survey plots used by Carbyn (1971) in Northwest Territories, Canada, with respect to black spruce wetlands. 166

Table D-7. Interpretation of avian surveys by Gillespie and Kendeigh (1982) in Manitoba, Canada, with respect to black spruce wetlands. 166

Table D-8. Interpretation of descriptions by Erskine (1977) of avian habitat use in boreal Canada 167

Table D-9. Interpretation of avian surveys by Ewert (1982) in Michigan "bogs" with respect to black spruce wetlands 167

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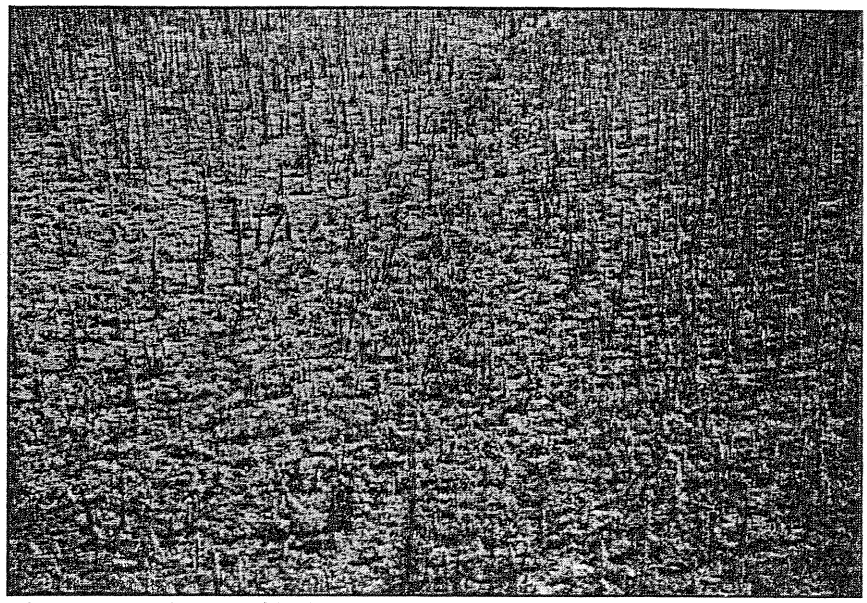

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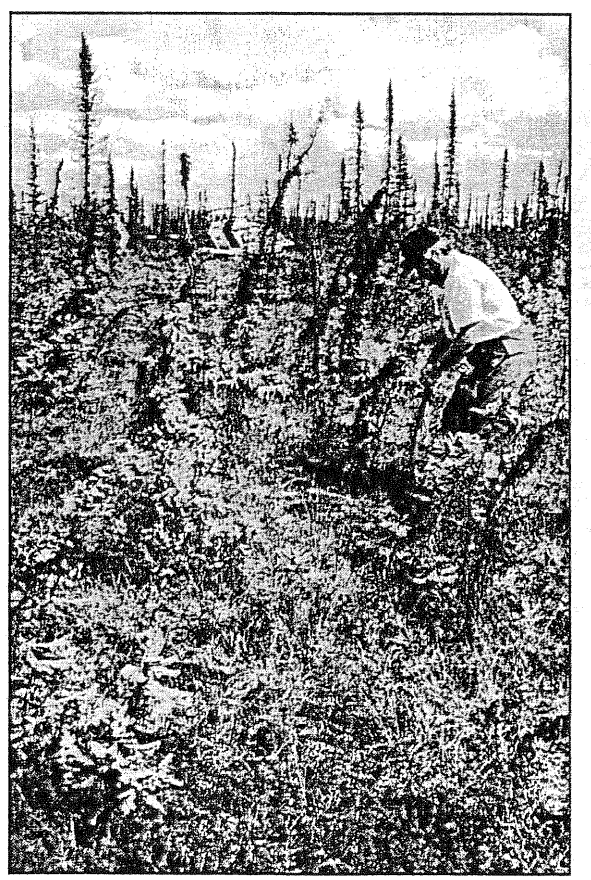
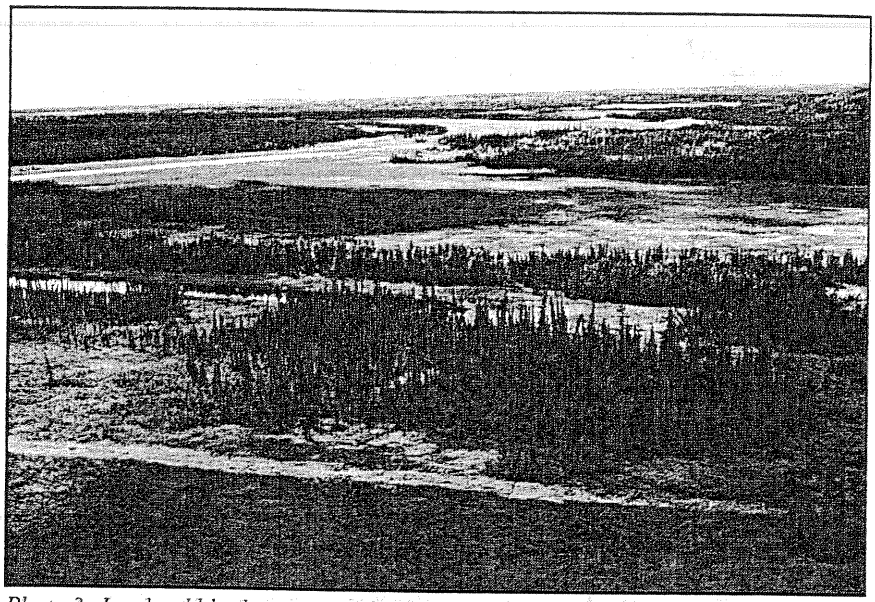


*Photo 2. Ground-level view of black spruce/*Sphagnum *wetland, Eagle Quadrangle, eastern Interior Region (photo courtesy U.S. Fish and Wildlife Service).*



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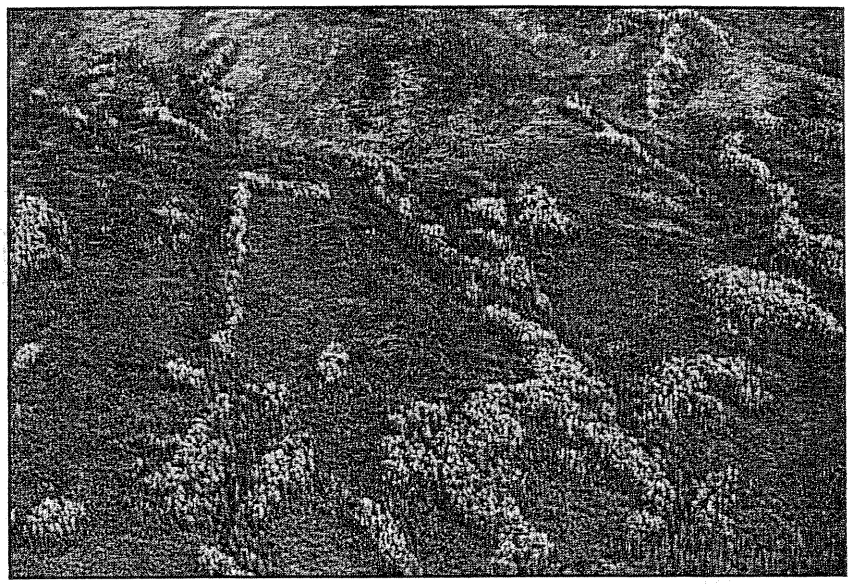

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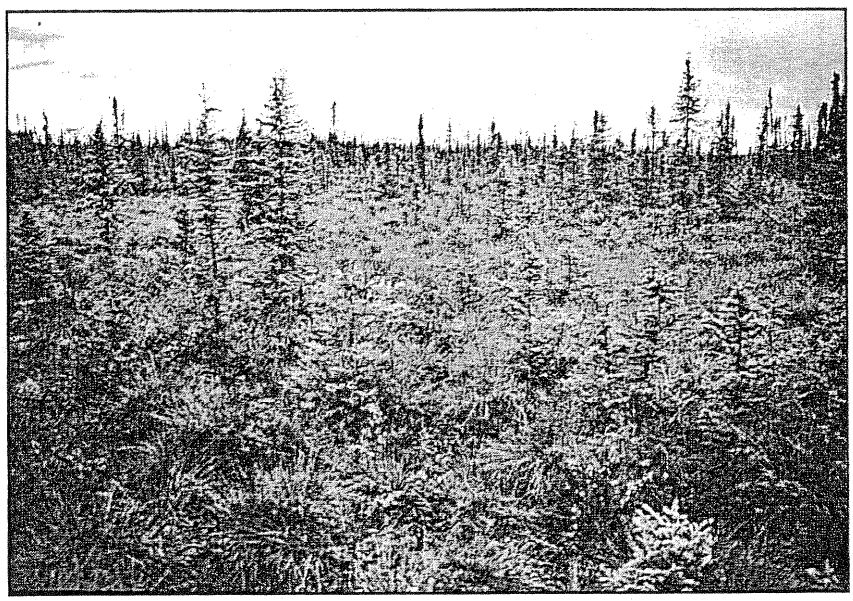

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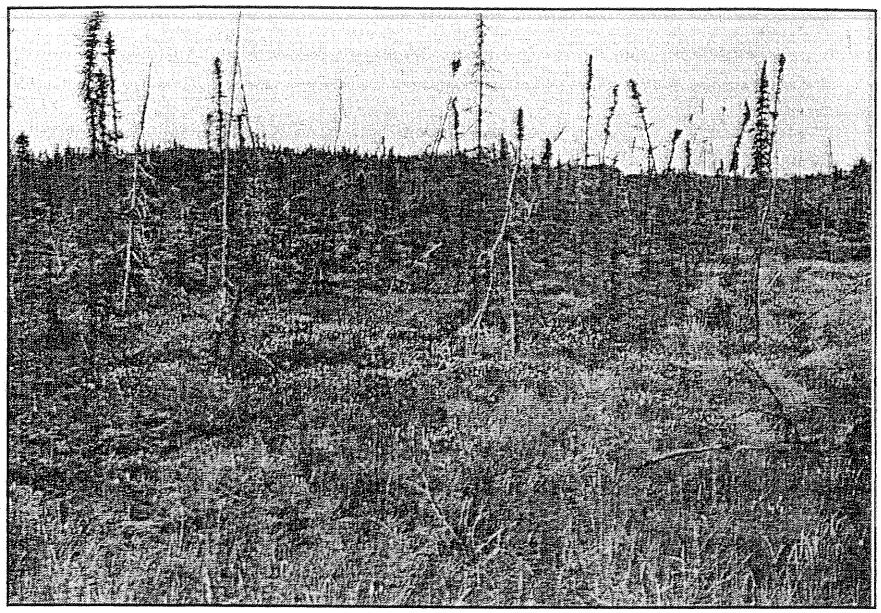

Photo 7. Black spruce/cotton grass wetland, Kenai Peninsula, Southern Region (photo courtesy U.S. Fish and Wildlife Service).

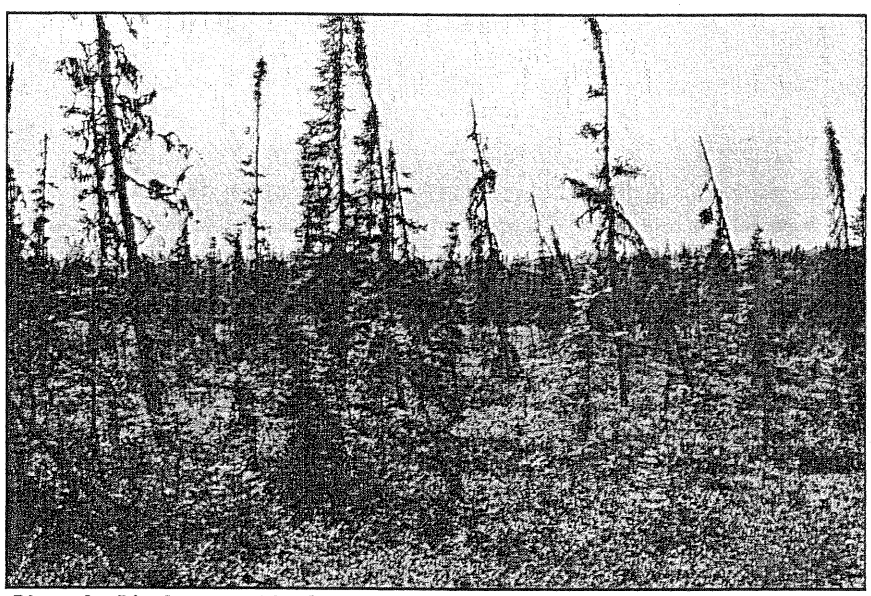

Photo 8. Black spruce/shrub wetland, Talkeetna Quadrangle, Southern Region (photo courtesy U.S. Fish and Wildlife Service).

INTRODUCTION

Alaska has 70.7 million ha of wetlands, approximately 63% of the remaining wetlands in the United States (Hall et al. 1994). Palustrine scrub-shrub and forested wetlands (see Appendix A for classification terminology) contribute about 51.7 million ha to Alaska's wetland area (Hall et al. 1994). In the Interior (Figure 1), most of the saturated forested wetlands (3.6 million ha) are classified as needle-leaved (i.e., conifer), and approximately half of the palustrine scrub-shrub wetlands (21.1 million ha) are dominated by black spruce (*Picea mariana*) (Hall et al. 1994; J. V. Hall, U.S. Fish Wildl. Serv., pers. commun.). Palustrine scrub-shrub and forested wetlands cover about 2.8 million ha of southern Alaska (Hall et al. 1994), much of which lies outside the distribution of black spruce. Wetlands supporting black spruce probably occupy about 14 million ha of Alaska, mainly in the Interior.

Open black spruce forests and woodlands often merge with sparsely treed or treeless *Sphagnum* peatlands (Viereck and Dyrness 1980) because size and stand density decrease with increasing soil moisture. These peat-accumulating wetlands develop in poorly drained lowlands and on cold slopes throughout the boreal forest where resistant bedrock, marine and lacustrine clays, glacial tills, or permafrost impede drainage (Heilman 1963; Brown and Péwé 1973; Zoltai, Tarnocai et al. 1988). Black spruce/moss woodlands occurring on peat sometimes are called "muskeg" (Gabriel and Talbot 1984:74, Natl. Wetlands Working Group 1988:437), although this term is imprecise and not generally used in contemporary wetland classification systems (Zoltai 1988), in part because similar communities occur on nonwetland sites (S. C. Zoltai, Can. For. Serv., pers. commun.).

Poorly drained black spruce stands occur in the Closed Needleleaf Forest, Open Needleleaf Forest, Needleleaf Woodland, Open Dwarf Tree Scrub, and Dwarf Tree Scrub Woodland hierarchical groupings of *The Alaska Vegetation Classification* (Viereck et al. 1992); scattered black spruce can occur in the Open Low Scrub grouping, as well. Lugo (1990:2) considers any wetland with "a significant component of woody vegetation, regardless of the size of the plants" as a forested wetland. For purposes of this report, a wetland (*sensu* Cowardin et. al. 1979, Natl. Res. Counc. 1995:59) containing black spruce of any size or stand density is a ***black spruce wetland*** (BSW).

Black spruce wetlands, by virtue of their abundance, are important boreal ecosystems. This abundance, and the regulated status of wetlands in the United States, engender conflicts with human economic development activities. Many communities in the Interior are surrounded by BSWs. Although such wetlands generally are not attractive for low-density residential development, commercial development, including high-density housing, may occur following wetland drainage or placement of fill. Regulatory decisions concerning conversion of these wetlands to other uses pursuant to Section 404 of the federal Clean Water Act require knowledge about their ***wetland functions*** (*sensu* Adamus and Stockwell 1983, Sather and Smith 1984) and hence their values to society.

Wetland functions are the physical, chemical, and biological processes that occur within wetlands. Such functions may be regarded as ecologic services provided by wetlands (Larson et al. 1988). These services are expressed at the level of ecosystem components (e.g., fish and wildlife populations, tim-

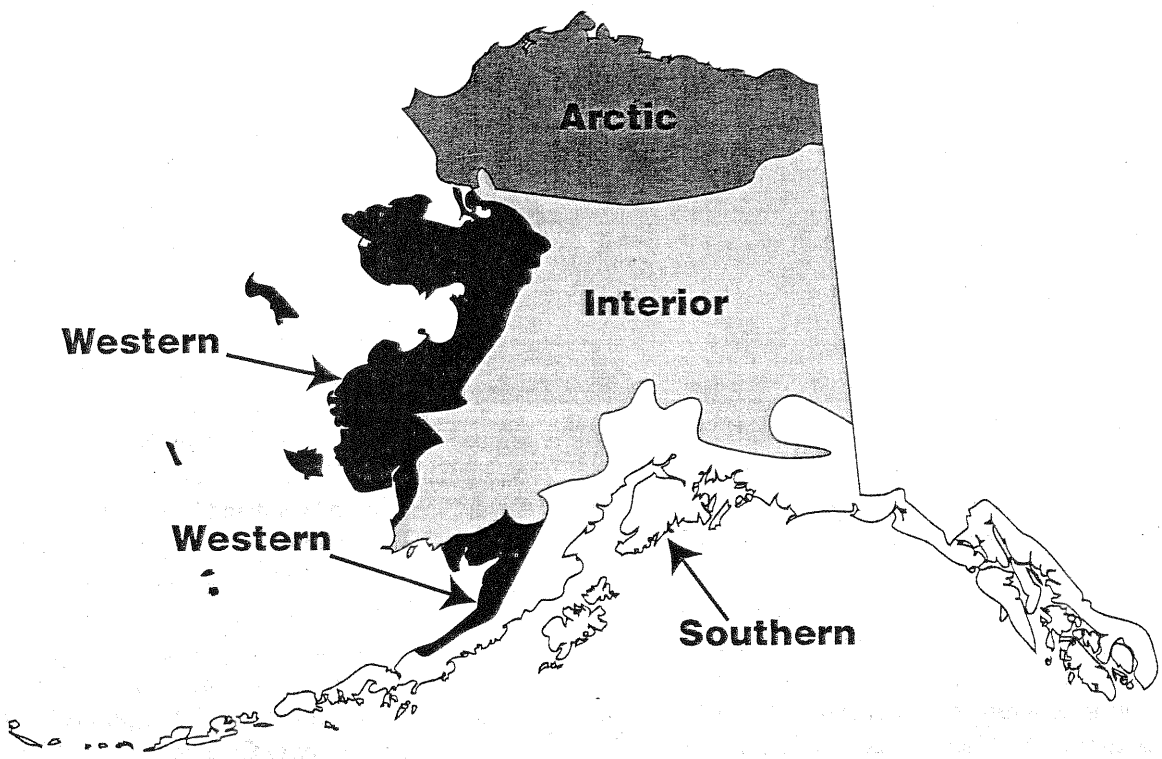

Figure 1. Physical subdivisions of Alaska (Hall et al., 1994).

ber stands), entire ecosystems (e.g., water storage, primary production), or global life support systems (e.g., biogeochemical cycling of elements), and humans may assign values to them (Odum 1979).

Several authors have grouped and described wetland functions based on available literature (Adamus and Stockwell 1983, Sather and Smith 1984). Other authors have discussed individual functions or closely related functions, for example hydrology (Carter et. al. 1979), water quality (Kadlec and Kadlec 1979), primary production and food chain support (Livingston and Loucks 1979), and habitat (Weller 1979). Socioeconomic aspects of wetlands are often called wetland functions (Sather and Smith 1984:58-68), but socioeconomics involves human perceptions and activities and thus values. Because this report does not discuss values, it will identify only socioeconomic "uses" of wetlands. These uses depend upon the physical, chemical, and biological processes, or functions, that shape individual wetlands.

Many people perceive few functions and low values for BSWs. Although hydrologic and ecologic aspects of BSWs have been studied in Alaska, particularly in relation to fire, permafrost, and ecologic succession, systematic examination of wetland functions associated with these communities has not occurred. Impacts of wetland conversion on hydrology, water quality, nutrient cycling, nutrient export, food chain support, fish and wildlife habitat, and recreation and heritage uses must be known before wetland avoidance, impact minimization, or compensatory mitigation can rationally be applied during the regulatory process.

The objective of this report is to provide a "functional profile" of Alaska's BSWs for use by scientists, wetland managers, commercial interests, and citizens. These groups can use the profile to identify

potential wetland research topics, provide a basis for regulatory and resource management decisions, design potential development projects to minimize impacts to wetland functions, and become informed participants in wetland conservation. In addition, functional profiles are an integral part of the Hydrogeomorphic approach to wetland assessment (Brinson 1993), a system under development for potential nationwide application by the U.S. Army Corps of Engineers. This profile should facilitate implementation of the hydrogeomorphic system in Alaska.

Because few directed studies of wetland functions exist for Alaska, this profile cites many studies conducted outside Alaska, usually within the boreal forest but occasionally including northern temperate locations. Wetland functions extrapolated from one area to another are likely to be correct in broad outline when reviewed for consistency with research conducted in the geographic area of interest but nonetheless should be used with caution. Future research should verify these functions and make clear the unique details of Alaska's BSWs.

This report first describes the northern coniferous (boreal) forest biome to establish the context within which BSWs occur. Descriptive material pertinent to these communities follows discussion of general wetland characteristics and classification systems to provide a vocabulary for the remainder of the profile. Activities potentially impacting BSWs, as well as research applicable to the functions of these wetlands, also are discussed. Finally, the main body of the profile identifies functions and socioeconomic uses of BSWs, analyzes their sensitivities to placement of fill and drainage, and identifies data gaps on a function-by-function basis.

A glossary is appended to the profile. Terms likely to be unfamiliar to nonspecialists appear in bold italics when first defined in the text and appear again in the glossary for ease of reference.

BLACK SPRUCE AND THE TAIGA ENVIRONMENT

Black spruce wetlands occur within the ***taiga***, the northern coniferous forest extending across northern North America (Figure 2) and Eurasia (Viereck 1975, Pruitt 1978:1-7, Oechel and Lawrence 1985). Long, cold winters; short, warm summers; relatively low precipitation; permafrost (in the north); and a fire-dominated landscape (in the west) are characteristic of this environment in North America (Viereck 1983, Kimmins and Wein 1986). The following discussion of climate, permafrost, and plant ecology demonstrates how the taiga environment establishes conditions that support black spruce forests and wetlands.

CLIMATE

Climate, in part, establishes the range of ecosystems that exist in the taiga (Van Cleve et al. 1991). Subarctic climates characterize this zone, which is a source region for continental polar air masses (Strahler 1963:329-344). Maritime influences may be present in coastal regions at the periphery of the boreal forest (Zasada 1976; Foster 1984; Wells and Hirvonen 1988; Zoltai, Tarnocai et al. 1988; Zoltai, Taylor et al. 1988). The following synopsis of climatic factors facilitates understanding ecosystem processes in taiga wetlands.

Temperature and Precipitation

Temperature extremes exemplify the primarily continental aspects of the taiga climate (Table 1). Mean monthly temperatures in Fairbanks, Alaska, vary much more on an annual basis for winter than for summer, with extreme low temperatures occasionally reaching -50°C (Bowling 1979, 1984). Precipitation (Table 1) varies from about 250 mm to more than 500 mm over the range of black spruce in Alaska (precipitation distributions mapped by Watson [1959 *in* Wahrhaftig 1965] and by Lampke [1979 *in* Rundquist et al. 1986]). Higher elevations receive more precipitation than do lowlands (Haugen et al. 1982, Slaughter and Viereck 1986).

Snowcover is essentially continuous between November and March or April because thawing conditions rarely occur during this period (Bowling 1979). Taiga snow (***api***) generally is uniformly distributed, with annual variation in depth of accumulation, and characterized by low density (Pruitt 1978:12-14). Several metamorphic processes act to increase or stratify snow density during the course of the winter (Marchand 1987:12-19). ***Pukak*** or depth hoar crystals grow in a columnar structure at the base of the snowpack forming a subnivean space that provides a favorable microclimate for overwintering plants and animals (Pruitt 1984).

Evapotranspiration

Evaporation and transpiration, in part, control soil moisture (Buckman and Brady 1969:240). Thornthwaite's (1948 *in* Lee 1980:178) estimator for potential evapotranspiration (PET) is based on mean monthly air temperature and approximated by evaporation from Class A pans (Ford and Bedford 1987). Water balances calculated using PET (Table 1) can be inaccurate (Ford and Bedford 1987), however, if underlying assumptions are not met (Buckman and Brady 1969:188-196, Lee 1980:154-181, Ingram 1983).

The difference between measured precipitation and runoff provides an alternative estimator of evapotranspiration that can yield much smaller values than calculated PET (Lee 1980:170-174, Ford and Bedford 1987). About half of annual precipita-

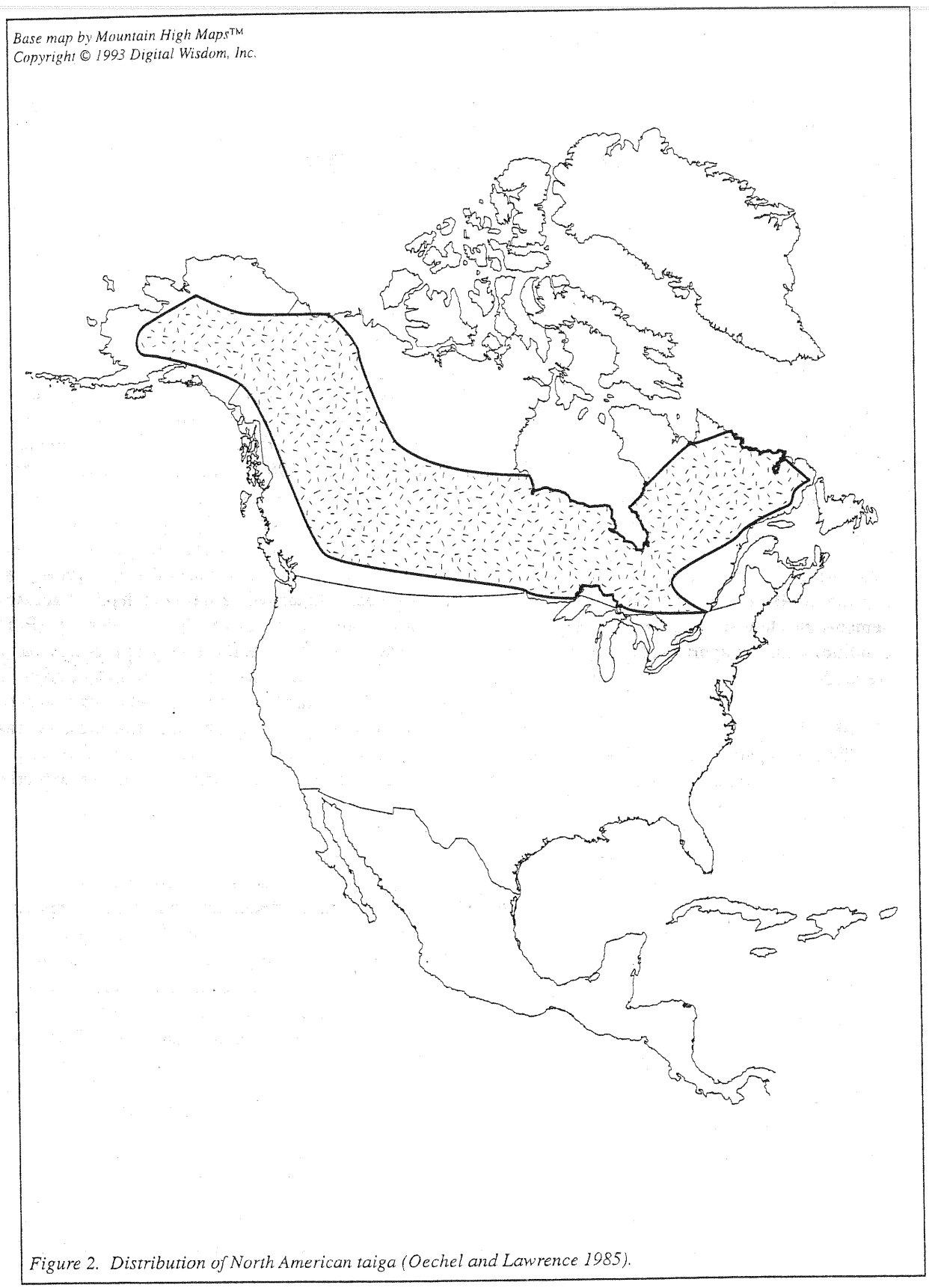

Figure 2. Distribution of North American taiga (Oechel and Lawrence 1985).

Table 1. Representative climatic data for interior Alaska (Fairbanks).

Climatic Variable (units)	Variable Value	Source
January Mean Temperature (°C)	-24.4	Haugen et al. (1982:6-8)
July Mean Temperature (°C)	17.1	Haugen et al. (1982:6-8)
Freezing Degree-Days (°C-day)	3,084	Haugen et al. (1982:6-8)
Thawing Degree-Days (°C-day)	1,799	Haugen et al. (1982:6-8)
Growing Season (frost-free days [0°C])	89 to 90	Ping (1987), Sharratt (1992)
Total Precipitation (mm)	284	Ping (1987)
Precipitation as Snowfall (%)	35	Slaughter and Viereck (1986)
Potential Evapotranspiration (mm)	350 to 450	Slaughter and Viereck (1986)
Precipitation Deficit (mm)	188	Slaughter and Viereck (1986)
December Solar Radiation ($kJ \cdot m^{-2} \cdot day^{-1}$)	231	Slaughter and Viereck (1986)
June Solar Radiation ($kJ \cdot m^{-2} \cdot day^{-1}$)	22,375	Slaughter and Viereck (1986)

tion appears as runoff from a small taiga drainage basin near Fairbanks, which implies that the remainder appears as evapotranspiration, a value equivalent to 31% of calculated PET (Dingman 1971). Thus, although interior Alaska is semiarid (Van Cleve et al. 1991) to subhumid (D. K. Swanson, Nat. Resour. Cons. Serv., pers. commun.), it has relatively low evapotranspiration rates, permitting wet soils to exist (Patric and Black 1968 *in* Slaughter and Viereck 1986). Wetlands supplied solely by precipitation theoretically could not exist where net evaporative water balances were negative (Ford and Bedford 1987). Indications that actual evaporative water balances are positive in the Alaskan taiga help account for the existence of precipitation-driven wetlands in this environment.

Solar Radiation

Day length and the angle of incidence of solar radiation vary with latitude and the time of year. Consequently, average daily solar radiation is unevenly distributed throughout the year at northerly taiga latitudes (Table 1) but more uniformly distributed at southerly latitudes (Strahler 1963:196). Seasonal radiation balances also vary widely in taiga regions (Pruitt 1978:8). An excess of outgoing long-wave radiation over incoming short-wave radiation under clear winter skies makes polar regions net heat sinks (Strahler 1963:206, Jayaweera et al. 1973).

Vegetation modifies the energy flux between the earth and atmosphere in significant ways, including influencing permafrost formation and the magnitude of seasonal frost phenomena in soils (Benninghoff 1963). Black spruce canopies intercept incoming short-wave solar radiation and reduce incident radiation reaching forest floors (Petzold 1981, Slaughter 1983). In addition to the effects of vegetation, topography strongly controls local climatic conditions through its influence on the intensity and duration of solar radiation incident on the ground surface (Slaughter and Viereck 1986, Van Cleve et al. 1991).

Topographic control of microclimates may be understood through the concepts of potential insolation and equivalent latitude (Dingman 1971, Koutz and Slaughter 1973, Dingman and Koutz 1974). Lee (1964 *in* Dingman 1971) provided an equation that relates slope inclination, aspect (azimuth), and actual latitude to an equivalent latitude in terms of solar radiation (potential insolation) striking a horizontal surface. Equivalent latitude affects the distribution of permafrost (Dingman 1971, Koutz and Slaughter 1973, Dingman and Koutz 1974, Collins et al. 1988) and forest communities (Figure 3) in interior Alaska.

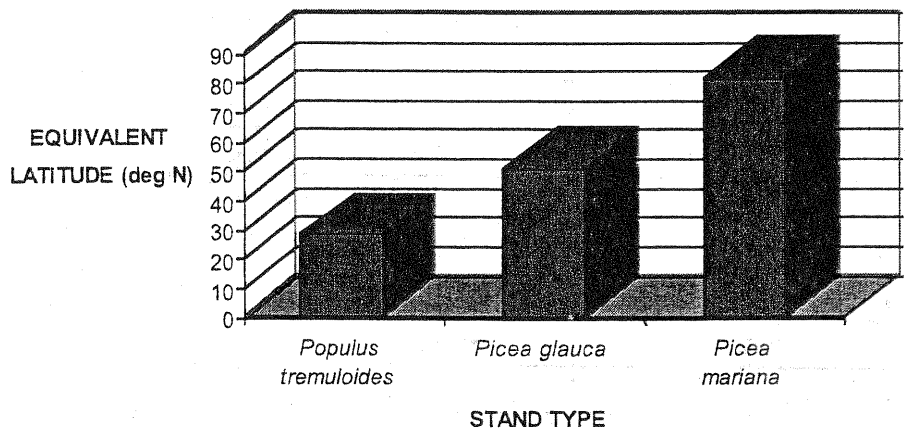

Figure 3. Equivalent latitudes for several forest research stands at 65 degrees N latitude (Slaughter and Viereck 1986).

PERMAFROST

Soil, rock, or other substrates that continuously remain at temperatures below 0°C for ≥2 yr are ***permafrost*** (Brown and Péwé 1973, Pruitt 1978:17-18). The physical characteristics of permafrost substrates strongly influence taiga ecosystems, including wetlands and wetland functions. This section discusses permafrost distribution, formation, and degradation; geomorphic features associated with permafrost; and the effect of permafrost on soil moisture.

Distribution

Permafrost may be continuous or discontinuous in its distribution (Péwé 1975:44). Across North America, the geographic zone of continuous permafrost is more or less coincident with the Arctic (tundra) and the zone of discontinuous permafrost with the Subarctic, which coincides with all but the southernmost portion of the taiga (Pruitt 1978, Ping et al. 1992; cf. maps in Brown and Péwé [1973], Bliss [1981], and Oechel and Lawrence [1985]). In Alaska, the Brooks Range roughly separates continuous permafrost from the zone of discontinuous permafrost (Figure 4) extending southward nearly to the coast of the Gulf of Alaska (Brown and Péwé 1973). Permafrost is encountered very rarely in southern Alaska, where mean annual air temperatures are warmer than in the Interior (Péwé 1975:44, Ping et al. 1992). Permafrost occurs in mountains in areas where it is absent at lower elevations (Brown and Péwé 1973).

Formation and Degradation

Permafrost forms or degrades in response to the thermal balance of the ground (Péwé 1975:47). Fluctuations in thermal balances of soils may manifest themselves rapidly in "warm" frozen soils (i.e., only slightly below 0°C) typical of the zone of discontinuous permafrost because the amount of heat gain necessary to induce thaw is less than for "cold" permafrost (Péwé 1975:47, Ping et al. 1992). Factors influencing this balance include regional climate, vegetation, and topography, which in turn influence microclimatic conditions such as snow cover (Brown 1963, Washburn 1973, Péwé 1975:47, Ping 1987, Collins et al. 1988).

Relict permafrost can occur where the mean annual air temperature (MAAT) is ≤0°C, but the -1°C or -2°C isotherm is the southern limit of equilibrium permafrost distribution (Brown and Péwé 1973, Ping et al. 1992). Mean annual ground temperatures are 3.6°C warmer than MAATs in disturbed terrain (Haugen et al. 1983), which may support the -2°C MAAT limit for discontinuous permafrost. Warmer

soil temperatures occur where winter snow cover is continuous as compared to areas without continuous cover (Ping 1987).

Surface organics affect permafrost formation and degradation (Harris 1987). Organic mats have low thermal diffusivities when dry, inhibiting heat flow into underlying mineral soil, but have higher diffusivities when wet, allowing evaporative cooling of the ground surface (Riseborough and Burn 1988). In addition, saturated, frozen peat conducts heat better than drier, thawed peat so that the organic layer impedes summer heat transfer into the ground more than winter transfer to the atmosphere (Brown and Péwé 1973). Permafrost degrades (i.e., seasonal thaw increases) following removal of forest vegetation by fire (Viereck and Foote 1979*b*, Viereck 1982) or mechanical disturbance (Dyrness 1982, Viereck 1982, Evans et al. 1988). Land clearing at an interior Alaska site raised mean annual soil temperature (MAST) by 3.4°C and caused the permafrost table to retreat to ~9 m below the surface after a period of 34 yr (Ping 1987). Conversely, permafrost aggrades as mature forest communities develop and insulate soil surfaces (Viereck 1973*b*, 1983; Ping et al. 1992).

Thaw phenomena occur where ground ice may be present in soil pores, ice seams or lenses, massive wedges, pingos, or buried masses (Péwé 1975:48-49). ***Thermokarst*** topography results when permafrost thaws and "creates an uneven topography which consists of mounds, sinkholes, tunnels, caverns, short ravines, lake basins, and circular lowlands caused by melting of ground ice" (Péwé 1975:65). Thawing of large ice masses, which can be initiated by loss of vegetative cover (Brown 1963, Washburn 1973, Péwé 1975:65), can produce striking features such as thermokarst pits; flowing water intercepted by these features can accelerate their formation (Péwé 1982:34-40).

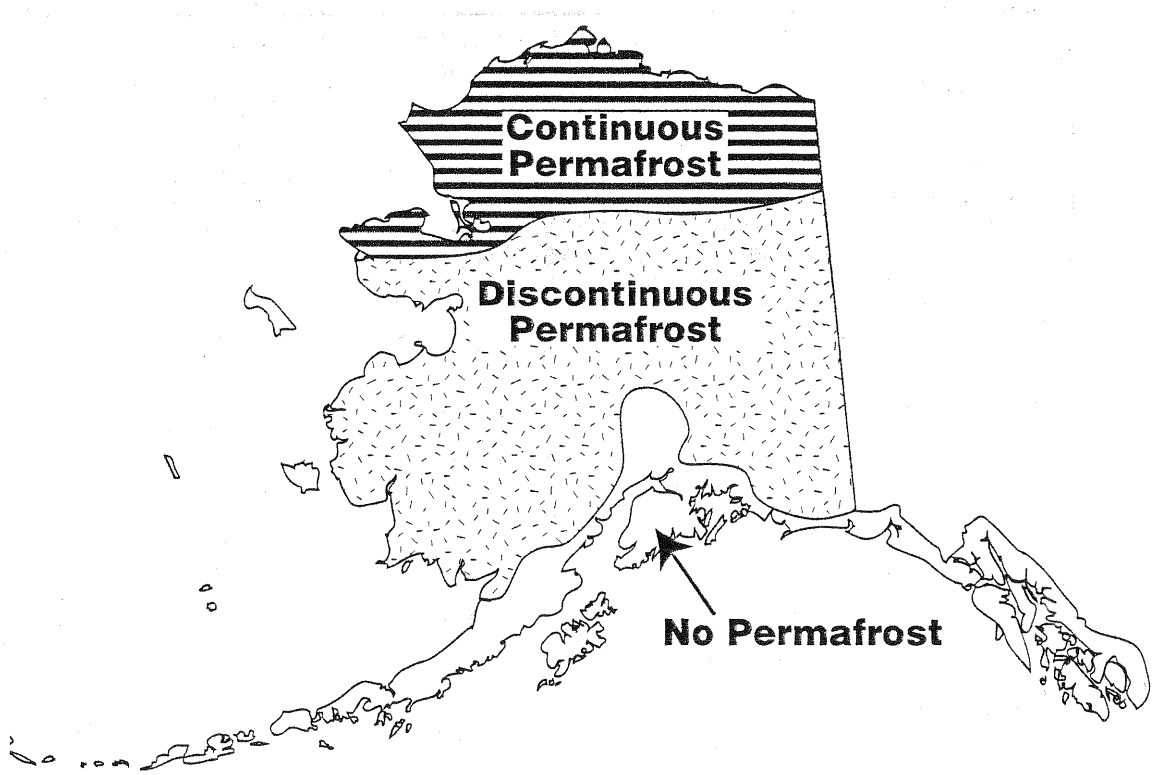

Figure 4. Permafrost distribution in Alaska (Ping et al. 1992)

Geomorphic Features

Water interacts with permafrost to produce interesting geomorphic features (Table 2). ***Palsas*** and ***peat plateaus*** are raised permafrost landforms occurring in peatlands (Zoltai 1972). Palsa and peat plateau formation and degradation are sensitive to vegetative cover and climatic conditions, including wind and snow cover (Thie 1974, Kershaw and Gill 1979, Seppälä 1982, Laprise and Payette 1988). Palsas may be initiated by wind scour on a peatland surface (Seppälä 1982). Moisture migrating to the frozen core of a palsa produces segregated ice, raises the palsa surface, and enables further wind scour (Brown and Péwé 1973, Péwé 1975:48, Kershaw and Gill 1979, Seppälä 1982).

Open-system ***pingos*** form in colluvium and valley fill material near slope bases, often with south or southeast aspects and muskeg or "bog" vegetation around, but not on, the pingos (Holmes et al. 1963, Brown and Péwé 1973, Péwé 1975:56, Ferrians 1988). ***Patterned ground,*** with polygons typically 3 to 12 m across in interior Alaska (Péwé 1982:28), occurs both in the zone of continuous permafrost, where ***ice wedges*** are generally active (i.e., still growing), and in the zone of discontinuous permafrost, where wedges may be active or inactive (Brown and Péwé 1973, Hamilton et al. 1983). Inactive wedges may partially or completely thaw and leave casts useful for studying paleoenvironments (Brown and Péwé 1973, Péwé 1975:52-56).

Fire (Péwé 1982:35, Zoltai 1993), or windthrow that raises tip-up mounds (Wallace 1948), may initiate thaw and surface subsidence. Ponded water and sediment are heated by the sun (Pavlov and Are 1984) to form ***thaw lakes***. Suggestions that thaw ponds and lakes are cyclic phenomena (Wallace

Table 2. Permafrost-related geomorphic features of wetlands

Geomorphic Feature	Description	Source
Palsa	Peat-covered mound or hummock from ~0.1 to 10 m in height and from ~3 to 100 m in diameter that contains a core of segregated ice and is found in peatlands	Brown and Péwé (1973), Péwé (1975:66), Kershaw and Gill (1979), Seppälä (1982), Natl. Wetlands Working Group (1988:417-420)
Peat Plateau	Landform with an internal structure similar to a palsa but having a flat surface that may cover several square kilometers	Kershaw and Gill (1979)
Pingo	Large mound or hill ranging from 30 to 1,000 m in diameter and from 3 to 70 m in height and containing massive ice heaved above the surrounding landscape by artesian or hydrostatic pressure and ice crystallization pressure	Holmes et al. (1963), Brown and Péwé (1973), Péwé (1975:56), Ferrians (1988)
Patterned Ground	The expression of an underlying polygonal pattern of ice wedges on the surface of the ground; may also occur through intense seasonal frost processes in nonpermafrost areas with severely maritime climates and low mean annual temperatures	Brown and Péwé (1973), Henderson (1968)
Ice Wedge	Massive structure ranging from 0.01 to 3 m in width and 1 to 10 m in height when viewed in transverse section (i.e., end-on view) and up to 15 m in length when viewed in longitudinal section (i.e., face-on view); active ice wedges grow by periodic cold-induced vertical cracking that allows surface water to enter the cracks and refreeze	Péwé (1975:49), Lachenbruch (1962 *in* Péwé 1975:51)
Thaw Lake	Cave-in lake on flat or gently sloping terrain underlain by fine-grained sediments formed when water ponds in a thermokarst depression and promotes radial thaw and bank caving; thaw may continue for long periods of time with eventual coalescence of ponds into larger lakes	Wallace (1948), Hopkins et al. (1955:140), Hopkins and Kidd (1988)

1948, Drury 1956:103, Viereck 1970) are supported by peat stratigraphy showing episodes of fire-induced permafrost degradation followed by peat accumulation and eventual permafrost aggradation (Zoltai 1993).

Effect on Soil Moisture

Permafrost profoundly affects soil moisture by forming a relatively impermeable zone in the soil profile, which often retains water near the ground surface (Dingman 1975:42, Pruitt 1978:21, Ping et al. 1992). Many wetlands in interior and arctic Alaska thus exist as a result of permafrost (Batten 1990). Permafrost also influences physical phenomena such as the hydrologic characteristics of watersheds (Dingman 1975:2).

Cold, wet soils on permafrost sites, in part, control ecologic processes, including typical vegetation communities and their successional development (Viereck 1970, Van Cleve et al. 1991). For example, black spruce occupies the coldest, wettest sites supporting forest stands in interior Alaska (Van Cleve and Yarie 1986). Nevertheless, factors such as fire or land-clearing activities may allow rapid thawing of permafrost, drainage of soils, improved nutrient status, and change in vegetation communities or feasible land uses (Viereck 1973*a*; Van Cleve, Dyrness et al. 1983; Ping 1987; Ping et al. 1992).

TAIGA ECOSYSTEMS

Frequent disturbance by the forces of nature creates the mosaic of plant communities and ecosystems characteristic of the taiga. One such force, Pleistocene glaciation and subsequent deglaciation, created the context within which present-day taiga ecosystems have developed. This section describes the succession of Holocene plant communities, zones of taiga vegetation, representative present-day communities containing black spruce, and processes that account for the dynamic nature of taiga ecosystems in terms of perturbation and ecologic succession.

Paleoecology

Modern taiga ecosystems developed following deglaciation of northern North America, although much of Alaska (Péwé 1975:21-24) and portions of Yukon Territory (Hughes et al. 1981) were not glaciated during the Pleistocene. Nonetheless, the Pleistocene environment differed from that of today. A largely treeless (Matthews 1970) steppe-tundra of grasses and forbs (Ager 1975:87), the Mammoth Steppe (Guthrie 1990:226-272), covered unglaciated terrain during the Wisconsinan glacial stage, although scattered stands of spruce may have persisted in central Alaska (Péwé 1975:87).

After local deglaciation ~14,000 yr BP (e.g., Prest 1976 *in* Ritchie et al. 1983), much of interior Alaska (Table 3) and northwestern Canada (Table 4) supported herbaceous or shrub-tundra vegetation. White spruce (*Picea glauca*) appeared ~10,000 yr BP in the Mackenzie Delta, ~8,500 yr BP in eastern Alaska (Edwards and Brubaker 1986), and as late as ~7,700 yr BP for more easterly areas of the Northwest Territories (MacDonald 1983). Black spruce became abundant 7,000 to 6,000 yr BP (Edwards and Brubaker 1986, Cwynar 1988, Cwynar and Spear 1991) and, with local exceptions, has persisted in boreal forest of northwestern Canada and interior Alaska.

Climatic cooling after ~5,000 yr BP (MacDonald 1983, Ritchie et al. 1983), and apparent changes in soil moisture at some sites, altered plant communities. Black spruce woodlands in central Yukon were replaced by shrub tundra (Cwynar and Spear 1991) and alder (*Alnus* sp.) invaded a southwestern Yukon forest-tundra site, which subsequently fluctuated between abundant sedge, juniper (*Juniperus* sp.), and ericaceous vegetation and abundant resin birch (Wang and Geurts 1991). The cooler climate caused the treeline to retreat southward in northern Canada, but little evidence for this has been found in Alaska (Viereck and Van Cleve 1984).

Zones of Taiga Vegetation

Within the North American taiga, tree size and canopy cover vary with latitude (Bliss 1981, Rowe 1984, Oechel and Lawrence 1985) and form four zones of vegetation: forest-tundra ecotone, open boreal woodland, main boreal forest, and boreal-mixed forest ecotone (Oechel and Lawrence 1985). ***Forest-tundra*** is the transition between taiga and tundra (Pruitt 1978:33). In this zone, tundra is interspersed with sparse or clumped white and black spruce with prominent lichen ground cover; tamarack (*Larix laricina*) may occur on wetter sites (Zoltai, Tarnocai et al. 1988; Timoney et al. 1992). The relatively broad zone of forest-tundra found in

Table 3. Paleoecologic history of black spruce in interior Alaska.

Event	Time Period (yr BP)	Vegetation Type	Key Taxa
Wisconsinan glaciation - cold, dry climate	>14,000	Steppe-Tundra	Grasses, *Artemisia*, other forbs[1]
Deglaciation - warmer, moister climate	14,000 to 9,000	Shrub Tundra	Graminoids, *Artemisia*, shrub birches (*Betula* spp.)[2]
Invasion by spruce	8,500 to 7,000	Boreal Forest	White spruce, paper birch (*Betula papyrifera*), resin birch (*Betula glandulosa*), alder (*Alnus* spp.)[2]
Black spruce abundant - cooler, moister climate	6,500 to Present	Boreal Forest	White spruce, black spruce, paper birch (declining), alder, willows (*Salix* spp.), dwarf arctic birch (*Betula nana*), Ericales[1-5]

1. Ager (1975:87-88)
2. Edwards and Brubaker (1986)
3. Hamilton et al. (1983)
4. Thorson and Guthrie (1992)
5. Péwé (1975:88)

Table 4. Paleoecologic history of black spruce in Yukon and western Northwest Territories.

Event	Time Period (yr BP)	Vegetation Type	Key Taxa
Wisconsinan glaciation - cold, dry climate	>14,000	Mostly covered by ice sheet	
Deglaciation - warmer, moister climate	14,000 to 11,000	Herb Tundra	Grasses, *Artemisia*[1]
Increase of woody vegetation	11,000 to 9,500	Shrub Tundra and Deciduous Woodland	Balsam poplar (*Populus balsamifera*), *Artemisia*, shrub birches, American green alder (*Alnus crispa*), grasses, willows[1-2]
Invasion by spruce	9,500 to 6,500	Boreal Forest and Shrub Tundra	White spruce, juniper, American green alder, balsam poplar, quaking aspen (*Populus tremuloides*), willow, shrub birches[2-5]
Black spruce abundant - cooler climate	6,500 to 4,000	Boreal Forest and Shrub Tundra	Black spruce, American green alder, white spruce[2-3]
Local decline of black spruce - SW Yukon - drier climate	4,100 to 1,900	Boreal Forest	White spruce, juniper, lodgepole pine (*Pinus contorta*)[3]
Local invasion of pine - SW Yukon	1,900 to Present	Boreal Forest	lodgepole pine[3]

1. Ritchie et al. (1983)
2. Cwynar (1988)
3. Cwynar and Spear (1991)
4. Wang and Guerts (1991)
5. MacDonald (1983)

northern Canada (Timoney et al. 1992) is much reduced in Alaska because the Brooks Range coincides with northern limit of trees (except balsam poplar) (Viereck 1975, 1979). Forest-tundra does occur in western Alaska, however (D. K. Swanson, Nat. Resour. Conserv. Serv., pers. commun.).

White and black spruce stands with patchy lichen cover (e.g., *Cladina mitis, C. rangiferina, C. stellaris* [=*alpestris*]) dominate open boreal woodland, but tamarack, paper birch, quaking aspen, and balsam poplar occur on suitable sites (Oechel and Lawrence 1985; Zoltai, Tarnocai et al. 1988). Further south, the main boreal forest contains closed-canopied stands of conifers including white spruce, black spruce, tamarack, jack pine (*Pinus banksiana*), lodgepole pine, balsam fir (*Abies balsamea*), subalpine fir (*A. lasiocarpa*), and hardwoods including quaking aspen, balsam poplar, and paper birch (Oechel and Lawrence 1985; Zoltai, Taylor et al. 1988). The boreal-mixed forest ecotone lies at the southern edge of the taiga and thus does not occur in Alaska.

Black Spruce Communities

Representative types of interior Alaska's mature forest communities (Foote 1983) fall into two major groups: the white spruce site type and the black spruce site type (Table 5). Black spruce stands, pure or codominant with aspen, birch, or white spruce, often occur on slopes and cool, moist valley bottoms (Foote 1983:28) and may be underlain by permafrost (Viereck and Little 1972:18). Black spruce also occurs on relatively dry, nutrient-poor residual soils over bedrock (M.T. Jorgenson, ABR, Inc., pers. commun.).

Tree species commonly associated with black spruce in Alaska include white spruce, tamarack, paper birch, and sometimes quaking aspen. White spruce occurs in mixed stands with black spruce near treeline, near the base of south-facing slopes, and as a successional stage on floodplains (Viereck 1970, 1975; Viereck and Dyrness 1980; Foote 1983:43-46). Although tamarack has a more restricted range than black spruce in Alaska and is disjunct from the remainder of the North American population (Harlow and Harrar 1968:116-117,126; Viereck and Little 1972:50; Zoltai 1973), it can be found in mixed stands with black spruce in wet lowlands of the Interior (Viereck and Dyrness 1980; D. K. Swanson, Nat. Resour. Conserv. Serv., pers. commun.). Paper birch, often an element of post-fire succession (Viereck and Little 1972:138), grows in mixed stands with black spruce on mesic sites but tends to die out in spruce stands more than 120 yr old (Viereck and Dyrness 1980, Foote 1983:32-35). Aspen frequently occurs in pure stands (Viereck and Little 1972:76-77) but sometimes is mixed with black spruce in successional stands on warm sites (Foote 1983:29-32) or well-drained floodplain terraces (Viereck and Little 1972:16-17

Ecologic Succession

Periodic disturbances by fire (Viereck 1973*a*, 1975, 1983; Van Cleve, Dyrness et al. 1983; Dyrness et al. 1986) and fluvial processes (Drury 1956; Viereck 1970, 1975; Van Cleve et al. 1980, Walker et al. 1986) "reset" ecologic succession in taiga ecosystems and create a mosaic of plant communities (Van Cleve et al. 1991). Fire frequency varies across the North American taiga (Table 6) with less frequent fires in humid eastern taiga than in drier western areas (Viereck and Schandelmeier 1980:12-13). Fire is a major allogenic (external) force initiating secondary succession in the taiga (Kimmons and Wein 1986).

Fires can leave the forest floor lightly burned, scorched, or unburned (Dyrness and Norum 1983) or, if severe, expose mineral soil, which is a favorable substrate for germinating seeds (Noste et al. 1979*a*). In addition, fire may eliminate buried, viable seeds and underground parts of shrubs in severely burned patches but not in lightly burned patches (Viereck and Schandelmeier 1980:46-47). Varying moisture content of forest floor organic material accounts for the mosaic pattern associated with taiga fires (Dyrness and Norum 1983). Post-fire succession may start with germination of seeds arriving from off site, germination of seeds surviving on site, or resprouting of surviving vegetation (Dyrness et al. 1986). Black spruce has ***semiserotinous cones*** that retain seeds for periods of years (Zasada 1986) and thus black spruce sites exhibit greater reproduction from on-site seed sources and from resprouting than do white spruce sites (Foote 1983:99-100).

No universal sequence of taiga succession exists (Viereck 1983) because successional sequences following fire depend on fire characteristics and severity, prefire vegetation, regional patterns, site aspect

Table 5. Representative black spruce community types of interior Alaska (Foote 1983).

Black Spruce Site Type	Description	Comments
Picea mariana/ Vaccinium uliginosum - Ledum groenlandicum/ Pleurozium schreberi	Black spruce, bog blueberry (*Vaccinium uliginosum*), Labrador-tea (*Ledum groenlandicum*), feathermoss on slopes and valley bottoms	Lichens are not abundant, but American green alder, resin birch, and mounds of *Sphagnum* mosses frequently occur
Picea mariana/ feathermoss - lichen	Similar to preceding type, but abundant lichens are mixed with the feathermoss	*Sphagnum* spp. are not common
Picea mariana/ Sphagnum spp. - *Cladina* spp.	Black spruce, *Sphagnum* mosses with intermixed lichens on north-facing slopes and wetter valley bottoms	Tamarack may occur in these stands (Viereck and Little 1972:18)
Populus tremuloides - Picea mariana/Cornus canadensis	Quaking aspen, black spruce, bunchberry (*Cornus canadensis*) on drier sites	Succeeds to black spruce and feathermoss
Picea mariana - Betula papyrifera/Vaccinium uliginosum - Ledum groenlandicum	Paper birch, black spruce, bog blueberry, Labrador-tea, feathermoss in slightly wetter sites than preceding community type	Succeeds to a black spruce community
*Picea mariana - Picea glauca/Betula glandulosa/*lichen	White spruce, black spruce, resin birch, lichens on drier sites near treeline	May not succeed to pure stands of either spruce species or might become monospecific black spruce in the rare event that fire did not occur for a long time (Strang and Johnson 1981)

Table 6. Fire recurrence intervals for North American taiga locations.

Location	Recurrence Interval (yr)	Source
Newfoundland	400 (includes man-caused fires)	Wilton and Evans (1974 *in* Viereck and Schandelmeier 1980:13)
New Brunswick	230 to >1,000 (varies by community type and elevation)	Wein and Moore (1977)
Labrador	"Extremely long" (most stands >250 yr old)	Foster (1984)
Quebec	~190 (30-yr period of record) 10,417 (single decade in 30-yr period)	Payette et al. (1989 *in* Timoney and Wein 1991)
Quebec	~130 (spruce/feathermoss)	Cogbill (1985)
Northwest Territories (transect, Hudson Bay to Mackenzie River)	343 (40-yr period) 216 to 717 (single decades in 40-yr period)	Timoney and Wein (1991)
Northwest Territories and Yukon (Mackenzie River)	80 to 90	Rowe et al. (1974 *in* Viereck 1983)
Alaska (Porcupine River)	<60 (spruce stands)	Yaric (1981 *in* Dyrness et al. 1986)
Alaska (interior taiga)	100 to 200 ≤400 (longest reported interval)	Viereck (1983), Gabriel and Tande (1983 *in* Dyrness et al. 1986)

and slope (potential insolation), site moisture, proximity of seed sources, and other factors (Viereck 1973*a*, Viereck and Schandelmeier 1980:47-49, Oechel and Lawrence 1985, Van Cleve et al. 1991). Viereck and Schandelmeier (1980:47-55) identify black spruce/feathermoss and black spruce/lichen woodland patterns of succession. Black spruce/feathermoss succession has six generalized stages: newly burned, moss-herb, tall shrub-sapling, dense tree, hardwood, and spruce (Foote 1983:49-100).

The black spruce/lichen woodland pattern of succession (Viereck and Schandelmeier 1980:47-55) occurs in three stages: pioneer mosses and liverworts, occasionally with substantial cover by vascular plants; open-canopy tree cover over fruticose lichens and ericaceous shrubs, sometimes with feathermosses; and increasing tree and feathermoss cover with lichen dominance shifting to favor *Cladina stellaris* and *C. rangiferina* over *Cladonia crispata* (Viereck and Schandelmeier 1980:47-55). Many black spruce/lichen stands are not wetlands (D. K. Swanson, Nat. Resour. Conserv. Serv., pers. commun.). Finally, hydric (wet) black spruce sites, such as floodplain terraces escaping fire for long periods, may succeed to treeless wetlands or cycle between such wetlands and black spruce (Drury 1956, Viereck 1970, Viereck and Schandelmeier 1980:53).

Post-fire secondary succession in black spruce often produces little change in the species composition of vascular plants, especially for incompletely burned stands (Black and Bliss 1978, Jasieniuk and Johnson 1982, Viereck 1983, Oechel and Lawrence 1985, Zoladeski and Maycock 1990), and differences between heavily and lightly burned stands rapidly diminish with time (Viereck and Foote 1979*a*). In contrast, species composition of nonvascular plants changes with time. Black and Bliss (1978), identified four stages of post-fire succession for *Picea mariana/Vaccinium uliginosum* communities in the Northwest Territories: three similar to those of black spruce/lichen woodland (above) and a fourth characterized by increased cover and density of black spruce from vegetative reproduction and increased cover by lichens such as *Cladina stellaris, C. mitis*, and *C. rangiferina*. The fourth stage occurs after 200 yr but is rare because of fire. Post-fire lichen-bryophyte succession in the absence of change in vascular species composition also occurs in *Picea mariana/Cladina stellaris* woodland in northern Quebec (Morneau and Payette 1989).

Erosion and deposition in river floodplains disrupt succession by undercutting and washing away the alluvial deposits upon which older plant communities have been established and by forming new depositional surfaces upon which primary succession can take place (Van Cleve et al. 1980, Kimmins and Wein 1986, Walker et al. 1986). Young surfaces increase in height with seasonal flooding and silt deposition, gradually building terraces (Walker et al. 1986) and altering physical and chemical site conditions (Van Cleve et al. 1980). Active movement of river channels and cycles of alluviation and downcutting produce a mosaic of habitats in river floodplains (Drury 1956:15-18, Péwé 1975:68). Given sufficiently long periods without fire, black spruce may replace white spruce on old terraces as permafrost forms and soils become waterlogged (Viereck 1970, Zasada 1986).

Succession-Permafrost Relationships

Succession in subarctic taiga forest affects aggradation and degradation of permafrost. Fire or other disturbance can remove vegetative cover and reduce forest floor thickness, increasing depth of thaw in permafrost soils (Brown 1963, Viereck 1973*b*, Viereck and Foote 1979*b*, Van Cleve and Viereck 1983, Viereck and Van Cleve 1984, Dyrness et al. 1986, Ping 1987, Evans et al. 1988). Thickness of the ***active layer*** ("the layer of ground above the permafrost which thaws and freezes annually" [Gabriel and Talbot 1984:7]) in a burned stand of black spruce increased for 9 yr following an Alaskan forest fire, reaching a depth of 1.87 m, and a bladed fire line thawed to 2.27 m after 8 yr (Viereck 1982). An experimental burn that only slightly reduced thickness of the organic layer produced only small increases in thaw depth whereas treatments that mechanically removed one half of the organic layer or the entire organic layer produced much greater depths of thaw (Dyrness 1982).

Conversely, recovery of vegetation and accumulation of organic matter during secondary succession can decrease the depth of the active layer (Heilman 1966, Viereck 1983). In upland stands of black spruce, feathermosses and some *Sphagnum* mosses become abundant in the dense tree stage of development 40 to 60 yr after fire; active layer thickness

decreases to prefire values at about this time (Zoltai 1975, Van Cleve and Viereck 1983), or at least within 100 yr (Viereck and Van Cleve 1984). Similarly, permafrost attributed to a thick insulating layer of moss and organics was present in a mixed floodplain stand of 200-yr old white and black spruce (presumably of primary successional origin) but absent in three younger stands (Viereck 1970).

BLACK SPRUCE SPECIES CHARACTERISTICS

Black spruce is an important, widespread species in northern North America and occurs in a variety of environmental settings. Black spruce has genetic potentials that govern its response to various environmental conditions in terms of appearance, tolerance of those conditions, and method of reproduction. The following discussion outlines the distribution and characteristics of black spruce as a species, range of environments within which black spruce occurs, and adaptations of black spruce to the conditions with which the species must cope.

Distribution

Black spruce occurs across North America from Labrador south to New Jersey and Pennsylvania in the east and from British Columbia north to Yukon Territory and Alaska in the west (Harlow and Harrar 1968:124-127, largely coincident with the taiga as defined by Pruitt (1978:1-7). Although black spruce grows on extensive upland areas in the northern portion of its North American range, to the south this species is often restricted to peatlands and may occur as a pioneer tree on floating mats of vegetation (Harlow and Harrar 1968:125). Black spruce is restricted to wetlands in kettle-hole depressions at the southern edge of its range in Minnesota (P. H. Glaser, Univ. Minn., pers. commun.).

Black spruce dominates the forest-tundra southeast of a point between Great Bear and Great Slave lakes, Northwest Territories; white spruce dominates to the northwest of this point (Timoney et al. 1992). Although white spruce also defines the northern and western limits of the taiga in Alaska (Viereck 1975), black spruce is the major conifer of the open boreal woodland zone to the south of the forest-tundra (Oechel and Lawrence 1985) and covers 44% of interior Alaska (Viereck et al. 1986). Black spruce occurs from the southern slopes of the Brooks Range southward to the Kenai Peninsula and from the Canadian border westward to Norton Sound, although it is absent on the Yukon-Kuskokwim Delta and in the western portion of the Alaska Range (Viereck and Little 1972:51-52).

Treelines are influenced by latitude, altitude, and climate, which perhaps limit forest growth through low summer temperatures (Dahl 1986). Additional factors include past climate, glaciation, and fire (Oechel and Lawrence 1985). Latitudinal treeline for black spruce across central North America is the tundra-taiga boundary, but white spruce occurs on this boundary in western Canada (Timoney et al. 1992) and Alaska (Viereck 1979). In Alaska, black spruce commonly grows on cold, wet sites of less than 610 m elevation, but the altitudinal treeline may reach 823 m (Viereck and Little 1972:51).

Growth Forms and Densities

Black spruce trees reach heights of 9 to 12 m and diameters of 150 to 300 mm (Harlow and Harrar 1968:125) on favorable sites. Individual trees can reach heights of 24 m in Minnesota (Heinselman 1963). In Alaska, these spruces more typically are 4.5 to 9 m tall and 75 to 150 mm in diameter with "narrow pointed crown[s]" (Viereck and Little 1972:51). The species also may grow as a shrub, generally in the shape of a small tree, or as ***krummholz*** (stunted, scrubby, twisted growth forms of species genetically capable of tree growth [Gabriel and Talbot 1984:63]) at treeline (Payette et al. 1982). Specific growth forms depend upon environmental conditions experienced during the lives of individual trees and include mat, infranival cushion, supranival skirted, whorled, and tree shapes (Lavoie and Payette 1992).

The stem density (Table 7) and canopy coverage of black spruce stands vary with site conditions and stand age. In the forest-tundra, trees may occur as clonal stands or single stems (Timoney et al. 1992) and by definition reach very low densities as the transition from taiga to tundra occurs. Black spruce in Alaska occurs in communities with crown canopies classified as closed (60-100% cover), open (25-60% cover), and woodland (10-25% cover) (Viereck et al. 1992). Black spruce woodlands occupy transitions between treeless wetlands and drier forests and also occur on dry uplands and at treeline, sometimes in association with white spruce (Viereck 1979,

Viereck and Dyrness 1980). Closed-canopied forests characterize the main boreal region of Canada (Zoltai, Taylor et al. 1988).

Adaptations

Factors such as soil moisture, soil chemistry, competition with other species, and response to browsing influence the distribution and abundance of black spruce. In terms of moisture tolerance, black spruce occurs on well-drained soils over much of its range but also grows in *Sphagnum* peatlands (Harlow and Harrar 1968:125). In Alaska, black spruce dominates cold, wet sites (Van Cleve and Yarie 1986, Viereck et al. 1986) but also occurs on drier, nutrient-deficient sites (M. T. Jorgenson, ABR, Inc., pers. commun.). This distribution indicates that black spruce tolerates a wide range of soil moisture conditions.

Silvicultural drainage of forest soils in Europe (Putkisto 1980, Remröd 1980, Vasander 1984) and North America (Haavisto and Wearn 1987, Härkönen 1987, Hillman 1987) has been attempted or proposed to promote tree growth, including that of black spruce. In Alberta, leader growth in black spruce did not initially respond to drainage (Lieffers and Rothwell 1987), but after a 3- to 6-yr delay tree ring growth increased to a maximum rate, which occurred 13 to 19 yr following drainage (Dang and Lieffers 1989). Wang et al. (1985) noted similar growth responses in black spruce on drained sites. Although wet sites do not provide optimum conditions for growth of black spruce, the species is adapted through a strategy of nutrient conservation to occupy these poor environments (Van Cleve and Dyrness 1983*a*).

Black spruce occupies sites characterized by low pH (Table 8) in Alaska (Van Cleve, Oliver et al. 1983) and the Northwest Territories (Jasieniuk and Johnson 1982). Compared to other interior Alaska forest types black spruce forest floors have low base element saturation; long turnover times for organic matter, nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg); high biomass accumulation; and low element (N, P, K, Ca, Mg) concentrations (Van Cleve, Oliver et al. 1983). Substrate quality in black spruce stands is poor (Flanagan and Van Cleve 1983). Low temperature and poor litter quality interact to reduce mineralization rates, potentially contributing to successional changes leading to sites dominated by black spruce (Chapin 1986). Black spruce requires only about one-third as much N, P, and K as white spruce and as little as one-tenth as much as quaking aspen (Van Cleve, Oliver et al. 1983).

Black spruce competes with other plants, such as mosses (Van Cleve and Viereck 1983, Oechel and

Table 7. Stem densities of several immature and mature black spruce stands, interior Alaska (Foote 1983:43-48,76-92).

Species Composition	Site Description	Stand Age (yr)	Stem Density (ha^{-1})
Black spruce	Moist	60 to 130	300 (mature)
Black spruce	Mesic	1 to 5	18,000
Black spruce	Mesic	91 to 200	1,700 (mature)
Mixed white and black spruce	Dry treeline	55 to 195	400 (mature)

Table 8. Soil pH at several black spruce sites in interior Alaska.

Stand Location	Number of Stands	Material	pH	Source
Upland	4	Organic	3.3 to 3.7	Troth et al. (1976)
Upland	3	Mineral	4.12 to 5.09	Noste et al. (1979b)
Lowland	1	Organic	3.60 to 4.80	Viereck (1970)
Lowland	1	Mineral	5.22	Viereck (1970)

Van Cleve 1986). Mosses efficiently trap nutrients, which are not available to vascular plants until the mosses decompose (Oechel and Van Cleve 1986). Moss production in mature black spruce stands may exceed tree foliage production by a factor of 3 (Van Cleve, Dyrness et al. 1983) and, coupled with low rates of decomposition (Van Cleve, Viereck et al. 1983), helps build thick organic layers (Oechel and Lawrence 1985).

There is some question whether or not black spruce can persist over long periods in successful competition with mosses and possible ***paludification*** (the process of ***bog*** expansion that occurs as peat accumulation impedes drainage [Natl. Wetlands Working Group 1988:438] of forest soils (Viereck 1983). Sparsely treed *Sphagnum* bogs develop on north-facing slopes that have escaped burning for significant periods (Heilman 1966, 1968). Paludification of lowland black spruce stands, perhaps coupled with disturbance that initiates thaw, may form treeless wetlands (Drury 1956:30-35, Viereck 1970). The ability of black spruce to persist in the absence of fire or other disturbance may be inversely related to the degree of swamping that occurs on a given site. In some Minnesota peatlands, woody peat is overlain by *Sphagnum* peat indicating the earlier presence of forest in what are now treeless bog drains (runoff channels) (Glaser 1987:50-52).

Black spruce is adapted to a low-nutrient environment (Bryant and Kuropat 1980, Bryant and Chapin 1986) through a strategy of nutrient conservation (Van Cleve and Yarie 1986) that includes a slow growth rate (Bryant et al. 1983). Because browsing of stress-adapted plants depletes stored, scarce nutrient capital, chemical compounds that discourage browsing by herbivores should be present in such plants (Grime and Anderson 1986). This expectation is confirmed for black spruce: the species has a high resin content (Bryant et al. 1983), herbivorous birds and mammals avoid black spruce when alternative browse is available (Bryant and Kuropat 1980), and actual or simulated browsing severely damages black spruce (Bryant and Kuropat 1980, Fox and Bryant 1984).

Reproduction

Black spruce reproduces by sexual and vegetative means (Harlow and Harrar 1968:126). Living *Sphagnum* mosses provide an adequate seedbed for black spruce regeneration (Johnston 1977:7), an adaptive advantage over other tree species (D. K. Swanson, Nat. Resour. Conserv. Serv., pers. commun.), but sexual reproduction in black spruce also is adapted to post-fire regeneration. Seedfall in undisturbed black spruce stands is gradual and less intense than in burned stands where seedfall can be heavy (Viereck and Dyrness 1979, Zasada 1986). Seedling density increased over a 3-yr period following fire in interior Alaska (Viereck and Foote 1979*a*). In northern Quebec uplands, sexual regeneration is most vigorous from 5 to 14 yr following fire, perhaps because microclimates for seedling establishment cool and moisten at this time (Morneau and Payette 1989); seedling establishment in this region declines as increasing lichen cover inhibits spruce germination beginning ~20 yr after burning (Sirois and Payette 1991).

Fire sometimes exposes mineral soil, which provides the best conditions for germination and establishment of black spruce (Viereck 1973*a*, Zasada 1986). Artificial seeding was most successful on heavily burned plots; germination failed on scorched or lightly burned plots (Zasada et al. 1983). Seedlings established most successfully on lightly and heavily burned hillside plots but only sparsely established on a heavily burned ridgetop following a natural fire in interior Alaska (Viereck and Foote 1979*a*). In general, black spruce regenerates best on heavily burned sites (Dyrness et al. 1986) with unburned tree crowns holding cones as a seed source (Zasada 1986).

Vegetative reproduction in black spruce occurs by ***layering***, which is the rooting of lower branches and growth of new individuals to form a clone (Zasada 1986). Layering predominates in older, undisturbed stands (Zasada 1986) characterized by lichens or thick moss layers, which may be unfavorable for seedling establishment (Chrosciewicz 1980, Aksamit and Irving 1984, Morneau and Payette 1989). Vegetative reproduction can maintain clonal black spruce stands (Legere and Payette 1981), change mixed stand composition (Strang and Johnson 1981), or increase stand density (Black and Bliss 1978).

BLACK SPRUCE WETLANDS

In North American taiga, black spruce, sometimes growing in mixed stands with tamarack, is the tree species most often associated with treed wetlands. Wetlands occupy 20 to 30% of the taiga landscape (Zoltai, Tarnocai et al. 1988; Zoltai, Taylor et al. 1988), although the percentage rises to ~50% in the southern boreal forest (Larson 1991). Hydrologically linked complexes of groundwater-influenced communities (***fens***) surrounding slightly higher, precipitation-influenced communities (bogs) (Heinselman 1963, 1970; Glaser et al. 1981), are the most common of these peat-forming wetlands (Larson 1991). Black spruce wetlands also occur in isolated locations to the south of the boreal forest (Mitsch and Gosselink 1986:288-291, Larson 1991) and on extensive glaciolacustrine deposits in Minnesota (Heinselman 1963, 1970). The following chapter defines terms necessary to understand the functions of BSWs and describes their classification and vegetation.

WHAT IS A WETLAND?

The reader should base specific understanding of the functions of Alaska's BSWs on general familiarity with wetland definitions and characteristics and wetland classification systems used in northern North America. The explanatory material contained in this section of the profile provides such familiarity with terminology and concepts. Additional information may be found in the comprehensive wetland textbook by Mitsch and Gosselink (1993) and the recent National Research Council (1995) report on wetland characteristics and boundaries.

Definitions and Defining Characteristics

Wetland definitions (Table 9) range from vernacular names (e.g., marshes, swamps, and ***mires*** [Gore 1983, Maltby 1986:28]) to descriptions of physical, chemical, and biological characteristics necessary for a wetland to exist (e.g., hydrologic regime, soils, and vegetation [Gore 1983, Mitsch and Gosselink 1986:16-20). Definitions may be based on science or developed for purposes of regulation. North American wetland definitions generally incorporate characteristics of vegetation, soils, and hydrology that allow practical delineation of wetland areas.

Hydrology is "probably the single most important determinant for the establishment and maintenance of specific types of wetlands and wetland processes" (Mitsch and Gosselink 1986:55). The season, frequency, depth, and duration of saturation or flooding control development of wetland soils and vegetation (Lugo, Brown et al. 1990; Maltby 1991). Wetland hydrology, in turn, is influenced by the source of water input (precipitation, groundwater discharge, surface flow); type of water output (surface outflow, groundwater recharge, evapotranspiration); biotic factors (e.g., paludification); energy inputs (e.g., tides, wind); and the balance between water input, output, and storage on various time scales (Mitsch and Gosselink 1986:55-77, Kangas 1990, Maltby 1991). These influences sometimes make wetland hydrology difficult to measure, but field indicators and other data sources can verify the presence or absence of wetland hydrology (Tiner 1989, Natl. Res. Counc. 1995:108-109).

Wetland soils are ***hydric***: "soil[s] that [are] saturated, flooded, or ponded long enough during the growing season to develop anaerobic conditions in the upper part" (Natl. Tech. Comm. Hydric Soils 1991:1). These soils are listed in the publication

Table 9. Representative wetland definitions.

Purpose and Scope	Wetland Definition	Source
Conservation (global): *Ramsar Convention on Wetlands of International Importance Especially as Waterfowl Habitat*	"Areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt including areas of marine water, the depth of which at low tide does not exceed 6 m [just over 19 ft]"	Maltby (1991:9)
Science/ classification (Canada)	"Land that has the water table at, near, or above the land surface or which is saturated for a long enough period to promote wetland or aquatic processes as indicated by hydric soils, hydrophytic vegetation, and various kinds of biological activity that are adapted to the wet environment"	Tarnocai (1980 *in* Zoltai 1988:3)
Science/ classification (United States)	". . . wetlands must have one or more of the following three attributes: (1) at least periodically, the land supports predominantly hydrophytes; (2) the substrate is predominantly undrained hydric soil; and (3) the substrate is nonsoil and is saturated with water or covered by shallow water at some time during the growing season of each year"	Cowardin et al. (1979:3)
Science/reference (United States)	". . . an ecosystem that depends on constant or recurrent, shallow inundation or saturation at or near the surface of the substrate. The minimum essential characteristics of a wetland are recurrent, sustained inundation or saturation at or near the surface and the presence of physical, chemical, and biological features reflective of recurrent, sustained inundation or saturation. Common diagnostic features of wetlands are hydric soils and hydrophytic vegetation. These features will be present except where specific physicochemical, biotic, or anthropogenic factors have removed them or prevented their development"	National Research Council (1995:59)
Regulatory (United States)	". . . those areas that are inundated or saturated by surface or ground water at a frequency and duration sufficient to support, and that under normal circumstances do support, a prevalence of vegetation typically adapted for life in saturated soil conditions. Wetlands generally include swamps, marshes, bogs, and similar areas. (33CFR328(b); 1984)"	Mitsch and Gosselink (1993:27)

Hydric soils of the United States (Natl. Tech. Comm. Hydric Soils 1991), based on criteria that include references to soil taxonomy (Soil Surv. Staff 1994) combined with drainage characteristics, water table position, soil permeability, and frequency of ponding or flooding. ***Redoximorphic features*** in soils - patterns of color related to chemical reduction or oxidation of iron (Fe) or manganese (Mn) - can be used, with caution, to assist field identification of aquic (wet) conditions (J. Bouma, Rep. of Int. Comm. on Aquic Soil Moisture Regimes, Circular 10).

Wetland plants exhibit structural and physiological adaptations to their environment (Larsen 1982:248-257, Mitsch and Gosselink 1986:130-140). Such plants are ***hydrophytes***: "macrophytic plant life growing in water, soil, or on a substrate that is a[t] least periodically deficient in oxygen as a result of excessive water content" (Tiner 1989:17). The U.S. Fish and Wildlife Service, in cooperation with national and regional interagency review panels, has prepared national, regional, and state lists of vascular plant species that occur in wetlands (Reed 1988:2-7). These species are further rated with respect to their frequency of occurrence in wetlands,

some plants being obligate (restricted to wetlands) and others facultative (not restricted to wetlands) wetland residents. Weighted sampling procedures are available to determine whether or not the vegetation on a given site predominantly comprises hydrophytes (Tiner 1989).

Recently, the National Research Council (1995:64) has suggested that, in the most general sense, defining characteristics of wetlands are water, substrate, and biota. This suggestion recognizes that organisms (e.g., mosses, aquatic invertebrates) other than vascular plants can serve as biological indicators and that some wetlands have substrates other than hydric soils (Natl. Res. Counc. 1995:136-137).

Mires

Some BSWs are ***peatlands*** or mires, peat-forming ecosystems having ≥0.4 m peat thickness and generally separated into bogs and fens based on vegetation, water source, and water chemistry (Table 10), all of which are related variables (Sjörs 1950, 1963; Boelter and Verry 1977; Gore 1983; Gabriel and Talbot 1984:71-72; Zoltai 1988; Swanson and Grigal 1989). Peat-forming vegetation includes mosses, grasses and sedges, and woody plants (Clymo 1983). Bogs are ***ombrotrophic*** mires, meaning they receive water exclusively as precipitation (Gabriel and Talbot 1984:77), which typically has a low nutrient content (i.e., water that is oligotrophic) (Gore 1983, Damman 1987). In contrast, fens are ***minerotrophic*** mires (Boelter and Verry 1977, Gore 1983), meaning they receive water that contains moderate to high concentrations of nutrients (i.e., water that is mesotrophic or eutrophic) from contact with mineral soil (Gabriel and Talbot 1984:71). Intermediate transition sites or poor fens also occur

Table 10. Representative characteristics of bogs and fens.

Mire Type	Water Source	Trophic Status	Pore Water pH	Pore Water Ca+Mg (mg/L)	Dominant Vegetation
Bog	Precipitation (ombrotrophic)	Oligotrophic	<4.4[1] 4.5[5] <4.6[6]	<5[6]	*Sphagnum*, lichens, heath shrubs, stunted trees[6,8]
Poor Fen	Precipitation/ groundwater (weakly minerotrophic)	Transition	>4.0 to <4.9[3] 4.4 to 5.6[2] 4.7[5] 5[4]	<6[9]	*Sphagnum*, black spruce[7]
Fen	Precipitation/ groundwater (minerotrophic)	Mesotrophic	5.5 to 6.0[6]	≥9[10]	Brown mosses, sedges, forbs, shrub birches, willows, tamarack[7]
Rich Fen	Precipitation/ groundwater (highly minerotrophic)	Eutrophic	6.8 to 7.9[4]	≥22[4]	Flarks: brown mosses, sedges[4] Strings: brown mosses, shrub birch, tamarack, black spruce[4]

1. Swanson and Grigal (1991)
2. Swanson and Grigal (1989)
3. Comeau and Bellamy (1986)
4. Slack et al. (1980)
5. Zoltai and Johnson (1987)
6. Zoltai (1988)
7. Zoltai, Taylor et al. (1988)
8. Zoltai, Tarnocai et al. (1988)
9. Gauthier (1980 *in* Zoltai 1988)
10. Schwintzer (1978 *in* Zoltai 1988)

(Sjörs 1950, Comeau and Bellamy 1986).

Peatland communities array along a moisture-nutrient gradient (Jasieniuk and Johnson 1982). Swanson and Grigal (1989) predicted pH class and thus trophic status of Minnesota mires with a simple vegetation key based on pH tolerances of common mire plants. Although all species that grow in raised bogs also occur in fens, raised bogs can be distinguished by the absence of fen indicator species (i.e., species restricted to fens) (P. H. Glaser, Univ. Minn., pers. commun.). Zoltai and Johnson (1987) characterized plant species associated with classes of peatlands of various trophic status based on Ca concentration. Vegetation responded to small changes in Ca levels at low Ca concentrations but was less sensitive at higher concentrations.

The reader should note that the Canadian system of wetland classification defines mesotrophic to encompass the majority of fens (Zoltai 1988), which is at variance with the usage of mesotrophic by Swanson and Grigal (1989) to represent scarce poor fens. Also, some European authors (e.g., Eurola et al. 1984) describe oligotrophic wetlands, along with mesotrophic and eutrophic wetlands, as a subset of minerotrophic wetlands, reserving ombrotrophic for mires of the very lowest nutrient status. In contrast, oligotrophic appears to describe the nutrient status of ombrotrophic wetlands in the North American literature. This report follows the Canadian classification system in usage of mesotrophic and the North American literature in usage of oligotrophic.

Relationship of Black Spruce Wetlands to Mires

Wetlands with ***Histosol***s, soils having >0.4 m of organic material, are mires, but wetlands with soils having histic epipedons (organic layers ranging from 0.2 to 0.4 m) are not mires by the Canadian definition (S.C. Zoltai, Can. For. Serv., pers. commun.). The 0.4-m criterion for minimum peat depth is based on the maximum rooting depth of most wetland plants (Zoltai 1988). Roots of most plants in ericaceous BSWs of interior Alaska, however, tend to be confined to organic soil horizons, even when those horizons are <0.4 m thick (D.K. Swanson, Nat. Resour. Conserv. Serv., pers. commun.).

Black spruce wetlands with histic epipedons form peat and occupy a continuum from mire to sites possibly influenced by mineral soils (Table 11). Studies reviewed for this profile did not address potential relationships between organic layer thickness and mire-like characteristics of wetlands. Nevertheless, literature addressing bogs and fens should be at least partially applicable to BSWs with histic epipedons. Sites supporting dwarf trees (<3-m tall) appear to have higher probabilities of being mires than do sites supporting forest and woodland (Table 11), but Histosols can occur in forest and woodland as well, at least as inclusions.

Table 11. Organic layer thickness and typical soils of Alaska Vegetation Classification (Level IV) classes dominated by black spruce (Viereck et al. 1992:66,74,82,109,111).

Level IV Classification	Organic Layer Thickness (m)	Soils
Closed Black Spruce Forest	Typical: 0.2 Maximum: 1.0 (*Sphagnum* mounds)	"well-drained alluvial gravels to poorly drained Cryaquepts"
Open Black Spruce Forest	Typical: 0.05 to 0.2 ("forest floor")[1] Maximum: >1.0	"Histic Pergelic Cryaquepts and sometimes Cryochrepts"
Black Spruce Woodland	Typical: 0.1 to 0.3	"Cryaquepts or, more rarely, Cryochrepts"
Open Black Spruce Dwarf Tree Scrub	Minimum: 0.3	Histosols and Histic Pergelic Cryaquepts?
Black Spruce Dwarf Tree Woodland	Minimum: 0.3	Histosols and Histic Pergelic Cryaquepts?

1. It is not clear that Viereck et al. (1992) mean "forest floor" to include all organic horizons. Histic Pergelic Cryaquepts are stated to be the most frequent soils, which is at variance with organic layers <0.2 m.

VEGETATION

Characterization of BSWs in terms of specific plant communities across northern North America is difficult. Neither the United States nor the Canadian wetland classification system (Appendix A) directly uses specific plant communities as classification units. Nevertheless, several approaches for characterizing the vegetation of BSWs present themselves: examine descriptions of classified wetlands to identify those supporting black spruce and evaluate black spruce community types to identify their respective probabilities of being wetlands.

Wetland Classes and Forms Supporting Black Spruce

Black spruce wetlands primarily fall within the Palustrine Forested Needle-leaved Evergreen and Palustrine Scrub-Shrub Needle-leaved Evergreen classes of the U.S. Fish and Wildlife Service classification system (Cowardin et al. 1979) and frequently have saturated water regimes. Wetlands dominated by cotton grass (*Eriophorum* spp.), sedges, or other nonwoody vegetation, except mosses or lichens, and supporting sparse (coverage ≤30%) black spruce, can fall within the Palustrine Emergent Wetland class. Emergent plants ("erect, rooted, herbaceous, hydrophytes" [Cowardin et al. 1979:19]) often dominate fens, where mosses may or may not be present, but *Sphagnum* mosses often dominate ground cover in bogs. Little additional general information about vegetation in BSWs can be extracted from National Wetlands Inventory maps or Cowardin et al. (1979).

The tolerance of black spruce for a variety of soil moisture and trophic conditions allows the species to appear in many plant communities. Some of these communities occur in both wetland and nonwetland settings, as well as in different wetland classes or forms. Plant communities vary between different types of bogs and fens across North America (Appendix B), but some taxa occur frequently (Table 12). Black spruce is more closely associated with ombrotrophic than minerotrophic conditions but is found in both types of mire.

Wetland Potential of Representative Black Spruce Community Types in Alaska

Published descriptions of black spruce community types provide some basis for inferring the probability that a particular type would be classified as a wetland or nonwetland. Community type descriptions providing species lists and densities or cover percentages can be compared to the regional list of wetland plants for Alaska (Reed 1988) to determine (approximately) whether or not characteristic vegetation is hydrophytic. Similarly, descriptive information on the presence or absence of permafrost and physical characteristics of sites (e.g., slope, aspect,

Table 12. Frequently occurring genera and species in North American bogs and fens.

Stratum	Bog Taxa	Fen Taxa
Tree	Black spruce, tamarack (sometimes)	Tamarack, black spruce (sometimes)
Shrub	Leatherleaf (*Chamaedaphne calyculata*), Labrador-tea (*Ledum* spp.), laurel (*Kalmia latifolia*), shrub birches, willow, blueberry (*Vaccinium* spp.), and bog-rosemary (*Andromeda polifolia*)[1]	Shrub birches, willow, sweetgale (*Myrica gale*), bog-rosemary, bog kalmia (*Kalmia polifolia*), buckthorn (*Rhamnus alnifolia*)[3]
Herb	Cloudberry (*Rubus chamaemorus*), cotton grass (sometimes)[2]	Sedges, cotton grass, buckbean (*Menyanthes trifoliata*), bladderwort (*Utricularia* spp.), arrow grass (*Triglochin maritima*), bulrush (*Scirpus* spp.), swamp horsetail (*Equisetum fluviatile*)[3]
Ground Cover	*Sphagnum* spp., lichens[2]	Mosses (e.g., *Drepanocladus revolvens, Scorpidium scorpioides, Sphagnum* spp., *Tomenthypnum nitens*)[3]

1. Viereck and Little (1972:19), Glaser (1987), Larson (1991)
2. Zoltai, Taylor et al. (1988); Larson (1991)
3. Zoltai, Tarnocai et al. (1988); Zoltai, Taylor et al. (1988); Larson (1991)

Table 13. Inferred probabilities that typical interior Alaska black spruce community types are jurisdictional wetlands based on stand descriptions from Foote (1983:28-48).

Community Type	Wetland Hydrology[1]	Hydrophytic Vegetation[2]	Wetland Probability
Picea mariana/ Sphagnum spp.-*Cladina*	Yes: permafrost and standing water present	Yes: OBL species, bog cranberry (*Vaccinium oxycoccos*), and *Sphagnum* mounds with no FACU species	High
Picea mariana/ Vaccinium uliginosum-Ledum groenlandicum/ Pleurozium schreberi	Often: permafrost generally present but may be absent on south-facing slopes	Yes: *Equisetum sylvaticum* is the only important FACU species	High-to-moderate: valley floors and north-facing slopes high, south-facing slopes low probability
Picea mariana-Betula papyrifera/ Vaccinium uliginosum-Ledum groenlandicum	Sometimes: north-facing slopes and valley floors may have permafrost	Yes: paper birch and prickly rose (*Rosa acicularis*) are the only important FACU species	Moderate: valley floors and north-facing slopes high, south-facing slopes low probability
Picea mariana/ Feathermoss-Lichen	Sometimes: north-facing slopes and valley floors may have permafrost	Yes: only one important species, *Geocaulon lividum*, is FACU	Moderate: valley floors and north-facing slopes high, south-facing slopes low probability
Picea mariana-Picea glauca/ Betula glandulosa	Unlikely: stony soils prevent permafrost probe, but thin organic layer discourages permafrost formation	Yes: but two important FACU species, white spruce and prickly rose, are present	Moderate-to-low: well-drained sites argue against wetland hydrology and hydric soils
Populus tremuloides-Picea mariana/ Cornus canadensis	Infrequent: permafrost occurs only in pockets	Yes (marginal): OBL species absent, FACU species (quaking aspen, prickly rose, bunchberry) prominent, only one important FACW species (black spruce)	Low: well-drained sites argue against wetland hydrology and hydric soils

1. Saturated soils assumed for sites with shallow permafrost.
2. Considering the three dominant species in each stratum, vegetation is hydrophytic under criteria used for the National Wetlands Inventory if there is a predominance (>50%) of "obligate" (OBL) (>99% estimated probability of occurring in wetlands), "facultative wetland" (FACW) (67-99% estimated probability of occurring in wetlands), and "facultative" (FAC) (34-66% estimated probability of occurring in wetlands) species (Reed 1988:9).

soil moisture) allows inferences about wetland hydrology and hydric soils. Table 13 presents such inferences for six of many possible black spruce community types of interior Alaska (Foote 1983:28-48). Summary physical descriptions of these community types appear in Appendix C.

Uncertainty in the probability of various community types being wetlands largely depends on site slope and aspect. Slopes lacking permafrost are unlikely to support wetland communities in the Interior. At least some east- and west-facing slopes may be free of permafrost (Jorgenson and Kreig 1988), but the bases of some south-facing slopes have permafrost soils. Collins et al. (1988) found positive mean annual soil temperatures on several slopes with approximately southeast to south-southwest aspects (131° to 202°).

Permafrost also can alter hydrology by raising

land surfaces. Peat plateaus with raised surfaces dominated by black spruce and lichens occur in Yukon, Mackenzie (S.C. Zoltai, Can. For. Serv., pers. commun.), and Alaska (S.S. Talbot, U.S. Fish Wildl. Serv., pers. commun.). These landforms have organic soils (peat thickness >0.4 m) but might not meet hydrologic criteria for wetlands. Site-specific investigation may be necessary to delineate wetlands within all but the wettest black spruce community types.

ACTIVITIES POTENTIALLY AFFECTING BLACK SPRUCE WETLANDS

Many activities associated with contemporary society have the potential to affect BSWs. These activities include filling, draining, flooding (wetland conversion), or clearing; disposing of wastes; or mining peat deposits. The following discussion outlines these activities in more detail.

Placement of Fill

Wetlands frequently are filled to provide stable surfaces for transportation, building construction, or resource development. Fill physically buries wetlands, radically changing their functions and values. Secondary effects of fills include deposition of chemical elements (particularly metals) in adjacent wetlands by airborne dust from fill surfaces (Santelmann and Gorham 1988) and alteration of drainage patterns.

Transportation corridors in interior Alaska often cross BSWs, although they may present particular difficulties for construction. Besides highways, overburden disposal sites and fills for pipeline workpads have been placed in BSWs (Pamplin 1979:50). Commercial facilities such as warehouses and storage yards require large areas of relatively low-cost land, as does high-density residential housing. Black spruce wetlands, especially those with minimal peat depths, meet these requirements and can be filled to provide a building surface. Commercial and residential development in BSWs has occurred in Anchorage, Fairbanks, and smaller communities in Alaska.

Mineral extraction, such as placer and hard rock mining for gold, often requires stripping overburden from the mineral-bearing material and piling it somewhere on the mine site. Overburden and tailings disposal sometimes occurs in BSWs. In the case of oil and gas extraction, production wells and facilities, and in some locations exploratory wells, occur on gravel pads. At this time, most oil and gas exploration and production in Alaska is in the tundra, but future production may occur in BSWs.

Drainage

Wetlands frequently are drained to facilitate residential and commercial development, transportation, agriculture, and forestry. Drainage effects include lower water tables, accelerated peat decomposition, and subsidence of ground surfaces (Verry and Boelter 1979; Lugo, Brown et al. 1990). Even highway and other ditches largely ineffective for extensive wetland drainage intercept lateral flow, dry out downslope wetlands, and alter dominant vegetation (Glaser et al. 1981).

Developers have drained BSWs in the Anchorage area, usually in conjunction with fill placement (Zenone 1976), and portions of those wetlands not currently undergoing commercial and residential development have been ditched in the past (e.g., Klatt Bog [Glass 1986*a*]). Farmers in Alaska drain permafrost BSWs simply by stripping vegetation and promoting thaw of permafrost that holds water near the ground surface (Ping 1987, Ping et al. 1992). Agricultural drainage is a major cause of wetland loss in the Lower 48 states (Tiner 1984:32) and Europe (Taylor 1983, Baranovskiy 1991). Ditches constructed to facilitate agriculture and highway construction have damaged mires in Minnesota (Glaser 1987:67).

Foresters have drained European spruce and pine forests (Putkisto 1980, Remröd 1980, Vasander 1984) and Canadian BSWs (Haavisto and Wearn 1987, Hillman 1987) to improve tree growth (Wang et al. 1985, Dang and Lieffers 1989). Drainage can allow earlier flowering (Lieffers and Rothwell 1987), reduce plant species diversity (Vasander 1984), and induce permafrost formation in fens (Swanson and Rothwell 1986). Air temperatures near ground level are expected to show greater extremes in drained wetlands, but this was not confirmed when tested in Alberta (Rothwell and Lieffers 1987).

Flooding

A variety of activities flood wetlands and convert them to shallow or deep open-water habitats. Conversion of one wetland form to another generally

alters its functions. Whether such alterations are net benefits or losses in terms of wetland values must be determined by site-specific evaluations.

Mining impoundments will affect BSWs in the Fairbanks area. On a smaller scale, linear wetland fills such as access roads or highways block local drainage and pond water, converting emergent wetlands to open-water habitats. Secondary impacts such as flooding can equal or exceed the area of fill placement (Walker et al. 1987). Secondary flooding effects of linear structures in the taiga include thermokarst development, altered vegetation, and transition from bog to fen conditions (Pomeroy 1985).

Clearing and Harvest of Woody Vegetation

Removal of vegetative cover from wetlands alters their character. Activities such as powerline installation (Grigal 1985) and maintenance, pipeline construction, agricultural development, and logging clear BSWs. Powerline construction and maintenance can compact and rut peat surfaces (Glaser 1987:70, Magnusson and Stewart 1987), reduce aerial biomass and species richness, cause erosion of surface peat (Sims and Stewart 1981), and result in herbicide use that adversely affects ericaceous vegetation and *Sphagnum* spp. (Magnusson and Stewart 1987). Clearing in permafrost terrain also can initiate thermokarst features (Péwé 1982:35). Disturbance associated with highway construction has been linked to formation of small thermokarst ponds (Senyk and Oswald 1983).

Logging for fuelwood and pulp occurs in BSWs. Impacts other than removal of biomass include disturbance of the peat surface by mechanized equipment, which may lower carbon (C) to N ratios to favor deciduous species (Brumelis and Carleton 1988, 1989); increased thaw depth in permafrost soils (Evans et al. 1988); nutrient depletion (Gordon 1983); potential fragmentation of bird habitat (Haila et al. 1987); potential for greater water yield and altered water quality in logged basins, based on studies of upland spruce systems (Nicholson 1988); loss of marten habitat (Snyder and Bissonette 1987); potential reduction of invertebrate food items for game birds (Stuen and Spidsø 1988); elimination of vegetative reproduction (Zasada 1986); and soil erosion (Aldrich and Slaughter 1983, Tallis 1983). These impacts may be positive or negative, depending on resource management objectives and values placed on various wetland functions. In Alaska, BSWs may be crossed by logging access roads, or otherwise be affected by harvest activities, but they currently are not targeted for harvest of wood (Aldrich and Slaughter 1983). Emerging wood harvest and utilization technologies could change this situation in the future.

Disposal of Waste

Society has often viewed wetlands as sites for disposal of solid waste. Solid waste buries wetlands, eliminating their functions and values, but has a secondary impact because landfill leachates contaminate ground water. A portion of Connors Bog in Anchorage, Alaska, originally a Palustrine Scrub-Shrub and Palustrine Emergent Wetland (Hogan and Tande 1983:116), was landfilled from 1958 to 1977 and later developed as commercial property and athletic playing fields (Glass 1986*b*). Similarly, the landfill currently in use in Fairbanks, Alaska, is located in an area of Palustrine Scrub-Shrub Wetland supporting black spruce. Leachate from the Connors Bog site is characterized by elevated levels of conductivity, total organic compounds, dissolved solids, and dissolved chloride; organic pollutants include benzene, ethyl benzene, methylene chloride, toluene, and dichloroethylene (Glass 1986*b*).

Today, society explores wetlands as providing final treatment and recycling mechanisms for sewage effluent and sludge (Stark and Brown 1988, Jørgensen and Mitsch 1989, Ma and Yan 1989). Peatlands used for wastewater disposal can maintain their functions and values at low loading rates, but impacts appear at high loadings. Wastewater impacts at a Minnesota site included loss of black spruce (Stark and Brown 1988). Wetlands receiving wastewater discharges in Michigan and Wisconsin tended to lose woody vegetation near the point of wastewater input and to develop extensive stands of cattail (*Typha* spp.) and duckweed (*Lemna* spp.) (Kadlec 1987). Increased biomass and reduced species diversity also characterize wetlands receiving wastewater (Kadlec 1987).

Mining of Peat

Peat mining for fuel has a long history in Europe and continues today (e.g., Taylor 1983). Large-scale peat harvest for energy production has been studied

in Minnesota, (Minn. Dep. Nat. Resour. 1984) but currently is not viable (Glaser 1987:68). Peat mining for horticultural purposes occurs on a small scale in the United States (e.g., ~567 ha in Minnesota through 1981 [Minn. DNR 1981 *in* Glaser 1987:67]).

Peat mining alters wetland characteristics by physical removal of vegetation, removal of organic substrates, and alteration of hydrologic conditions through drainage and reduced elevation of the land surface (e.g., Clausen and Brooks 1983*a*). Runoff from drained bogs chemically differs from runoff from undisturbed bogs (Table 14). Moore (1987) concluded that channelized and augmented runoff from bog drainage could increase nutrient and dissolved organic C (DOC) loading of receiving waters.

Peat mining may remove peat down to mineral soil or eutrophic peat may be left to support agricultural uses (Taylor 1983). Recovery of mined peatlands depends upon restoration of saturated conditions favorable to growth of peat-forming vegetation. In situations where peat removal is not complete and drainage ditches are blocked to retain soil moisture, revegetation of mined terrain can occur (Glaser 1987:69). Shallow ponds left after mining may be used by waterfowl.

RESEARCH

Scientists have not systematically studied the functions and values of wetlands dominated by black spruce, perhaps because research has focused on commercially important upland stands. Even research on a particular wetland type (e.g., palsa bog) numbering black spruce as a component of its vegetation may not yield information applicable to other wetland types supporting black spruce. Existing studies shedding light on the functions of BSWs include silvicultural and ecologic research on black

Table 14. Water quality variables that have shown increased levels in runoff from ditched or mined peatlands.

Variable	Location	Source
Water Temperature	Minnesota	Clausen and Brooks (1983*a*)
Conductivity	Minnesota	Clausen and Brooks (1983*a*)
	Quebec	Moore (1987)
Acidity	Minnesota	Clausen and Brooks (1983*a*)
Suspended Solids	Minnesota	Clausen and Brooks (1983*a*)
Fe	Minnesota	Clausen and Brooks (1983*a*)
	Quebec	Moore (1987)
Na	Minnesota	Clausen and Brooks (1983*a*)
	Quebec	Moore (1987)
Mg	Quebec	Moore (1987)
K	Quebec	Moore (1987)
Total Kjeldahl-N	Minnesota	Clausen and Brooks (1983*a*)
Ammonia-N	Minnesota	Clausen and Brooks (1983*a*)
	Quebec	Moore (1987)
Organic-N	Minnesota	Clausen and Brooks (1983*a*)
Total Dissolved P	Quebec	Moore (1987)
Dissolved Organic C	Quebec	Bourbonniere (1987), Moore (1987)

spruce forests and treeless mires, research in individual disciplines (e.g., hydrology) related to wetland functions, and directed research on wetland functions conducted in areas outside the distribution of black spruce. The following discussion outlines sources of information used in compiling this profile. Relevant citations appear elsewhere in the text.

Forestry Studies

Silvicultural research related to black spruce has focused on methods to improve timber production and promote regeneration following harvest. Because black spruce occurs on wet, lowland sites as well as in upland terrain, foresters and researchers have drained and fertilized forest soils to improve tree growth. The response of black spruce to these treatments provides information on nutrient deficiencies in treed wetlands and the ecologic tolerances of black spruce. This information, in turn, allows inferences about the ability of forested wetlands to use or immobilize nutrients, which is relevant to their water quality functions.

Foresters have studied harvest strategies and surface treatments to promote regeneration of logged stands. Clearcutting, strip cutting, and selective cutting are used for timber harvest in Canada. Prescribed burning, mechanical disturbance, and planting influence forest regeneration and stand composition. The response of black spruce to these silvicultural treatments reflects its biology and relationships with other species.

Ecologic Studies

Scientists have studied the structure and function of taiga ecosystems, including nutrient cycling, soil temperature, and fire. Some of the black spruce stands used as study areas in these research projects are wetlands. Wetland functions may be inferred from research findings concerning such stands and from an understanding of the controls on black spruce ecosystems.

Research shows that floodplain processes and fire are principal causes of primary and secondary succession in taiga ecosystems of interior Alaska. Successional changes affect soil temperature and moisture, as well as wildlife habitat. Relationships between soil moisture and plant communities relate to hydrologic functions, nutrient cycles provide information applicable to water quality functions, and synecologic research illuminates the trophic and habitat functions of ecosystems. Ecologic studies of individual species and groups of species in interior Alaska, northern Canada, and elsewhere also provide information on the habitat function of BSWs.

Research on treeless mires in Canada, the Great Lakes Region of the Lower 48 states, and Europe, including studies of their paleoecology, successional patterns, permafrost features, and response to disturbance, provides information on the relationships of treed and treeless wetlands and shifts between these forms. Understanding these relationships helps extrapolate information on treeless mires to BSWs. Studies of the vegetation, geomorphology, and classification of treeless mires in Alaska are few, however.

Physical Studies

Very little physical science research in Alaska and northern Canada directly examines the functions of BSWs, but hydrologic, permafrost, and water quality (including water chemistry) studies conducted in watersheds containing such wetlands provide information that can be synthesized to characterize these functions. Alaska hydrologic studies that identify specific wetland types, such as permafrost catchments dominated by black spruce, may be viewed as functional in nature. Water quality research in Alaska has addressed wetland responses to nutrient enrichment, evaluated the water quality function of mires in the Anchorage area, and compared water quality in permafrost-free and permafrost-dominated watersheds in the Interior. Additional information on the hydrologic and water quality functions of BSWs can be found in studies conducted outside Alaska.

Current Knowledge

Studies of treed and treeless bogs and fens largely have focused on their hydrology, soil and water chemistry, and vegetation. The origin and flow of water through these mires strongly influence their chemistry and thus their plant communities. Decomposing plants accumulate in mires as peat, which can alter mire hydrology with concomitant changes in chemistry and vegetation. Long-term climatic changes, short-term natural disturbances such as fire, and human-induced impacts influence mire characteristics and can produce cyclic excursions in mire

ecology. Mires often do not follow traditional hydroseral successional pathways.

European and Siberian studies of mires often emphasize wetland classification and description of vegetation. Other palearctic studies address mire stratigraphy, uses, values, and impacts. Canadian researchers have documented the stratigraphy, morphology, and vegetation of taiga mires, including the role of permafrost, but these investigations, like those of Europe and northern Asia, usually do not directly address wetland functions. The peatlands of glacial Lake Agassiz and other areas in northern Minnesota are particularly well-studied. Black spruce and tamarack dominate many wetlands in this region. Similarities among physical, chemical, and biological characteristics of circumpolar taiga peatlands allows inferences about the functions of Alaska's BSWs.

Few comprehensive studies of interior Alaska's BSWs exist. An early report described "bog" [treeless mire] vegetation and postulated cycles between treed and treeless wetlands. Later investigations described the vegetation of treeless taiga wetlands, forest community types that include BSWs, and the hydrology of permafrost basins supporting black spruce. Most Alaska research has not directly addressed the functions of BSWs and has not been multidisciplinary in nature.

In summary, integrated knowledge of BSWs in Alaska is sparse, but lines of evidence from a variety of locations and disciplines are available in the literature. Synthesis and analysis of this evidence yields a coherent picture of the wetland functions of these wetlands. This picture points the way to further research to fill data gaps.

HYDROLOGIC FUNCTIONS

Wetlands interact with the hydrologic cycle (Odum 1979). These interactions comprise the hydrologic functions of wetlands: groundwater recharge and discharge, flow regulation, and erosion control (Sather and Smith 1984:3-10). In Alaska, permafrost can modify wetland hydrology. This chapter addresses hydrologic functions of BSWs and identifies topics for further research.

GROUNDWATER DISCHARGE

Wetlands often discharge groundwater (Carter et al. 1979). Groundwater discharge can seep from an unconfined aquifer or flow from a confined (artesian) aquifer that intersects the ground surface. Permafrost can provide aquifer confinement (Kane and Stein 1983). Groundwater discharge is a wetland function that stabilizes water levels and facilitates ecologic processes such as fish spawning (Adamus and Stockwell 1983:7, Larson et al. 1988), rearing, and overwintering.

Where either continuous or discontinuous permafrost is present, the perennially frozen layer separates groundwater into suprapermafrost and subpermafrost zones (Kane and Stein 1983). ***Suprapermafrost groundwater*** occupies the saturated portion of the active layer; ***subpermafrost groundwater*** lies beneath the perennially frozen layer. ***Taliks***, thawed zones within permafrost (Gabriel and Talbot 1984:112), often occur beneath waterbodies. Taliks can penetrate the permafrost layer and allow hydrologic connections between suprapermafrost and subpermafrost zones (Woo 1986).

Suprapermafrost Groundwater

Active layers of BSWs having saturated organic soils underlain by permafrost can act as shallow unconfined aquifers (Slaughter and Kane 1979). Vertical infiltration rates are high (e.g., 2.18 $mm \cdot s^{-1}$), making overland flow unlikely (Dingman 1971:37, 1973). Dry bulk density of surface organics is low (0.02-0.04 $g \cdot cm^{-3}$), increasing to 1.45 $g \cdot cm^{-3}$ at the interface of organic and mineral soil (Slaughter and Kane 1979).

Snowmelt and rainfall rapidly enter the organic layer, but high-moisture permafrost prevents deep penetration into mineral soil (Kane 1980, Kane and Stein 1983). Consequently, suprapermafrost groundwater flows downslope within thawed organic soils and, at a much lower rate, within thawed mineral soils (Dingman 1973; Slaughter and Kane 1979; D. L. Kane, Univ. Alaska, pers. commun.). Substantial flow occurs in the organic layer during snowmelt on permafrost slopes (Kane et al. 1978). Flow within the organic layer following rainfall depends upon antecedent moisture conditions, and the ratio of runoff to rainfall increases with wetness of the watershed (Dingman 1973).

The hydrologic characteristics of permafrost slopes supporting BSWs in interior Alaska are similar in some respects to those of bogs. Precipitation infiltrates thick organic layers with little or no overland flow, lateral hydraulic conductivity exceeds vertical conductivity, and slope surfaces are ombrotrophic. Ombrotrophic BSWs do not receive groundwater and thus do not perform the groundwater-discharge function.

Black spruce also occurs in minerotrophic wetlands. Suprapermafrost groundwater discharging at the bases of bog-like slopes (e.g., Dingman 1973) probably becomes somewhat minerotrophic during downslope passage because seasonal thaw on slopes

nearly always reaches the interface between organic and mineral soil (D. L. Kane, Univ. Alaska, pers. commun.). Where the water table approaches the surface, groundwater influences vegetation through often parallel gradients of increasingly minerotrophic and hydric conditions (e.g., Vitt and Slack 1975, Calmes 1976:62, Jasieniuk and Johnson 1982).

Black spruce wetlands receiving suprapermafrost groundwater on valley floors appear to be minerotrophic. For example, shrub/sedge tussock vegetation (with variable amounts of black spruce and tamarack) on a valley floor of interior Alaska contrasts with black spruce/moss vegetation on the adjacent permafrost slope (Dingman 1971:29-31). The similar sedge tussock (i.e., *Eriophorum vaginatum*) community type is minerotrophic at sites near Fairbanks (Calmes 1976:47-48).

Black spruce wetlands supplied by discharge of suprapermafrost groundwater perform the groundwater-discharge function, albeit on a scale limited by the small storage capacity of the shallow active layer on up-gradient permafrost slopes. Suprapermafrost groundwater discharges for long recession periods following precipitation in permafrost basins, but essentially ceases during dry periods (Dingman 1973). Such discharges are short-term phenomena compared with groundwater discharges that can provide year-round baseflows in nonpermafrost areas.

Subpermafrost Groundwater

Vertical and horizontal circulation of groundwater can maintain taliks within permafrost (Hopkins et al. 1955) and allow discharge of subpermafrost groundwater at the surface. Examples include perennial springs in peatlands on alluvial and glaciofluvial fans (van Everdingen 1988), a mire lake fed by groundwater discharge (Kane and Slaughter 1973), and interior Alaska streams fed by springs (Kane et al. 1973). Discharge of subpermafrost groundwater to stream channels is not directly relevant to the functions of BSWs, although such wetlands may dominate the landscape within which the discharge occurs.

In contrast, discharge of subpermafrost groundwater to lakes, ponds, or flowages can supply fens located adjacent to, or covering the surface of, these waterbodies on grounded or floating peat mats (e.g., Kane and Slaughter 1973, Calmes 1976, Racine and Walters 1991). If black spruce is present, such fens are BSWs that perform the groundwater-discharge function, but this function cannot be extrapolated to all fens or to other BSWs. Laterally continuous permafrost immediately rules out discharge of subpermafrost groundwater. Hydrologic information (e.g., piezometer or water balance studies) or possibly topographic analysis (e.g., mire-dominated basin with no inlet but with an outlet), coupled with the presence of thawed soils, is necessary to show that discharge of subpermafrost groundwater is occurring in a given BSW.

Groundwater Discharge in Unfrozen Terrain

Southern Alaska largely is free of permafrost, which removes an impediment to groundwater discharge, but most pertinent studies in unfrozen terrain have occurred outside Alaska. Groundwater discharge has been documented in swamps (Roulet 1991, Woo and Valverde 1981), a cattail marsh (Gehrels and Mulamoottil 1990), an Alaska mire lake (DOWL Eng. 1983), a spruce-tamarack fen (Brown and Stark 1989), and spring fens (Almendinger et al. 1986; Zoltai, Taylor et al. 1988), and basin wetlands may penetrate regional water tables (Boelter and Verry 1977). Fens with large flows and deep water do not support trees, but black spruce can occur in tamarack and spring fens (Boelter and Verry 1977).

The spruce-tamarack fen studied by Brown and Stark (1989) showed strong, upward groundwater head gradients with diffuse groundwater discharge so that the entire fen performed the groundwater-discharge function. In contrast, spring fens (Appendix B) of Canada's Boreal Wetland Region are linear features continuously supplied by groundwater from point sources (Zoltai, Taylor et al. 1988). Treed "islands," which support black spruce (S.C. Zoltai, Can. For. Serv., pers. commun.), can occur in less minerotrophic areas of Canadian spring fens (Zoltai, Taylor et al. 1988) but presumably are not sites of groundwater discharge. Both types of fen may occur in Alaska but have not been specifically described for this location.

Bogs and spring fens in the form of unfrozen peat mounds that support black spruce occur in northern Minnesota, but BSWs with these characteristics have not been described in Alaska. Black spruce bogs, by definition, do not perform the groundwater-dis-

charge function. Treeless, ombrotrophic bog aprons or *Sphagnum* lawns surrounding forested bogs merge downslope into poor fen water tracks that channel minerotrophic runoff (Glaser 1987:24-34). Weakly minerotrophic lower bog aprons indicate either groundwater discharge (Siegel 1983) or the effects of peat decomposition (Glaser et al. 1981). Discharge from highly permeable surface organics (i.e., the ***acrotelm*** or aerobic, partly living upper layer of mires [Ingram 1983]) of a bog would be limited in volume, perhaps somewhat akin to discharge of suprapermafrost groundwater in northern regions.

Current research in the northern Minnesota peatlands indicates a drought-affected interplay between precipitation-driven water table domes under raised bogs and upward head gradients driven by regional groundwater (Siegel and Glaser 1987, McNamara et al. 1992, Siegel et al. 1995). Upward head gradients of sufficient duration and magnitude to frequently discharge groundwater at the surface of raised bogs would change them to fens. Spring fen mounds (Almendinger et al. 1986) and fen water tracks at least periodically discharge groundwater (Siegel and Glaser 1987) and thus perform the groundwater-discharge function.

In southern Alaska, groundwater discharges to Mosquito Lake in Anchorage (DOWL Engineers 1983) but apparently does not discharge to the BSW to the northeast, which slopes toward the lake. Groundwater also moves through peat deposits of Klatt Bog in Anchorage but apparently does not discharge to the undisturbed bog surface (Glass 1986*a*). Nearby Connors Bog is largely supplied by precipitation, but groundwater occasionally discharges to, or passes through, Connors Lake (Glass 1987*b*). The sedge fen occupying exposed lake bottom along the northwest shoreline of Connors Lake (Hogan and Tande 1983:29-32) could intermittently discharge groundwater, but there is no evidence that adjacent black spruce stands do so. Although detailed information is not available, black spruce stands in the Anchorage "bogs" may be ombrotrophic and thus not capable of performing the groundwater-discharge function.

Functional Summary

Many Alaska wetlands are ombrotrophic, unaffected by groundwater. Ombrotrophic BSWs, including bogs, do not perform the groundwater-discharge function. Groundwater discharge or surface runoff from mineral terrain influences minerotrophic wetlands, including fens. Black spruce (or tamarack) wetlands perform the groundwater-discharge function when they are supplied by upward groundwater flow, but the distribution and frequency of this phenomenon in Alaska are not known.

Site-specific documentation of groundwater discharge is required to ascribe the groundwater-discharge function to any particular minerotrophic BSW. Exposure of a suprapermafrost water table at the base of a moss-covered permafrost slope, evidence of a talik in terrain where permafrost can form a confined aquifer, a visually-apparent spring, a water balance study indicating groundwater discharge, or a piezometric study showing upward groundwater flow can provide such documentation.

Water chemistry is another potential indicator of the strength of the groundwater-discharge function for a given fen or fen-like wetland. Presumably, groundwater discharge dominates a rich fen to a greater degree than it does a poor fen when the same aquifer supplies both fens (i.e., Ca concentration and pH of the discharge is the same in both fens). Such comparisons are not valid between fens with different discharge sources because calcareous aquifers produce higher Ca and pH concentrations than do mineral-poor aquifers.

Functional Sensitivity to Impacts

The groundwater-discharge function of minerotrophic BSWs is impaired or eliminated by fill placement within the area of discharge. Poorly permeable fill (e.g., silt, clay) and compaction of underlying substrates reduce the hydraulic conductivity of the groundwater "window" through which discharge occurs. Fill outside the zone of groundwater discharge, and not otherwise impairing flow within the aquifer, is unlikely to directly affect discharge but might alter patterns of surface flow and affect down-gradient ecologic communities and water supplies. Lower hydraulic conductivities, coupled with reduced areas available for discharge, imply decreased rates of groundwater discharge in filled wetlands.

Mitigating the impact of fill on groundwater discharge might be possible in nonpermafrost terrain. Considering only the narrow "water-supply" aspect of groundwater discharge, a fill of shot rock (highly

permeable) or placement of perforated drains in a gravel bed beneath less permeable fill might permit lateral flow, which could continue to supply remaining wetlands or streamflow. Drains of this sort usually freeze and fail when placed on permafrost soils, however (D. L. Kane, Univ. Alaska, pers. commun.).

Wetland drainage is unlikely to adversely affect the water-supply aspect of the groundwater-discharge function of minerotrophic BSWs. Ditches or tiles that intercept groundwater and direct it to the same drainages that originally received such flows would maintain or increase downstream water-supply uses. Redirection of flow could alter downstream water supplies, however.

GROUNDWATER RECHARGE

Surface water infiltrates the ground to recharge aquifers. Although some wetlands, particularly those only seasonally holding water, may recharge groundwater, many wetlands apparently do not perform this function (Carter et al. 1979, Sather and Smith 1984:6). Black spruce wetlands share the variability of other wetlands with respect to the groundwater-recharge function.

The ***catotelm,*** highly-decomposed, anaerobic peat of low hydraulic conductivity, underlies the acrotelm (Ingram 1983). Thick deposits of peat therefore may perch bog water tables above regional water tables (e.g., Bay 1969) with flow (primarily lateral) limited to the acrotelm (Glaser 1987:18). Alternatively, downward head gradients imply that bogs recharge regional groundwater (Siegel 1983, Glaser 1987:20). Both views imply that bogs are sites of groundwater recharge, either of shallow, perched water tables or of regional water tables. Ombrotrophic BSWs should exhibit similar characteristics.

Fens vary in their capability to recharge groundwater. Groundwater discharge within a fen demonstrates a hydraulic connection to an aquifer and thus a potential for recharge in response to regional groundwater fluctuations (Glaser 1987:20). Fens that continually discharge groundwater (e.g., spring fens) do not perform the groundwater-recharge function. Fens fed primarily by surface flow could be underlain by soils of low permeability, which would reduce their potential for recharging groundwater. The variable recharge characteristics of fens require site-specific studies to document this hydrologic function. Minerotrophic BSWs should be comparable to fens with respect to groundwater recharge.

Suprapermafrost Groundwater

Shallow permafrost frequently characterizes bogs (e.g., Zoltai, Tarnocai et al. 1988) and other ombrotrophic wetlands within the region of discontinuous permafrost. Infiltration of precipitation recharges suprapermafrost groundwater (Williams and Waller 1963) as demonstrated by the following evidence: snowmelt satisfies the moisture deficit of the organic layer before significant runoff is initiated (Kane et al. 1981), near-surface flow occurs within the organic layer (Kane et al. 1978), rainfall intensity and duration control moisture retention of moss (Chacho and Bredthauer 1983), and streams in permafrost watersheds exhibit long recession periods following rainfall, probably due to suprapermafrost subsurface flow (Dingman 1971:80). Supra-permafrost groundwater provides insufficient volume for direct domestic water supply, although it does contribute water to waterbodies providing such supplies (Kane and Stein 1983). Permafrost BSWs perform the groundwater-recharge function, but only with respect to suprapermafrost groundwater.

Subpermafrost Groundwater

Many minerotrophic wetlands in the zone of discontinuous permafrost are underlain by permafrost (Calmes 1976; D. K. Swanson, Nat. Resour. Conserv. Serv., pers. commun.) and cannot recharge subpermafrost groundwater. Other minerotrophic wetlands, such as northern ribbed fens in the Hudson Bay Lowlands, Labrador, and Great Slave Lake Region, usually do not contain permafrost (P. H. Glaser, Univ. Minn., pers. commun.). Elsewhere, permafrost may be limited to specific geomorphic features such as the peat ridges of ribbed fens (Zoltai, Tarnocai et al. 1988). Thawed, minerotrophic BSWs might recharge subpermafrost groundwater if head gradients periodically were directed downward, but such recharge has not been demonstrated in Alaska.

Most recharge of subpermafrost groundwater in interior Alaska occurs in unfrozen uplands such as south-facing slopes (Kane and Stein 1983) and, for alluvial aquifers, by infiltration from larger rivers (Nelson 1978:16). The primary source of recharge in uplands is infiltration of snowmelt (Kane et al. 1978, Kane 1980, Kane et al. 1981, Kane and Stein 1983,

Gieck and Kane 1986). Black spruce wetlands generally should not be viewed as sites of recharge for subpermafrost groundwater without site-specific piezometric or water-balance studies.

Groundwater Recharge in Unfrozen Terrain

Permafrost becomes widely scattered in the southerly portions of the zone of discontinuous permafrost (Brown and Péwé 1973). In this region, seasonally frozen soils may affect infiltration and thus recharge of groundwater (Dingman 1975:40-43) but often have no effect where dry soils have the capacity to take up more moisture than snowmelt provides (D. L. Kane, Univ. Alaska, pers. commun.). Some wetlands recharge groundwater in unfrozen terrain.

A swamp (Woo and Valverde 1981) and a cattail marsh (Gehrels and Mulamoottil 1990) recharged groundwater in Ontario, although other portions of these wetlands discharged groundwater and exchanges probably were confined to thick organic layers. Black spruce bogs and fens on organo-karst terrain in the Hudson Bay Lowlands recharged groundwater via sinkhole complexes (Cowell 1983). In Minnesota, a basin bog with deep peat and a perched water table recharged groundwater to a limited extent by lateral flow through surficial peat to surrounding glacial till, and a peat bog with shallow peat exhibited vertical recharge to underlying and surrounding sand, but a fen did not recharge groundwater (Verry and Boelter 1979). Although poor fen water tracks occasionally can recharge groundwater (e.g., Siegel and Glaser 1987), site-specific hydrologic studies are required to demonstrate this function.

An unconfined aquifer of peat interbedded with gravel and sand lenses over clay and silt occurs in Anchorage, Alaska (Zenone 1976). Precipitation supplies most of the water to the aquifer in Klatt Bog, but percolation to the underlying, confined aquifers probably is much less than evapotranspiration losses (Glass 1986*a*). The unconfined aquifer of nearby Connors Bog transferred only an estimated 10 $mm \cdot yr^{-1}$ to the underlying confined aquifer (Glass 1986*b*). Ombrotrophic BSWs recharge groundwater in unfrozen terrain, but the magnitude of such recharge may be small.

Functional Summary

Ombrotrophic BSWs perform the groundwater-recharge function, but the magnitude of recharge generally is small. In regions of widespread discontinuous permafrost, ombrotrophic wetlands recharge only suprapermafrost groundwater. Where permafrost is absent, ombrotrophic wetlands recharge either shallow, perched water tables or deeper regional aquifers. In either case, vertical flow through deep layers of ***sapric*** (highly decomposed) peat may be small. Uplands and some riparian areas contribute more to regional groundwater recharge than do ombrotrophic wetlands. Minerotrophic BSWs should not be considered to perform the groundwater-recharge function unless site-specific piezometric or water-balance studies show that recharge occurs.

The trophic status of a BSW can indicate its potential for groundwater recharge: ombrotrophy indicates recharge whereas, in the absence of obvious surface inputs of Ca-rich water, strong minerotrophy indicates discharge. Weak minerotrophy is not an indicator for or against recharge because poor fens can arise from discharge of mineral-poor groundwater (Vitt et al. 1975 *in* Zoltai 1988), oxidative decomposition of peat in areas of concentrated flow (Glaser et al. 1981), and, possibly, fluctuating head gradients with occasional recharge (Glaser 1987:20). Laterally-extensive permafrost in a BSW indicates that the groundwater-recharge function, if present, is limited to suprapermafrost groundwater whereas thawed areas indicate potential recharge of subpermafrost groundwater.

Functional Sensitivity to Impacts

The groundwater-recharge function of BSWs is sensitive to fill placement. Compacted fill and underlying compressed peat have lower hydraulic conductivities than do the highly-permeable ***fibric peats*** (undecomposed) of undisturbed wetlands and thus would resist infiltration and percolation of precipitation. Fill runoff might flow to surface drainages rather than enter the groundwater system. Directing fill runoff to adjacent undisturbed wetlands capable of recharging groundwater could compensate for lost recharge area, if runoff loading of the remaining wetlands did not exceed their infiltration capacity. Siltation from fill surfaces could impair the ability of remaining wetlands to recharge groundwater, however.

The groundwater-recharge function of BSWs is

sensitive to drainage. Drainage converts groundwater flow to surface flow, shortening groundwater flow paths and reducing groundwater volumes potentially available for recharge. In wetlands having only near-surface groundwater (e.g., permafrost wetlands), drainage affects small volumes of water of localized significance. The adverse effect of drainage on recharge potentially is greatest for unfrozen BSWs that supply regional water tables, but studies reviewed for this profile did not demonstrate large recharge volumes for these wetlands.

The detrimental effect of drainage on groundwater recharge is ameliorated by the relatively low hydraulic conductivity of sapric peat. Effective drainage requires closely spaced ditches, as little as 30 to 40 m apart (Glass 1986*a*, Lieffers and Rothwell 1987). Boelter (1972 *in* Glaser et. al. 1981) found that even a deep ditch drained only the surface layer of peat at horizontal distances exceeding 5 m. Effective drainage of BSWs, therefore, is an expensive proposition, which could limit its application.

FLOW REGULATION

Flow regulation, sometimes referred to as flood control, occurs when wetlands interact with precipitation, surface runoff, and streamflow to modify the magnitude, timing, and duration of downstream flows (Carter et al. 1979, Sather and Smith 1984:3-5, Larson et al. 1988). Wetlands store precipitation in several ways: snowmelt and rainfall percolate into the soil, water fills surface depressions, and basin topography temporarily detains flow. Wetland vegetation reduces water velocity by increasing channel roughness (i.e., Manning's "n") (Carter et al. 1979), and evapotranspiration of stored surface water and groundwater reduces downstream flows (Larson et al. 1988). "Relative to inputs, wetland basins lose less water through runoff and more through evaporation than non-wetland basins under similar environmental conditions" (Roulet 1987:338). Wetlands potentially provide baseflows to streams but generally are less effective than upland areas because wetlands have high evapotranspiration losses (Carter et al. 1979).

Black spruce wetlands are heterogeneous with respect to flow regulation and differ with respect to storage capacities for precipitation and surface flows, proportions of stored water subsequently released to surface and subsurface flows, and time scales over which releases occur. Permafrost, seasonal frost, and high water tables limit the storage capacities of these wetlands and change the runoff responses of associated watersheds.

Subsurface Storage of Precipitation

High snowmelt runoff characterizes permafrost sites (Woo 1986, Roulet 1987); nevertheless, BSWs store snowmelt within the soil system. During winter, soil moisture moves into the overlying snowpack and desiccates the organic layer in response to temperature-driven vapor-pressure gradients (Slaughter and Kane 1979, Kane et al. 1981, Slaughter and Benson 1986, Woo 1986). The desiccated organic layer has low bulk density (Slaughter and Kane 1979) and accepts initial snowmelt (Kane et al. 1981), although runoff begins before the moisture deficit of the organic layer is completely satisfied (Chacho and Bredthauer 1983).

The water-holding capacity of the desiccated organic layer limits snowmelt water storage in permafrost wetlands because snowmelt generally cannot readily enter underlying high-moisture mineral soils. In these soils, water migrates toward the freezing front and forms a relatively impermeable ice-rich layer during freeze-up; this layer later inhibits snowmelt percolation during breakup (Kane 1980, Kane et al. 1981, Kane and Stein 1983). In contrast, dry, frozen mineral soils characteristic of permafrost-free uplands infiltrate snowmelt and produce little runoff (Kane 1980, Kane et al. 1981, Kane and Stein 1983). Snowmelt infiltration on nonpermafrost uplands greatly exceeds that in permafrost BSWs in interior Alaska.

Unfrozen BSWs also accept only limited snowmelt. Examples include seasonally-frozen wetlands (presumably peatlands) near James Bay, Canada, which have "wetland" streamflow regimes characterized by low infiltration into frozen ground and high snowmelt flows (Woo 1988); black spruce bogs in Minnesota, which have high water tables (Bay 1969, Verry and Boelter 1979); and fens, which also have high water tables (Verry and Boelter 1979, Glaser 1987:21). Similarly, high spring flows characterized Wisconsin basins with high proportions of wetlands and lakes (not differentiated) as compared to basins with no wetlands and lakes (Novitzki 1979). As in permafrost BSWs, snowmelt storage in seasonally-frozen wetlands appears small.

Black spruce wetlands more easily store water during summer, when frost and water tables are depressed, than during spring, when frost and water tables are high. Active layer thickness increases approximately linearly from May to September on undisturbed, forested, permafrost sites in interior Alaska and reaches a maximum in September or early October (e.g., Viereck 1982). The unsaturated portion of the active layer can accept precipitation until the water table reaches the surface, at which time overland flow occurs (Wright 1979, Woo 1986). In interior Alaska, precipitation quickly induced overland flow on a minerotrophic permafrost valley bottom with a high water table (Dingman 1973). Storage in permafrost BSWs is limited to the capacity of the active layer, which in summer is dependent upon depth of thaw (Woo 1986), antecedent moisture (Roulet 1987), groundwater flow, and evapotranspiration.

As in permafrost wetlands, rainfall infiltration can occur in nonpermafrost BSWs until the zone of saturation reaches the surface. Unsaturated peat thickness was <0.3 m after snowmelt, generally did not exceed 0.9 m at any time during 1983, and at one undisturbed location was ~0.2 m even in mid-summer for Klatt Bog in Anchorage, Alaska (Glass 1986*a*). Forested swamps that recharge groundwater (Woo and Valverde 1981) and discharge only a fraction of incident precipitation (Roulet1991), and fens with reversing groundwater head gradients (Almendinger et al. 1986, Siegel and Glaser 1987), imply that treed fens should store rainfall when water tables are below the surface. In contrast, floating-mat, treeless groundwater-discharge fens of interior Alaska (Racine and Walters 1991) intercept rainfall, but storage time within the mat should be negligible.

Water fluxes across the surfaces of ombrotrophic wetlands are downward whereas surfaces of minerotrophic wetlands receive upward or horizontal flows. Based on these characteristics, ombrotrophic BSWs likely infiltrate and store more rainfall than do minerotrophic BSWs. Water table position controls storage in both trophic classes, however.

Detention and Depression Storage of Precipitation

The topography and microtopography of peat-forming wetlands provide surface storage of snowmelt and rainfall and slow overland flow. On permafrost slopes, water fills microtopographic depressions as ***depression storage*** before runoff occurs (Woo 1986). Depressions filled to a depth greater than the elevation of the surface outlet moderate flow by providing ***detention storage*** (Woo 1986). Pits excavated in a permafrost slope quickly flooded with snowmelt (Kane et al. 1978), illustrating the potential for depression and detention storage by microtopographic features in BSWs.

Black spruce wetlands with slightly sloping surfaces also store water in surface depressions. Such depressions include the crescentic pools of domed bogs, "small wet depressions" of northern plateau bogs, ***flarks*** (wet depressions) separated by ***strings*** (peat ridges oriented transverse to the direction of flow) of northern ribbed fens, and entire collapse scar bogs and fens (Natl. Wetlands Working Group 1988:417-420). Microtopographic depressions in discontinuous permafrost terrain in Quebec stored 44 to 74% of total snowmelt runoff (FitzGibbon and Dunne 1981). The thaw ponds, depressions, and mounds of wet, ombrotrophic black spruce communities (Foote 1983:47) and the intertussock hollows of minerotrophic black spruce communities (D. K. Swanson, Nat. Resour. Conserv. Serv., pers. commun.) suggest modest depression and detention storage by BSWs of interior Alaska. Water table position (e.g., Bay 1969) and microtopography determine the volume available for surface storage in BSWs.

Release of Stored Precipitation and Effect on Streamflow

Water storage and release by BSWs affect streamflow. Partitioning of released water between surface and subsurface flows and evapotranspiration changes seasonally. Permafrost black spruce slopes release suprapermafrost groundwater during snowmelt. In an interior Alaska watershed, such slopes released ~51% of snowmelt, with the remainder retained within saturated organic soils of the active layer (Kane et al. 1981). Although the organic layer delayed runoff initiation for 4 days, daily streamflows lagged daily snowmelt by only 3 hours once significant runoff began (Kane et al. 1981). Most runoff of snowmelt groundwater in this watershed came from permafrost soils (Kane et al. 1981, Chacho and Bredthauer 1983); snowmelt infiltrated

mineral soils in the nonpermafrost areas (Kane and Stein 1983). Rapid release of snowmelt is consistent with a "wetland" streamflow regime (Woo 1988).

Permafrost black spruce slopes also release stored rainfall via suprapermafrost groundwater. Surface runoff from an intermittently-exposed suprapermafrost water table of a valley floor caused rapid streamflow response to rainfall in a permafrost basin, but slow flow of suprapermafrost groundwater from black spruce/moss slopes caused streamflow to recede slowly (Dingman 1971:67-80; 1973). A permafrost-dominated (53.2%) subwatershed exhibited higher peak flows (by an order of magnitude) and lower baseflows than an upland-dominated subwatershed (Slaughter and Kane 1979, Haugen et al. 1982). Other Alaska drainages with permafrost soils also have high peak flows and long recession times (Ford and Bedford 1987). The streamflow responses of these basins indicate that permafrost BSWs regulate flows to a lesser extent than do well-drained uplands.

Release of stored snowmelt and rainfall in nonpermafrost bogs in some respects resembles that of frozen BSWs. Flow from nonpermafrost bogs generally is absent in winter, high during snowmelt and periods of high precipitation, and low or absent during extended dry periods (Bay 1969, Boelter and Verry 1977, Glass 1986*a*). Approximately 66% of the annual water yield of unfrozen Minnesota bogs appears as spring runoff, due, in part, to seasonally high water tables; and summer streamflow from Minnesota bogs responds rapidly to rainfall, once storage is satisfied (Bay 1969), by "slow release of water from deeper peat horizons as water tables recede" (Bay 1969:99). Depressions within a subarctic "marsh" in a peatland basin supplied surface flow to streams and created long recessions during summer dry periods (Woo 1988). Downward groundwater head gradients in nonpermafrost bogs also may release some stored precipitation to regional water tables (e.g., Siegel 1983).

High summer evapotranspiration from mires reduces the amount of water released to streamflow or groundwater recharge (Verry and Boelter 1979); low spring and fall evapotranspiration has the opposite effect (e.g., Bay 1969, Woo and Valverde 1981, Gieck and Kane 1986, Riseborough and Burn 1988, Gehrels and Mulamoottil 1990). Evapotranspiration was the primary route for outflow from permafrost-free Klatt Bog and Connors Bog in Anchorage, Alaska (Glass 1986*a,b*), and a Minnesota watershed containing a bog exported 65% of incident precipitation as water vapor (Verry and Timmons 1982). Evaporation from *Sphagnum recurvum* cores exceeded that from a water surface by a factor of ~2 (Nichols and Brown 1980), demonstrating the powerful ability of mires to transfer stored water to the atmosphere.

Surface runoff is more likely to occur in minerotrophic wetlands with characteristically high water tables than in ombrotrophic wetlands with highly-permeable acrotelms. Flows from groundwater fens can occur throughout the year, mainly as a function of regional hydrogeology, and are more uniformly distributed than those of bogs, but rapid runoff of incident precipitation and losses to evapotranspiration may actually reduce their ability to regulate flows (Boelter and Verry 1977).

Black spruce wetlands release water primarily via groundwater and surface flow during snowmelt and via evapotranspiration during the summer. High rates of evapotranspiration, flat topography, and near-surface storage of incident precipitation characteristic of unfrozen bogs reduce peak flows and create long streamflow recession periods (Boelter and Verry 1977). Ombrotrophic permafrost BSWs appear to have similar characteristics. Minerotrophic BSWs can supply baseflows to waterbodies.

Functional Summary

Ombrotrophic BSWs on permafrost slopes demonstrate quantitatively small, short-term flow regulation by retaining some suprapermafrost groundwater during initial snowmelt and exhibiting microtopography conducive to detention and depression storage, should surface flow occur. The desiccated organic layers of frozen and unfrozen lowland bogs probably function similarly, but high water tables could reduce subsurface storage of snowmelt. Ombrotrophic BSWs regulate streamflow by quantitatively-small subsurface storage of rainfall, limited by the position of the water table. Evapotranspiration losses from ombrotrophic wetlands may cause streamflows to cease in dry weather, which might be considered an antiregulatory rather than regulatory function.

Minerotrophic BSWs fed by groundwater perform the flow-regulation function by providing long-

term baseflows but have limited ability to regulate streamflows by subsurface storage. Black spruce wetlands supplied by suprapermafrost groundwater provide only quantitatively small, short-term baseflows. Both permafrost and nonpermafrost minerotrophic wetlands may provide depression and detention surface storage, but the magnitude and significance of such storage has not been documented. Despite the ways in which black spruce wetlands act to regulate flows, in comparison with vegetated, well-drained uplands of low to moderate slope, the wetlands generally are less effective in performing the flow-regulation function.

Slope may indicate various aspects of the flow-regulation function of ombrotrophic black wetlands. Organic layers of ombrotrophic permafrost slopes should drain faster than those of lowland wetlands, provide more subsurface storage for subsequent precipitation events, minimize losses to evapotranspiration, and increase the amount of suprapermafrost groundwater supplied to the valley floor and hence to downstream flows. In contrast, relatively flat ombrotrophic wetlands would have lower hydraulic gradients than slope wetlands, potentially longer residence times for stored suprapermafrost groundwater, higher water tables and hence less subsurface storage capacity for subsequent precipitation events, and higher evapotranspiration losses. High evapotranspiration losses in lowland ombrotrophic wetlands might prevent most of the stored water from augmenting streamflow but should restore subsurface storage capacity during dry periods.

Groundwater discharge indicates the ability of a minerotrophic BSW to provide baseflows but is a negative indictor for flow regulation by subsurface storage. In unfrozen wetlands, discharge of groundwater implies provision of long-term baseflows, although such flows may accumulate largely as ***aufeis*** or ***naleds*** ("sheets of ice formed by the freezing of overflow water"; "stream icing" [Gabriel and Talbot 1984:12,75]) during winter. Discharge of suprapermafrost groundwater implies quantitatively-small, short-term additions to seasonal baseflows. Black spruce wetlands discharging sufficient water to provide long-term baseflows should have high water tables and little subsurface storage capacity to moderate runoff.

Functional Sensitivity to Impacts

Fill diminishes the flow-regulation function of ombrotrophic BSWs by reducing vertical infiltration of precipitation (i.e., subsurface storage), increasing surface runoff, eliminating detention and depression storage, and reducing evapotranspiration in filled areas, all of which potentially increase peak flows in down-gradient waterbodies. Because unvegetated fills conduct heat, ice-rich, fine-grained soils adjacent to fill embankments frequently thaw, subside, and intercept suprapermafrost groundwater and surface runoff. Linear fills (e.g., roads) and their peripheral zones of subsidence can direct intercepted flows to nearby streams, increasing peak flows. Little mitigation for loss of these aspects of flow regulation appears feasible without extensive hydraulic engineering.

The effects of fill on flow regulation in minerotrophic wetlands with seasonally-depressed water tables should parallel that of fill in ombrotrophic wetlands. For sites discharging groundwater, fill-induced loss of infiltration capacity may not be significant, but fill covering zones of groundwater discharge would reduce their ability to provide baseflows. Placement of highly-permeable fill or installation of subdrains on nonpermafrost soils could maintain groundwater discharge for downstream water supplies, however.

The flow-regulation function of ombrotrophic BSWs is sensitive to drainage. Drainage that effectively lowers wetland water tables can reduce evapotranspiration and increase the proportion of channel precipitation, which increase both water yield as surface runoff and peak flow (Verry and Boelter 1979). Mire drainage increases peat decomposition and can cause surface subsidence (Glaser 1987:67), the hydrologic effects of which are not clear. Little mitigation for increased surface runoff appears feasible without extensive hydraulic engineering.

Drainage of groundwater-discharge wetlands is unlikely to diminish their flow-regulation function for providing baseflows. Drainage should increase near-surface storage for precipitation and snowmelt by depressing water tables, which should increase short-term flow regulation. Nevertheless, short storage times could to some extent offset increased storage capacities in drained, minerotrophic BSWs.

EROSION CONTROL

Wetlands control erosion by stabilizing soil surfaces or dissipating energy of waves and currents (Carter et al. 1979). Black spruce wetlands affect rates of erosion by insulating mineral soils and promoting permafrost formation in the zone of widespread discontinuous permafrost. Elsewhere, BSWs mantle mineral soils with peat and provide mechanical stability for soil surfaces.

Thermal Stability in Permafrost Terrain

Permafrost BSWs thermally stabilize erodible soils by accumulating an insulating layer of peat, which in mature wetland stands typically ranges from 0.3 to 1.0 m in thickness (Foote 1983:47) and contributes to permafrost formation (Brown and Péwé 1973). The active layer may extend into mineral soil as the season of thaw progresses or may be confined to organic horizons, depending on peat thickness. Frozen soils protect against slope movements and erosion by running water, although the vegetative mat provides most erosion protection, and the thermal stability function of frozen soil is not necessarily confined to wetland environments (D. K. Swanson, Nat. Resour. Conserv. Serv., pers. commun.).

Permafrost BSWs also protect against thermokarst phenomena (see Péwé 1982). Factors disturbing this thermal equilibrium include windthrow (Wallace 1948), fires and firelines (Viereck 1982), vehicle traffic (Racine and Ahlstrand 1991), and clearing of land (Péwé 1982, Ping 1987). In nearly all cases, depth of thaw increases following disturbance and persists for years to decades depending upon the severity of disturbance. Thaw alone may not lead to erosion (Aldrich and Slaughter 1983, Racine and Ahlstrand 1991), but thaw coupled with removal of the organic mat (e.g., firelines [Viereck 1973*a*]) can produce severe erosion on slopes in interior Alaska. Thaw also can cause the ground surface to subside, pond water, and initiate growth of thermokarst lakes (Viereck 1973*b*, Burn and Smith 1988).

Mechanical Stability

The organic mat of BSWs, even when disturbed, isolates mineral soil from erosive forces. Rainfall erosion on a trail containing churned-up *Sphagnum* sp. and feathermoss in permafrost black spruce was ~3 times that from cutover and undisturbed permafrost-free forest plots with intact surface vegetation but ~6 times less than erosion from stripped mineral soil on another permafrost-free plot (Aldrich and Slaughter 1983). Likewise, hydraulic erosion on permafrost in peat-forming tussock-shrub alpine tundra subjected to multiple vehicle passes was small (Racine and Ahlstrand 1991). Activities that remove the organic layer, such as construction of bladed fire-control lines, expose underlying mineral soils to thaw and hydraulic erosion (DeLeonardis 1971 *in* Slaughter and Aldrich 1989).

Functional Summary

Black spruce wetlands perform the erosion-control function by insulating permafrost soils so that the bulk of the soil profile is immobilized in a frozen state and by mantling erodible mineral soils with a layer of peat resistant to erosion whether frozen or thawed. Erosion control by BSWs is not unique. Permafrost-free, well-drained forest stands also develop mats of organic material in later successional stages (e.g., Foote 1983), which protect mineral soils from erosive forces.

Thickness of the organic mat may serve as an indicator of the erosion-control function. Thick organic layers make it more likely that mineral soils will remain frozen throughout the season of thaw on permafrost sites and imply that moderate surface disturbance will not penetrate sufficiently to expose mineral soils to thaw and hydraulic erosion.

Functional Sensitivity to Impacts

The erosion-control function of BSWs probably is only slightly sensitive to fill placement that does not disrupt surface organics. Thaw subsidence at fill perimeters on permafrost sites could pond water and alter vegetation, but erosion would be unlikely on low to moderate slopes. If the organic mat is not intact, however, severe erosion can result when linear fills across long permafrost slopes intercept suprapermafrost groundwater and channel it as surface flow (pers. observation).

Draining may affect the erosion-control function of BSWs to a greater degree than filling. Ditches that penetrate peat to mineral soil expose the soil to erosion. On permafrost sites, lateral and vertical thaw around drainage ditches could cause erosion of slumping, fine-grained, ice-rich soils.

DATA GAPS

Hydrologic studies in subarctic and boreal areas rarely have focused specifically on the hydrologic functions of BSWs. Data gaps exist with respect to groundwater discharge and recharge, flow regulation, and sensitivity of hydrologic functions to impacts of fill placement and drainage.

Groundwater Discharge

Wetland literature reveals no comprehensive studies relating groundwater discharge to the vegetation and morphology of minerotrophic BSWs in Alaska, although botanical studies of groundwater-discharge fens are available for several boreal areas of Canada (e.g., Slack et al. 1980). Potential sites of groundwater discharge include large, floating-mat, groundwater-discharge fens on the Tanana Flats in interior Alaska (Racine and Walters 1991); perennial springs discharging subpermafrost groundwater on alluvial and glaciofluvial fans, as described for the Yukon Territory (van Everdingen 1988); and lakes receiving subpermafrost groundwater (Kane and Slaughter 1973). The distribution and abundance of such discharge sites and their hydrologic relationships, if any, with included or adjacent BSWs remain to be investigated.

Mixed stands of black spruce and tamarack occur in the Interior, apparently on permafrost, but have not been formally described (Viereck et al. 1992:77). Studies of wetland vegetation outside Alaska, however, often identify tamarack with fens (e.g., Zoltai, Tarnocai et al. 1988). Hydrologic investigations of Alaska spruce-tamarack stands would clarify their trophic status and sources of water.

Groundwater Recharge

The relationship between BSWs and recharge of regional groundwater has received little study in Alaska. Several unfrozen bogs in Anchorage, Alaska contributed little to regional groundwater supplies (Glass 1986*a,b*), but more extensive hydrologic study of unfrozen ombrotrophic wetlands and their relationships to regional water tables is necessary.

Some minerotrophic wetlands of interior Alaska have been reported as unfrozen (e.g., Drury 1956:19-21, Calmes 1976:8) based on probing 1 to 2 m from the surface rather than drilling to greater depths. Presence or absence of taliks extending to subpermafrost groundwater should be verified for various minerotrophic wetlands. Although groundwater recharge by fens probably is rare, seasonally-downward head gradients (Glaser 1987:19-20) could occur in Alaska. Piezometric studies within unfrozen BSWs would clarify their relationships to subpermafrost aquifers.

Flow Regulation

Hydrologic studies of flow regulation by relatively flat BSWs in interior Alaska, unlike those of permafrost slopes, are lacking. Whether or not the slopes of permafrost BSWs actually produce measurable differences in associated streamflow responses is not clear because some variables (e.g., higher hydraulic gradients and potentially higher subsurface storage capacity of ombrotrophic slopes as compared to floodplain bogs) may offset each other, and researchers have not conducted comparative studies. Evapotranspiration losses (Glass 1986*a,b*) and "nearly level bog topography and the large detention storage of surface peats" (Boelter and Verry 1977:17) provide short-term flow regulation in unfrozen lowland bogs, but this conclusion should be verified for the range of Alaska BSWs. The role of minerotrophic BSWs in maintaining biologically important streamflows in Alaska also should be investigated.

Erosion Control

The erosion-control function of undisturbed BSWs is well-established. Peat layers protect erodible soils from the erosive force of flowing water whereas gross disturbance of such layers can produce severe erosion.

Functional Sensitivity to Impacts

The hydrologic sensitivity of Alaska BSWs to impacts of fill placement and drainage remains largely unexplored. Glass (1986*a*) measured flows from ditches draining portions of nonpermafrost Klatt Bog in Anchorage, Alaska, but similar studies for permafrost BSWs are not evident.

No direct studies of fill placement versus the hydrologic functions of groundwater discharge and recharge, flow regulation, and erosion control are apparent in the literature on northern mires. At this time, hydrologic effects of fill placement must be inferred from the physical characteristics of fills and BSWs. Directed studies of fill placement on wetland hydrology are necessary to confirm such inferences.

WATER QUALITY FUNCTIONS

The physiological processes of microorganisms, plants, and animals coupled with slow water velocities and physical settling of particulates are the main factors affecting water quality in wetlands (Sather and Smith 1984:11). These physical, chemical, and biological processes buffer changes in the quality of water discharged from wetlands (Kadlec and Kadlec 1979). Water quality functions of wetlands include nutrient transformation, retention, and removal (Larson et al. 1988), which can improve water quality where wetlands receive high loadings of N and P from human activities (van der Valk et al. 1979, Sather and Smith 1984:11-20). Wetlands also can retain sediment and immobilize or degrade toxic pollutants. This chapter examines sediment retention, nutrient uptake, nutrient transformation, and contaminant removal by BSWs and topics for further research on their water quality functions.

SEDIMENT RETENTION

Sediment retention or trapping is considered either a hydrologic or a water quality function because of its relation to erosion control and consequent effect on water quality (Carter et al. 1979, Sather and Smith 1984:6-7, Larson et al. 1988). Settling and "filtering" by near-surface flow through organic material retain sediment in wetlands. Because sedimentation is inversely proportional to water velocity (Boto and Patrick 1978 *in* Brown and Stark 1989), slow wetland flows are conducive to settling of suspended solids (Elder 1988).

Low-velocity or nearly stagnant flows characterize basin wetlands (Brown 1990). Closed basins retain nearly all inorganic sediment (Carter et al. 1979), and open basins retain significant quantities, although resuspension can occur in some systems (Kadlec and Kadlec 1979). Even wetlands on slopes retain sediment if water velocities are low (Novitzki 1979).

The microtopographies and permeable moss mats of BSWs enhance their potential for sediment retention. *Sphagnum* mosses form hummocks on bog surfaces, and the strings and flarks of northern ribbed fens provide microtopographic relief (e.g., Zoltai, Tarnocai et al. 1988). The combination of peat barriers and depressions retains water and impedes rapid runoff. Suspended solids in water seeping through fen strings are likely to settle out within the organic matrix.

Flows across the surfaces of ombrotrophic BSWs (e.g., infiltration of snowmelt and precipitation) primarily are downward and should carry sediment particles into the moss mat. Flows across the surfaces of minerotrophic BSWs primarily are upward or horizontal, but downward head gradients may exist at times (Glaser 1987:20). Although sediment retention may be inhibited in the immediate area of upward groundwater flows, horizontal and downward flows could carry particulates into the substrate. Once within the organic matrix of a peat-forming wetland, particulate material should not be exposed to sufficiently high water velocities to become remobilized.

Suspended Solids in Wetland Runoff

One measure of a wetland's ability to retain sediment is the concentration of total suspended solids (TSS) in runoff from the wetland. Low levels of TSS imply wetland sediment retention. Measurements of suspended solids yields from undisturbed and disturbed mires provide evidence for the sediment-retention function of BSWs.

Northern peatlands receiving wastewater reduce TSS concentrations (Kadlec 1987). Although ombrotrophic BSWs should effectively remove suspended solids from anthropogenic waste streams, conversion to minerotrophic wetlands likely would result (D. K. Swanson, Nat. Resour. Conserv. Serv., pers. commun.). Undisturbed ombrotrophic wetlands rarely should receive natural sediment loadings in excess of atmospheric deposition.

Minerotrophic, organic-substrate wetlands remove suspended solids from influent anthropogenic waste streams and storm water: TSS concentration declined 76% downstream of a discharge into a *Typha-Scirpus* marsh (Kent 1987), and another cattail marsh retained 94 to 98% of influent sediment loads (Gehrels and Mulamoottil 1990). Similarly, a spruce-tamarack fen in Minnesota retained 34%, and an associated marsh 44%, of influent TSS (Brown and Stark 1989).

In interior Alaska, TSS concentrations measured over several years in an undisturbed drainage containing a high proportion of permafrost BSWs averaged 0.23 $mg \cdot L^{-1}$ and were <8 $mg \cdot L^{-1}$ even during high flows, comparable to a paired forested watershed containing little permafrost (Hilgert and Slaughter 1983, 1987). Nevertheless, TSS concentrations in permafrost watersheds can briefly rise to much higher levels during snowmelt runoff (e.g., 1,337 $mg \cdot L^{-1}$ declining to <200 $mg \cdot L^{-1}$) than are typical for the remainder of the year (Chacho 1990).

Runoff from relatively undisturbed, non-permafrost peatlands shows mean TSS concentrations on the same order as that from BSWs; disturbed, nonpermafrost mires show slightly greater TSS concentrations (Table 15). Levels of suspended solids measured in runoff from undisturbed, and to some extent disturbed, mires are comparable to those found in typical undisturbed, nonglacial streams in Alaska (cf. U.S. Geol. Surv. 1978:279-351).

Functional Summary

Black spruce wetlands appear to perform the sediment-retention function. Few quantitative comparisons of TSS concentrations in runoff from BSWs with runoff from other wetlands and uplands are available, but the physical structure of peatlands argues for sediment retention. Black spruce wetland surfaces often show microtopographic variation, are composed of permeable peat, and have slow water velocities. Minerotrophic BSWs, often characterized by surface flows and inputs of runoff from upland areas, have a greater opportunity to remove suspended solids from the water column than do ombrotrophic wetlands, which primarily receive inputs from precipitation and have little or no surface flow.

Indicators of the sediment-retention function include features that slow water movement such as

Table 15. Typical concentrations of total suspended solids (TSS) in runoff from nonpermafrost peatlands.

Mire Type	Mire Location	TSS ($mg \cdot L^{-1}$)	Notes	Source
Bog	Minnesota	5.1	Average runoff value	Clausen and Brooks (1983*b*)
Poor Fen	Minnesota	5.3	Average runoff value	Clausen and Brooks (1983*b*)
Fen	Minnesota	5.4	Average runoff value	Clausen and Brooks (1983*b*)
Bog	Minnesota	13.7	Average runoff value - peat mining present	Clausen and Brooks (1983*a*)
Connors[1] "Bog"	Anchorage, Alaska	5.6 to 22.5	Surface water samples - surface disturbance present	Fugro Northwest, Inc. (1980)
Klatt "Bog"[1]	Anchorage, Alaska	5.8 to 53.0	Surface water samples - surface disturbance present	Fugro Northwest, Inc. (1980)

1. Mire includes fen areas.

permeable moss surfaces, *Sphagnum* hummocks, pools, strings, and flarks. Sites with significant inputs of suspended solids may show visible sediment deposits as well.

Functional Sensitivity to Impacts

The sediment-retention function of BSWs is sensitive to placement of fill. Snowmelt and precipitation carry suspended solids off fill surfaces, erode fill slopes, and deposit sediment in remaining wetlands or drainageways. Increased inputs of suspended solids combined with reduced wetland areas for sediment retention increase unit-area sediment loadings, which may reduce sediment-retention capacities. Fill reduces cross-sectional areas of flow paths within minerotrophic wetlands having surface flow, which may increase water velocity and also reduce sediment-retention capacity. Likewise, fill in ombrotrophic wetlands with little or no surface flow may force shallow groundwater to the surface rendering sediment retention less effective.

Paving or armoring fill surfaces or re-establishing dense vegetative cover with an organic surface layer, minimizing fill area, and reducing influent TSS concentrations (e.g., establishing up-gradient vegetative buffers) could partially mitigate the impacts of fill on sediment retention by remaining BSWs. Although paving or armoring would prevent erosion of the fill, it would not prevent runoff of other anthropogenic solids (e.g., sand) and would adversely affect several other wetland functions.

The sediment-retention function of BSWs is sensitive to drainage, as shown by higher levels of TSS in runoff from mined bogs, which usually are drained, than in runoff from undisturbed bogs (e.g., Clausen and Brooks 1983*a*). In permafrost wetlands, ditching in thaw-unstable materials such as ice-rich ***muck***, a mixture of well-decomposed organic material and mineral soil (Gabriel and Talbot 1984:73), could produce severe erosion. Drainage also may increase surface and subsurface flow velocities, and hence decrease sediment retention, in response to increased hydraulic gradients in the vicinity of drainage ditches. These effects should be more apparent for minerotrophic sites with surface flows than for ombrotrophic sites.

The adverse effects of drainage on sediment retention can be self-limiting as water tables fall because hydraulic conductivities (and thus groundwater flow velocities) decrease with depth (Boelter and Verry 1977, Verry and Boelter 1979), and drained minerotrophic areas can become ombrotrophic (e.g., Glaser et al. 1981). Avoiding ditch excavation in permafrost BSWs and limiting ditch depths in unfrozen wetlands to avoid mineral soils would reduce erosion potential. Settling ponds incorporated in wetland drainage systems might partially mitigate lost sediment-retention capacity.

NUTRIENT UPTAKE

Wetland plants remove sufficient nutrients from influent water to meet growth requirements, and some vascular plants concentrate excess nutrients in tissue by luxury consumption, although leaching and decomposition subsequently release many of the stored nutrients (Kadlec and Kadlec 1979). Nevertheless, accumulated detritus retains some nutrients (Adamus and Stockwell 1983:23). Peatlands in general accumulate N and P in organic substrates (Whigham and Bayley 1979). In BSWs, nutrient demands and cycling by trees, shrubs, and herbaceous vegetation are supplemented by those of a thick moss layer.

Moss Layer

Mosses dominate the ground cover of ombrotrophic BSWs: feathermosses in drier stands and *Sphagnum* mosses in wetter sites (Foote 1983:46-48,69-79). In bogs, nutrients reach the moss layer via atmospheric deposition (Malmer 1988) and litterfall from tree, shrub, and herbaceous vegetation; thus, mosses are "filters" that intercept nutrient inputs to the forest floor by virtue of their position above the root zone of vascular plants (Oechel and Van Cleve 1986). Nutrient demand by mosses can exceed that supplied by throughfall and litterfall for several elements (Figure 5). Mosses effectively compete with black spruce on permafrost-dominated sites, with element uptakes sometimes exceeding those of aboveground components of black spruce (Oechel and Van Cleve 1986).

Mosses are nutrient sinks because they rapidly take up nutrients (e.g., N and P) and retain them until moss tissues decompose (Weber and Van Cleve 1984, Oechel and Van Cleve 1986, Malmer 1988, Urban and Eisenreich 1988). Feathermosses retained >90% of recoverable ^{15}N 28 months following application to a black spruce site (Weber and Van Cleve

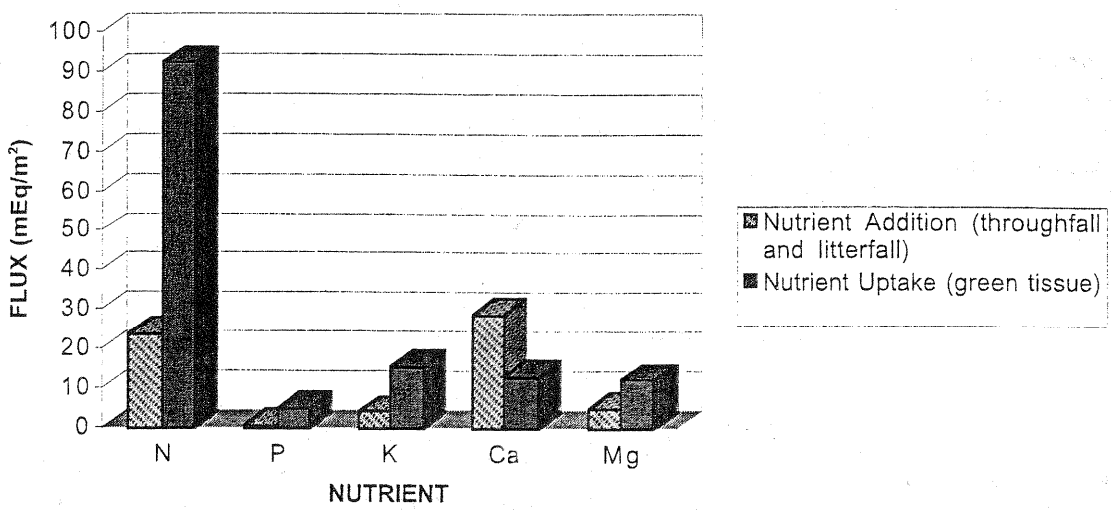

Figure 5. Nutrient uptake by green moss tissue in a permafrost black spruce stand, interior Alaska, as compared to nutrient addition by precipitation throughfall and litterfall (Oechel and Van Cleve 1986).

1981), with minimal export by leaching, reducing its availability to vascular plants rooted in deeper organic matter (Weber and Van Cleve 1984). Mosses decompose "about 10% as fast as vascular plant tissue" (Oechel and Van Cleve 1986:122).

Moss production (e.g., ~120 $g \cdot m^{-2} \cdot yr^{-1}$) can exceed that of aboveground production of trees (e.g., 102 $g \cdot m^{-2} \cdot yr^{-1}$) in BSWs (Oechel and Van Cleve 1986). The productivity of moss on a variety of black spruce sites averaged 100 $g \cdot m^{-2} \cdot yr^{-1}$ as compared to 33 $g \cdot m^{-2} \cdot yr^{-1}$ for tree foliage (Van Cleve, Dyrness et al. 1983). Slow decomposition of moss in black spruce stands, combined with significant annual production, produced accumulations of organic matter averaging 7.6 $kg \cdot m^{-2}$ for several interior Alaska sites, with ~50 yr turnover times for organic matter in forest floors (Van Cleve, Oliver et al. 1983).

"Photosynthesis and productivity of forest floor mosses in the taiga" are severely nutrient limited (Oechel and Van Cleve 1986:133) as shown by the responses of mosses to nutrient addition. Two sources of added nutrients have been studied in peat-forming wetlands: fertilizers applied for experimental or silvicultural purposes and sewage effluent applied for wastewater treatment. Fertilizer increased both growth and photosynthesis of *Sphagnum nemoreum*, increased photosynthesis in new shoots of *Hylocomium splendens* but caused salt damage to overwintered shoots, and decreased growth in *H. splendens* and *Pleurozium schreberi* (Skre and Oechel 1979). Similarly, Bartsch (1991 *in* Bartsch and Schwintzer 1994) noted increased production in fertilized *Sphagnum* mosses.

Small quantities of sewage effluent and inorganic fertilizer caused *Sphagnum* shoots near fertilizer pellets to become intensely green, probably indicating increased production, with retention of added nutrients in the uppermost portion of *Sphagnum* cores (Sanville 1988). Concentrations of total P (TP) were high in the upper 2 cm of cores from plots treated with P, alone or in combination with N and/or sewage (Sanville 1988). The positive responses of *Sphagnum* mosses to nutrient addition imply significant potential for nutrient uptake in ombrotrophic BSWs. Although wetlands containing *Sphagnum* can

remove nutrients from wastewater (Verry and Timmons 1982), species composition is likely to change, as occurred in a fen receiving sewage effluent in Minnesota (Brown and Stark 1989).

Tree, Shrub, and Herb Layers

Low soil temperature and high soil moisture reduce element cycling (and thus nutrient availability to vascular plants) in permafrost black spruce stands (Van Cleve et al. 1991). These stands have the lowest tree productivities and nutrient fluxes among Alaska's treed taiga sites (Van Cleve, Dyrness et al. 1983; Viereck et al. 1983). Conditions of low nutrient availability in BSWs suggest that their trees, shrubs, and herbs should efficiently acquire and retain nutrients. Conversely, adaptation of these plants to a low-nutrient environment suggests potentially limited capacities for uptake of nutrients, as shown by Van Cleve, Oliver et al. (1983) for black spruce (Figure 6).

Vascular plants primarily acquire nutrients through their roots, presumably enhanced by mycorrhizal associations with fungi, which are common in taiga species (Flanagan 1986) such as black spruce (Tyrrell and Boerner 1987, Summerbell 1989) and mountain-cranberry (*Vaccinium vitis-idaea*) (Dickinson 1983). Black spruce roots elongated at greater rates than other taiga tree species on cold, wet sites, probably favored by high soil moisture (Tryon and Chapin 1983). Fine roots, responsible for absorbing nutrients, made up 72% of root biomass on a permafrost black spruce site (Tryon and Chapin 1983). Black spruce produces biomass more efficiently (i.e., ratio of annual biomass production to element requirement) than do taiga hardwoods and partially offsets low nutrient uptake by retaining nutrients, adding an annual increment of 113 $g \cdot m^{-2}$ of aboveground biomass while losing only 43 $g \cdot m^{-2}$ to litterfall in one study (Van Cleve, Oliver et al. 1983).

Shrubs within ombrotrophic and weakly minerotrophic BSWs also are adapted to low nutrient availability: shallow rooting depths allow early uptake of nutrients by shrubs in the spring (Chapin 1983*a*, Tryon and Chapin 1983), evergreen ericaceous plants (e.g., Labrador-tea) conserve scarce nutrients within plant tissues (Larsen 1982:148),

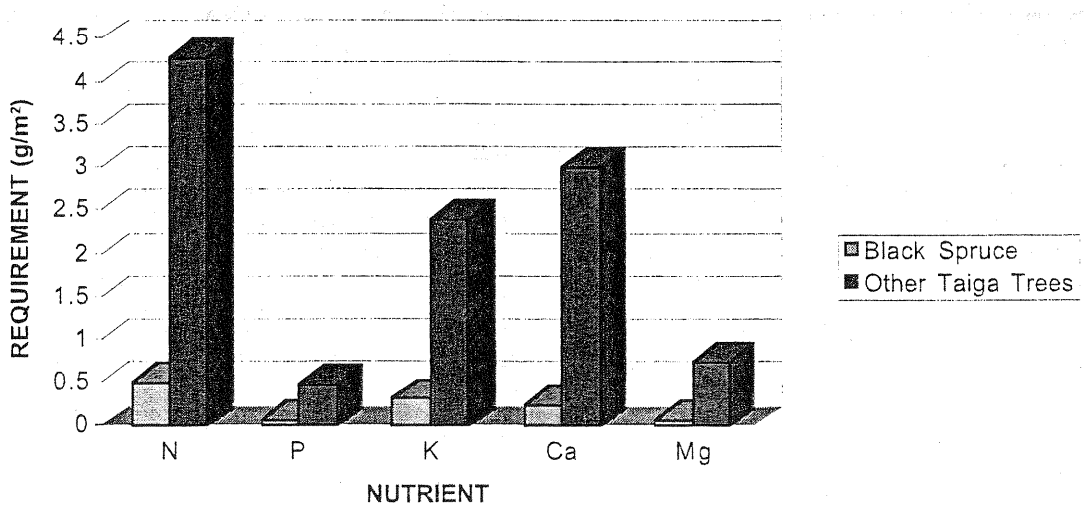

Figure 6. Comparative nutrient requirements for black spruce and other taiga trees as a group (white spruce, quaking aspen, paper birch, and balsam poplar) (Van Cleve, Oliver et al. 1983).

evergreen shrubs exhibit earlier fine root growth in the spring than do deciduous shrubs (Kummerow et al. 1983), and shrubs adapted to low-nutrient environments have slow growth rates (Bryant et al. 1983). Evergreen and deciduous plants adapted to bog environments both produce photosynthate more efficiently with respect to N than do nonbog plants (Larsen 1982:149).

Shrubs play a larger role in nutrient uptake and cycling in BSWs than suggested by their small biomass (Chapin 1983*a*). Chapin (1983*a*) reported that Labrador-tea and bog blueberry accounted for only 0.8% of aboveground vascular plant biomass but 2.8% and 2.4% of the standing crop of N and P at a permafrost forest site. Shrubs as a group accounted for 24% and 19% of annual uptake of N and P by aboveground portions of vascular plants (including trees) and 16% of their annual biomass increment. Annual biomass turnover for shrubs at this site was 34 to 43%. Rapid biomass turnover in wetland shrubs suggests that uptake would remove anthropogenic nutrients from the soil solution, deposit them in plant structures, and return them to the forest floor as litterfall over the course of several years. A portion of the litterfall nutrients from shrubs potentially would be bound in forest floor organic matter with turnover times of 100 to 1000 yr, as Flanagan and Van Cleve (1983) postulated for the mineral nutrient cycle of deciduous trees.

Responses of vascular plants to experimental and silvicultural fertilization and application of sewage effluent demonstrate potential nutrient uptake in BSWs. Fertilized (N, P, and K) leatherleaf produced a significant growth response in a bog (Bartsch 1994) but not in a poor fen, indicating nutrient deficiency in the bog environment (Bartsch and Schwintzer 1994). With respect to ericaceous plants, Reader (1980) cites research showing that 50 kg $N \cdot ha^{-1}$ should compensate for naturally occurring deficiencies in bog soils. At least some of the plants and soil characteristics of tundra are shared by taiga wetlands (Kummerow et al. 1983), implying that taiga plants should show similar responses to N-fertilized tundra cores, which approximately doubled leaf area and total aboveground biomass (Billings et al. 1984).

Fertilizer trials with seeded annual ryegrass (*Lolium temulentum*) in a disturbed, wet graminoid-low shrub meadow (at least partially minerotrophic) with mucky peat soils revealed N, P, and K deficiencies (Helm et al. 1987). Aboveground biomass of vascular plants in Alaska mire plots fertilized with N+P and sewage effluent+N+P increased compared to controls, and some graminoids showed a significant response to P alone, suggesting both N and P deficiencies in the mire (Sanville 1988). Actual wastewater discharges impose high nutrient loads on wetlands (Kadlec 1979), often increasing vascular plant biomass (Figure 7). Ombrotrophic wetlands receiving large quantities of effluent likely would soon become sparsely-treed fens or treeless marshes.

Nitrogen deficiency limits tree growth in boreal forests (Weetman 1982), and forest floors on cold, wet sites (e.g., BSWs) have particularly low concentrations of available N (Flanagan and Van Cleve 1983). Taiga conifers respond to N fertilization with increased growth, although the response is less in black spruce than in other tested species (Weetman 1982). Diameter increments of black spruce treated with 112 or 224 kg $N \cdot ha^{-1}$ on a gleyed-soil site receiving groundwater seepage increased significantly over controls (Foster et al. 1986). Black spruce seedlings grown under controlled conditions show no significant growth response to phosphate fertilization, however (Chapin et al. 1983).

Minerotrophic BSWs may not be nutrient deficient with respect to plant growth requirements, but their characteristic plants (e.g., sedges) can respond to additional nutrients by virtue of adaptations to high-nutrient environments. Upland taiga tree species have much higher maximum growth rates than mire conifers, yet show marked responses to nutrient addition (Chapin 1986). Tamarack, characteristic of fens, has a greater maximum growth rate than black spruce, characteristic of bogs (Chapin 1986).

A speculative route of nutrient uptake by BSWs is assimilation of atmospheric ammonia. Langford and Fehsenfeld (1992) presented evidence that the canopy of a montane-subalpine forest of lodgepole pine, ponderosa pine (*Pinus ponderosa*), spruce, fir, and aspen in Colorado acted as a sink for anthropogenic ammonia. Conversely, the forest acted as a source of ammonia at low ambient ammonia concentrations. Taiga forests, and by extension black spruce mires, may or may not respond to atmospheric ammonia in the same way as the montane-subalpine forest.

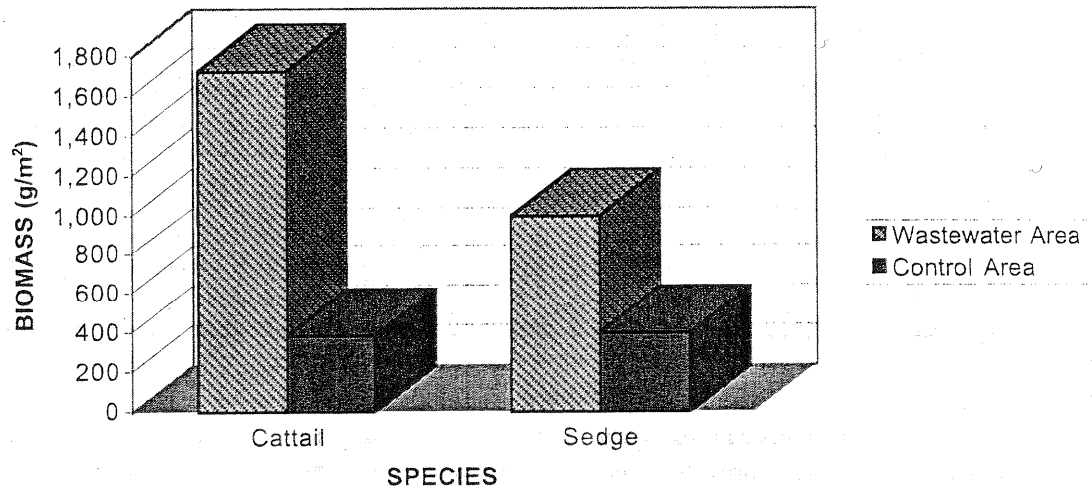

Figure 7. Cattail and sedge biomasses at wastewater discharge and control sites, Hay River, N.W.T. (Kadlec 1987).

Functional Summary

Black spruce wetlands perform the nutrient-uptake function. Ombrotrophic and weakly minerotrophic wetlands are nutrient-poor environments, and many of their characteristic plants, including black spruce, can assimilate anthropogenic nutrients as shown by increased net primary production following nutrient addition. *Sphagnum* mosses - positioned to intercept nutrients in precipitation, throughfall, and litterfall - effectively compete with vascular plants for nutrients. Shrubs rapidly turn over biomass, removing nutrients from the soil solution and shunting them to accumulating organic material. Plants characteristic of minerotrophic BSWs also respond to nutrient addition.

Nutrient uptake is not confined to BSWs; upland taiga communities share the ability to remove nutrients from anthropogenic sources (e.g., wastewater discharge, nonpoint-source pollution). Ombrotrophic sites receive only atmospheric inputs of nutrients and thus have a limited opportunity for nutrient removal, although nutrient-poor runoff from bogs could serve to dilute anthropogenic nutrients in receiving waters. Minerotrophic BSWs that receive surface water, in contrast, have ample opportunity for uptake of waterborne anthropogenic nutrients. Because all plant communities take up nutrients from their environments, no specific indicators of the nutrient-uptake function need be applied to vegetated wetlands.

Functional Sensitivity to Impacts

The nutrient-uptake function of BSWs is sensitive to fill, which, unless vegetated, has little capacity for nutrient uptake. Runoff from fill surfaces would carry nutrients deposited on, or contained within, those surfaces into adjacent wetlands and increase their nutrient loadings. Revegetating fill surfaces to achieve dense vegetative cover could ameliorate excessive nutrient loading from fill runoff in the absence of high anthropogenic nutrient inputs (e.g., fertilization), but such surfaces could not remove waterborne nutrients within the wetland.

Draining BSWs reduces, but does not eliminate, uptake of waterborne nutrients by wetland plants. Ditching channelizes flow so that waterborne nutrients have less contact with plant root zones and have shorter residence times within wetlands. Rates of

decomposition, and hence nutrient release from organic matter, are likely to increase as wetland soils are drained and become increasingly aerobic. Nutrient release from drained soils could diminish the capacity of wetland plants for uptake of anthropogenic nutrients by increasing total nutrient availability. To the extent that natural wetland surfaces and vegetation are maintained following drainage, the functional capability to take up nutrients remains present, although opportunities for nutrient uptake are reduced in the absence of surface and near-surface flows.

NUTRIENT TRANSFORMATION

Chemical reactions and biotic metabolic activity transform nutrients entering wetlands (Mitsch and Gosselink 1993:120-142). Nutrients can reside for various times in different chemical forms (e.g., organic and inorganic), tending to smooth influent nutrient pulses, and can leave wetlands in other forms. Some forms of nutrient elements may enter sinks and effectively be removed from short-term cycles. Chemical transformations of nutrients occur as oxidation-reduction or ***redox potentials*** (potentiometric measures of the oxidizing or reducing intensity of a solution [Wetzel 1983:298]) vary with concentrations of oxygen (Mitsch and Gosselink 1993:123-126) and, to a lesser extent, humic acids (Wetzel 1983:301). Microbial oxidative-respiratory reactions transform organic and inorganic compounds under aerobic and anaerobic conditions (Mitsch and Gosselink 1993:166).

Nitrogen

Nitrogen is a major anthropogenic nutrient transformed by wetlands. The primary N transformations are fixation, conversion of gaseous N (N_2) to organic N (or to ammonium [Wetzel 1983:235, Alexander and Billington 1986]); mineralization, conversion of organic N to ammonium N (NH_4-N); nitrification, conversion of NH_4-N to nitrite N (NO_2-N) and then to nitrate N (NO_3-N); and denitrification, conversion of NO_3-N to N_2 (Mitsch and Gosselink 1993:128-130). The extent to which each of these processes occurs determines the primary forms taken by N in BSWs and whether such wetlands act as sources or sinks for various forms of N.

Fixation: Microbes, which may be aerobic or anaerobic, heterotrophic or autotrophic, symbiotic or free living, and may belong to several taxonomic groups including the cyanobacteria (blue-green algae) and actinomycetes, use the enzyme nitrogenase to fix N (Waughman and Bellamy 1980, Dickinson 1983). Symbiotic bacteria associated with lichens, mosses, and vascular plants, as well as asymbiotic bacteria, fix N in mires and BSWs (Granhall and Selander 1973, Granhall and Hofsten 1976, Waughman and Bellamy 1980, Billington 1981, Dickinson 1983, Florence and Cook 1984).

Rates of N fixation by heterotrophic bacteria increase from ombrotrophic to minerotrophic site conditions but decline somewhat for extremely rich fens (Waughman and Bellamy 1980). Waughman and Bellamy (1980) found low levels of heterotrophic nitrogenase activity in several bogs with pH < 4, and heterotrophic bacteria accounted for most N fixation in a black spruce bog in Minnesota (Urban and Eisenreich 1988). Asymbiotic N-fixing bacteria, including *Azospirillum* spp. and *Azotobacter* spp., associated with black spruce and tamarack, respectively, in wet lowland stands in Alberta (Florence and Cook 1984). Actinomycetes symbiotic with alder and sweetgale roots fix N in fens (Moore and Bellamy 1974:79, Dickinson 1983).

Autotrophic microbes also fix N. Granhall and Selander (1973) found that moss-associated cyanobacteria (blue-green algae) fixed most N in wetter areas of a permafrost bog, but heterotrophic N-fixing bacteria were active in peat hummocks. Mosses with epiphytic cyanobacteria showed higher fixation than those containing intracellular cyanobacteria or those associated with free-living cyanobacteria. Despite lower rates of N fixation, intracellular cyanobacteria persist at lower pH concentrations than extracellular forms. Cyanobacteria occur in hyaline cells of *Sphagnum riparium* and *S. lindbergii* at extracellular pH concentrations as low as 4.2, but the symbionts are absent at pH 3.8, characteristic of some other *Sphagnum* communities (Granhall and Hofsten 1976).

Cyanobacteria associated with lichens (e.g., *Nephroma* spp. and *Peltigera* spp.) and mosses fix most N in high-latitude wetlands (Alexander and Billington 1986). Lichens containing symbiotic cyanobacteria show high levels of N fixation (Granhall and Selander 1973), exceeding those of lichens without phycobionts by 1 to 2 orders of magnitude in an Alaska study (Alexander and Billington

1986). Lichens containing symbiotic cyanobacteria fix N at higher rates than complexes of mosses and cyanobacteria, but mosses can account for the majority of N fixation by virtue of their abundance at Alaska black spruce sites (Billington 1981:55). Between-site and interannual variation in N fixation apparently is small in black spruce ecosystems, with nitrogen fixation (based on acetylene reduction) ranging from 0.9 to 1.4 kg $N \cdot ha^{-1} \cdot yr^{-1}$ for two permafrost and nonpermafrost black spruce sites (Billington and Alexander 1983). These values are similar to those found for wetlands in other subarctic and arctic locations (Alexander and Billington 1986).

Mineralization: Nitrogen resides in forest floors of taiga black spruce for an average of 61 yr as compared to 18 yr for temperate coniferous forests (Van Cleve, Oliver et al. 1983). Mineralization (ammonification [Mitsch and Gosselink 1993:129]) removes N from long-term storage during decomposition of organic matter by transforming organic N to NH_4-N, a rapidly cycling but volatile form easily taken up by living organisms. Bogs apparently cycle N exclusively as NH_4-N (Urban and Eisenreich 1988), the dominant form of inorganic N in black spruce stands of interior Alaska (Weber and Van Cleve 1984).

Substrate quality, including C/N ratios, energy limitations imposed by lack of easily-degradable C compounds, and nutrient content of litter, as well as temperature and moisture, affect organic matter decomposition (Moore 1981; Flanagan and Van Cleve 1983; Fox and Van Cleve 1983; Van Cleve, Oliver et al. 1983; Flanagan 1986; Van Cleve and Yarie 1986). Birch, poplar, and aspen stands have higher temperature sums above 0°C, lower soil moistures, lower C/N ratios, and higher rates of N mineralization than do black spruce stands (Van Cleve and Yarie 1986). Low rates of mineralization coupled with accumulating organic matter would be consistent with a wetland acting as a sink for N.

Nitrogen concentrations in Alaska peat soils are highest some distance below the surface; therefore, low temperatures in the zone of maximal N concentration minimize rates of mineralization (Heilman 1966). Mineralization and immobilization of N in forest floors of black spruce stands occur mainly in moss layers subject to environmental variation rather than in colder underlying organic matter, and these events are more frequent on warmer, nonpermafrost sites with lower C/N ratios (i.e., more favorable for decomposition) than on permafrost sites (Weber 1982). Heating an experimental black spruce site in interior Alaska increased decomposition and released N, P, and K (Van Cleve, Oliver et al. 1983).

Precipitation promotes mineralization by wetting moss layers (Weber and Van Cleve 1984), but drainage increases peat decomposition (Glaser 1987:67) and thus mineralization of N. The effects of fertilization on mineralization are not clear. Mire drainage and fertilization with P and K for silvicultural purposes increased mineralization (Remröd 1980) but mineral fertilizers reduced mineralization on drained peatlands converted to agriculture (Baranovskiy 1991) and suppressed microbial respiration in forest litter (Flanagan 1986).

Mineralization rates in North American wetlands may vary with latitude. Mineralization and plant uptake dominate rapid cycling of N in temperate bogs (Urban and Eisenreich 1988), but taiga black spruce ecosystems, including permafrost BSWs, mineralize only small amounts of N (Van Cleve, Oliver et al. 1983; Van Cleve and Yarie 1986). Alaska BSWs mineralize less N than taiga hardwood stands and much less than a temperate Minnesota bog but about the same amount as the acrotelm of an European blanket peat (Table 16).

Nitrification: Bacteria or fungi transform reduced forms of N to more oxidized forms in the process of nitrification (Wetzel 1983:234-235, Flanagan 1986, Mitsch and Gosselink 1986:97). Nitrate is the end product of these transformations but, as an anion, is not retained by the cation exchange capacity of wetland peat (Moore and Bellamy 1974:122-123, Weber and Van Cleve 1981, Mitsch and Gosselink 1986:97). High rates of nitrification tend to make a wetland a source, rather than a sink, for NO_3-N.

Nitrifying bacteria occur in poor fens (Dickinson 1983), but nitrification is absent under anaerobic conditions (Wetzel 1983:236) and much reduced or absent in ombrotrophic peatlands (Moore and Bellamy 1974:98-99, Dickinson 1983, Mitsch and Gosselink 1986:98, Urban and Eisenreich 1988). Tannins and other dissolved organic compounds inhibit nitrifying bacteria (Rice and Pancholy 1972, 1973 *in* Wetzel 1983:236), which may account for their low numbers in bogs. Flux between NH_4-N and NO_3-N in a blanket bog (0.03 kg $N \cdot ha^{-1} \cdot yr^{-1}$) was inconsequential as compared to NO_3-N input via rain-

Table 16. Comparative N mineralization in several European and North American mires and forest stands.

Site Type and Location	N Mineralization (kg $N \cdot ha^{-1} \cdot yr^{-1}$)	Source
Bog - Minnesota	43 to 59	Urban and Eisenreich (1988)
Black spruce - Quebec	11	Weetman and Webber (1972 *in* Bonan 1990a)
Black spruce - Alaska	7.9 to 18	Van Cleve et al. (1981), Flanagan and Van Cleve (1983)
Blanket peat - Europe	9	Dickinson (1983)
Birch, poplar, aspen - Alaska	24 to 58	Flanagan and Van Cleve (1983)

fall (1 kg $N \cdot ha^{-1} \cdot yr^{-1}$) (Dickinson 1983).

Nitrification rates in North American mires are not well documented, but studies of taiga forest ecosystems are pertinent. Incubated organic matter from a mature black spruce-lichen woodland yielded nearly equal concentrations of NH_4-N and NO_3-N (Figure 8), but Moore (1981) characterized nitrification as low in the subarctic soils tested. In contrast, concentrations of NO_2-N and NO_3-N in an Alaska permafrost BSW generally were <0.1 mg $N \cdot kg^{-1}$ soil (Sparrow and Sparrow 1988).

Pools of NH_4-N consistently are larger than pools of NO_3-N in Alaska black spruce stands (Table 17). Ratios of NH_4-N pools to NO_3-N pools, calculated for individual samples from Weber and Van Cleve (1984), range from approximately 3.8 to 22.8 for permafrost sites and from 1.4 to 18.3 for nonpermafrost sites, consistent with the ratio (>10) reported for permafrost black spruce by Van Cleve and Dyrness (1983*b*). Small pools of NO_3-N do not necessarily indicate comparably low rates of nitrification if plants rapidly assimilate NO_3-N, but $^{15}NO_3$-N transformations appear slow in black spruce forests (Weber 1982:66-67,89). Glucose increased NO_3-N concentrations in black spruce stands, perhaps by fungal nitrification (Flanagan 1986). This finding may indicate a greater capacity for nitrification than normally is expressed under ambient conditions in BSWs.

Alaska's BSWs frequently develop in later stages of post-fire secondary succession as permafrost aggradation or paludification saturates near-surface soils. Low nitrification rates might be expected in these wetlands because nitrification declines during later stages of secondary succession in some seres (Vitousek et al. 1989). Based on their acidic, anaerobic conditions, as well as typical successional status, ombrotrophic BSWs probably show little nitrification. Although comparative data are lacking, surface layers (aerobic) of minerotrophic BSWs might be expected to show greater nitrification than those of ombrotrophic wetlands.

Denitrification: Denitrification by bacterial reduction of NO_2-N and NO_3-N to N_2 can occur under aerobic conditions but occurs most intensely under anaerobic conditions, although acidic water and low temperatures depress rates of denitrification (Wetzel 1983: 237-238). Bacterial denitrifiers occur in mires, including those dominated by *Sphagnum*, and are more common than nitrifying bacteria (Dickinson 1983) but are sparse at pH < 5.5 (Larsen 1982:156). A European blanket bog denitrified 1 kg $N \cdot ha^{-1} \cdot yr^{-1}$, a rate that balanced input of NO_3-N by rainfall (Dickinson 1983). Most literature suggests that significant denitrification does not occur in ombrotrophic mires because nitrification is largely absent (Urban and Eisenreich 1988).

Soil profiles of BSWs are largely anaerobic, which would favor denitrification, but are often acidic, which would depress denitrification. Counts of denitrifying bacteria in the organic horizons of control plots in a BSW were <100 $cells \cdot g^{-1}$ soil whereas counts from experimentally-oiled plots approached 10 million $cells \cdot g^{-1}$ soil, suggesting that oil-killed vegetation released substrates that enhanced microbial activity (Sparrow et al. 1978). This observation indicates a latent capacity of BSWs, particularly minerotrophic wetlands, to transform anthropogenic inputs, possibly including NO_3-N. Significant denitrification would make a wetland a sink for N as gaseous output of N_2 removed N from internal cycling (Larsen 1982:156) and potentially

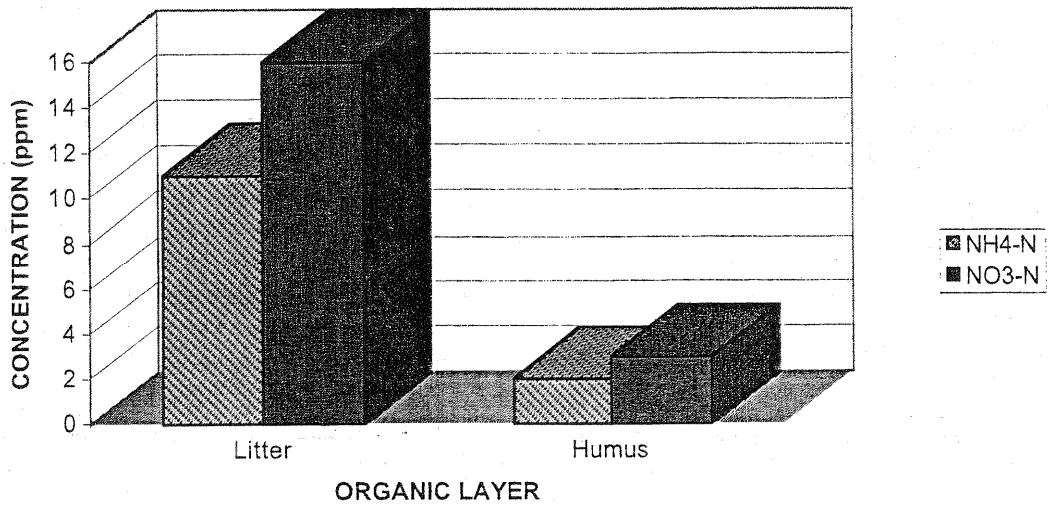

Figure 8. Concentrations of NH_4-N and NO_3-N in incubated organic material from a mature black spruce-lichen woodland, Quebec (Moore 1981).

Table 17. Pools of NH_4-N and NO_3-N in wetland and nonwetland Alaska forest stands.

Site Type	NH_4-N (kg N·ha^{-1})	NO_3-N (kg N·ha^{-1})	Comment	Source
Permafrost black spruce	0.3 to 0.4	NA[1]	Organic horizon - range over summer	Sparrow and Sparrow (1988)
Permafrost black spruce	3.24	0.15[2]	Forest floor estimates	Van Cleve and Dyrness (1983b)
Permafrost black spruce	3.02 to 20.63	0.34 to 2.04	Fermentation and humus layers - range for various sampling dates	Weber and Van Cleve (1984)
Nonpermafrost black spruce	0.60 to 32.13	0.34 to 2.60	Fermentation and humus layers - range for various sampling dates	Weber and Van Cleve (1984)
White spruce floodplain	1.8	trace	Forest floor	Walker (1989)

1. NA = not available.
2. Units given as mass·volume^{-1} in cited report, but text context (i.e., direct comparison of forest floor pool sizes for NH_4-N and NO_3-N) implies mass·area^{-1} intended for both estimates.

decreased waterborne output of NO_3-N.

Phosphorus

Chemists treat P as dissolved or suspended (particulate) and subdivide each form into reactive, acid-hydrolyzable, and organic fractions for analytical purposes (Am. Public Health Assoc. et al. 1992:4-108 to 4-109). Inorganic P occurs as orthophosphates, which include PO_4^{-3}, HPO_4^{-2}, and $H_2PO_4^{-1}$, depending on pH (Mitsch and Gosselink 1993:140); and acid-hydrolyzable or condensed phosphates, including polyphosphates such as detergents and suspended mineral particles such as Fe^{+3} and Ca^{+2} phosphates (Wetzel 1983:255-256, Am. Public Health Assoc. et al. 1992:4-108). Most waterborne P in freshwater systems is in suspended organic form, mainly derived from biological processes, but smaller dissolved pools of a low molecular weight organic P compound and colloidal P are present and exchange with other pools of P (Wetzel 1983: 255,257,270). Actual forms of P in wetland ecosystems may not correspond to analytical fractions used in limnologic or water quality studies, however (Wetzel 1983:256).

Phosphorus commonly limits biological production and, in excess, can cause waterbodies to become eutrophic (Wetzel 1983:255,284-291; Lowe et al. 1992) because cyanobacteria can fix the additional N necessary to support biomass production (J. LaPerriere, Univ. Alaska, pers. commun.). Biological assimilation occurs primarily as dissolved inorganic P (Mitsch and Gosselink 1993:140), which is incorporated in organic compounds: nucleic acids, commonly the largest fraction in vascular plants; phospholipids, also common in plant tissue; proteins; esters; and nucleotide phosphates (Chapin and Kedrowski 1983, Wetzel 1983:255-258, Mitsch and Gosselink 1993:139). Once biologically transformed to organic form, P becomes less available and may be stored for significant periods in living and dead plant tissues, ameliorating the effects of anthropogenic P on waterbodies.

Wetlands often transform, and may be sinks for, various inorganic and organic fractions of P (van der Valk et al. 1979). Mitsch and Gosselink (1993:141) and Wetzel (1983:255-258) describe three general mechanisms whereby PO_4-P is removed from solution: precipitation, adsorption, and uptake by living organisms. Leaching and mineralization return organic P to solution.

Precipitation: Phosphorus precipitates when PO_4 forms insoluble complexes with metallic ions such as Fe^{+3}, aluminum [Al^{+3}], and Ca^{+2} under oxidizing conditions (Stumm and Morgan 1970 *in* van der Valk et al. 1979, Wetzel 1983:255-258, Mitsch and Gosselink 1993:141). Anaerobic conditions at the sediment-water interface in lakes are known to release Fe^{+2} and PO_4^{-3} to the water column whereas oxygenation of this zone precipitates $FePO_4$ (Wetzel 1983:261-263). Tundra ponds in northern Alaska show little precipitation of P minerals, however (Prentki et al. 1980). Anaerobic (reducing) conditions in BSWs potentially would act against precipitated P remaining insoluble in saturated horizons. In addition, salts such as $AlPO_4$ become more soluble at pH < 6 (Wetzel 1983:258), a condition present in ombrotrophic and weakly minerotrophic peat-forming wetlands.

Adsorption: Mechanisms of PO_4-P adsorption in BSWs are not well-documented. Phosphate adsorbs (binds) to mineral surfaces and organic material, a process sometimes supplemented by chelation and formation of chemical complexes (Wetzel 1983:255-258, Mitsch and Gosselink 1993:141-142). Phosphate adsorbs to peat, even in mires receiving large anthropogenic nutrient inputs (Whigham and Bayley 1979, Kadlec 1987, Brown and Stark 1989, Mitsch and Gosselink 1993:141). A calcareous fen peat sorbed an order of magnitude more P than an acid *Sphagnum* peat (Isirimah and Keeney 1983*b* *in* Sikora and Keeney 1983).

Complexes of ferric hydroxides adsorb P in lakes (Wetzel 1983:255,261), although humic and fulvic acids may hold Fe and PO_4 in solution in peatland lakes (Engstrom 1984). Sediment P contents of Fe-rich peats in tundra ponds strongly correlated with their Fe contents as a result of PO_4 sorption (Prentki et al. 1980), and Fe concentrations that reached 30 mg $Fe \cdot g^{-1}$ in mineral soil horizons of a Quebec spruce-lichen woodland apparently bound P (Moore 1980). Representative Fe concentrations in the uppermost 1 m of Canadian mire peats ranged from 0.5 to 29.7 mg $Fe \cdot g^{-1}$ (Zoltai, Tarnocai et al. 1988; Zoltai, Taylor et al. 1988), about 1 order of magnitude less than those of Alaska tundra ponds (Prentki et al. 1980) but perhaps sufficient to cause P adsorption. Measured P concentrations in several Canadian mires (Table 18) generally exceeded predicted P

concentrations (e.g., <228 μg P·g^{-1}), based on Fe concentrations (e.g., <3.7 mg Fe·g^{-1}), using the regression equation of Prentki et al. (1980) for tundra ponds. This result is consistent with, but does not necessarily demonstrate, P adsorption to Fe and peat in taiga mires.

Sorption processes for P may become saturated near points of heavy loading, such as occurs from wastewater discharge (Kadlec 1987, Kent 1987) but may occur sooner for PO_4-P than for TP (Jones and Amador 1992). Orthophosphates, approximated by soluble or dissolved reactive P (DRP), are rapidly converted to total suspended P (TSP) in many freshwater systems (Prentki et al. 1980, Wetzel 1983:256, Mitsch and Gosselink 1993:140). Following PO_4-P saturation of subtropical marsh peat, microorganisms that apparently constituted the suspended-P fraction appeared to undergo hydrophobic and ionic interactions with the peat (i.e., adsorption) and thus provided a continuing route of TP removal (Jones and Amador 1992).

Uptake By Organisms: Biotic uptake transforms PO_4-P to organic P in microscopic and macroscopic organisms. A hypertrophic lake receiving 90% of TP in dissolved form yielded ~70% TSP in the water column (Lowe et al. 1992). Likewise, losses of P in runoff from tundra (wetland) soils occur primarily as organic fractions (Gersper et al. 1980). Processes such as settling or adsorption to peat can remove TSP from the water column (Stark and Brown 1988, Jones and Amador 1992) or from the soil solution, and organic suspended material can enter food chains.

Phosphorus deficiency is common in northern regions (Tamm 1968 *in* Miller et al. 1979). Availability of P in a peat-forming wetland of interior Alaska was only one-third that of an adjacent permafrost-free birch forest (Chapin and Kedrowski 1983); a shrubby sedge meadow was deficient in P with respect to growth of seeded annual ryegrass (Helm et al. 1987); and content of PO_4-P was greater in organic layers of permafrost black spruce stand in Alaska than in underlying mineral soil, but the majority of P was not in available form (Grigal 1979). Pool sizes for total P apparently can exceed those for available P by several orders of magnitude in black spruce stands (Table 19).

Table 18. Phosphorus concentrations in several Canadian taiga mires with Fe concentrations <3.7 mg Fe·g^{-1} (Zoltai, Taylor et al. 1988).

Wetland Type	P Concentration (μg P·g^{-1})
Northern Plateau Bog	183 to 620
Boreal Fen	384 to 1736
Flat Bog	278 to 451
Basin Bog	263 to 825

Peatlands appear to accumulate less P in aboveground vegetation than do wetlands with mineral substrates (Whigham and Bayley 1979), but lack of available P creates biotic demand. Green moss tissue annually took up 4.8 mEq P·m^{-2} on a permafrost black spruce site even though throughfall and litterfall only supplied 0.6 mEq P·m^{-2} (Oechel and Van Cleve 1986). Fertilization increased photosynthesis in the mosses *Sphagnum nemoreum* and *Hylocomium splendens*, and P increased annual growth in *S. nemoreum* (Skre and Oechel 1979). In *Sphagnum* mosses, P concentrates in the youngest tissue (Malmer 1988, Sanville 1988) and is retained until the mosses become litter (Malmer 1988).

Mycorrhizal fungi efficiently acquire P for associated vascular plants (Miller et al. 1979) but uptake in BSWs is affected by several factors: growth strategies of individual species, soil temperature, soil moisture, dissolved ions, and evergreen versus deciduous leaf habit (Tilton 1978, Chapin and Tryon 1983, Grime and Anderson 1986, Hom 1986). Although taiga trees and shrubs absorb PO_4-P at lower rates in cold wetlands than in warm uplands, evergreen species - and the deciduous bog blueberry - take up PO_4-P at low concentrations on cold sites more effectively than do deciduous species in general (Chapin and Tryon 1983). Understory shrubs representing only 0.8% of aboveground vascular plant standing crop accounted for 19% of P assimilated by aboveground portions of vascular plants on a permafrost black spruce site (Chapin 1983*a*). Vascular plants in bogs fertilized with P had higher TP contents than controls (Sanville 1988).

Tree species adapted to low-nutrient environments show less growth response to high PO_4-P concentrations than those adapted to high-nutrient environments (Chapin et al. 1983). Black spruce has the lowest capacity for absorption of PO_4-P among taiga trees (Chapin 1983*b*), with a minimum P re-

quirement of only 0.7 kg P·ha^{-1} in interior Alaska (Van Cleve, Oliver et al. 1983), and has lower foliar P content on cold sites than on warm sites (Heilman 1968, Hom 1986). By retaining needles for >20 yr (Hom and Oechel 1983) black spruce mitigates its low capacity for uptake of PO_4-P and maximizes storage time for organic P. Litterfall P content in black spruce averaged only 0.2 kg P·ha^{-1} as compared to 5.3 kg P·ha^{-1} for paper birch (Van Cleve, Oliver et al. 1983). Similarly, tamarack foliar P inversely correlates with site wetness and positively correlates with specific conductivity, a measure of dissolved ions (minerotrophy), the latter perhaps accounting for a finding of lower tamarack foliar P in a bog than in a fen (Tilton 1977, 1978).

Leaching and Mineralization: Two mechanisms, leaching and mineralization, liberate stored PO_4-P from biomass, sometimes making wetlands seasonal sources of PO_4-P even when they are sinks for TP (e.g., Gehrels and Mulamoottil 1990). Leaching loss of P from black spruce foliage is smaller than that from several other taiga trees (Chapin and Kedrowski 1983). Such loss accounted for only 0.01 to 0.04% of total foliar nutrient concentration in a Wisconsin mire (Tyrrell and Boerner 1987).

Phosphate leaches from fresh litter in wetlands, but older litter may accumulate P (van der Valk et al. 1979), roughly paralleling accumulation of organic matter (Miller et al. 1979). Pools of TP in interior Alaska black spruce stands (Table 20) are >3 times that of aboveground tree components (Van Cleve, Oliver et al. 1983). Leaching removed 3 to 4 times more P from these stands than was added by precipitation (Table 20).

Table 19. Phosphorus concentrations and pools in organic and mineral layers of several taiga black spruce stands.

Site Type and Location	Concentration (ppm)	Pool Size (kg P·ha^{-1})	Comment	Source
Upland black spruce - Alaska	NA[1]	96	Organic layer TP	Troth et al. (1976)
Upland black spruce - Alaska	1.7 to 20.8[2]	NA	Mineral soil extractable P increased with depth up to 0.15 to 0.30 m	Troth et al. (1976)
Spruce-lichen woodland - Quebec	11.6 to 26.6[3]	0.21 to 0.49	Organic layer available P	Moore (1980).
Spruce-lichen woodland - Quebec	4.2 to 6.4	NA	Mineral soil available P	Moore (1980).

1. NA = not available.
2. Extractable P presumably is PO_4-P.
3. Available P presumably is PO_4-P.

Table 20. Phosphorus-related characteristics of interior Alaska black spruce stands.

Variable	Quantity	Source
Biomass (kg·ha^{-1})	76,460	Van Cleve, Oliver et al. (1983)
TP Pool (kg P·ha^{-1})	73	Van Cleve, Oliver et al. (1983)
Exchangeable P[1] (kg P·ha^{-1})	0.80	Van Cleve, Oliver et al. (1983)
P Input by Precipitation (kg P·ha^{-1})	0.05 to 0.07	Van Cleve, Oliver et al. (1983)
P Output by Leaching (kg P·ha^{-1})	0.20	Van Cleve, Oliver et al. (1983)
P Mineralization Rate[2] (kg P·ha^{-1}·yr^{-1})	1.5 to 1.8	Flanagan and Van Cleve (1983)
P Turnover Time (yr)	99	Van Cleve, Oliver et al. (1983)

1. Presumably PO_4-P.
2. White spruce and black spruce stands.

Organic decomposition mineralizes PO_4-P at rates that may increase under anaerobic conditions (Gersper et al. 1980). Decomposition rates vary in response to type of litter, soil temperature, and available energy sources for decomposers (Flanagan 1986, Van Cleve and Yarie 1986). High-nutrient litter decomposes more quickly than low-nutrient litter (Flanagan and Van Cleve 1983). Needles of black spruce and the lichen *Cladina stellaris* decompose more slowly than leaves of resin birch in a Quebec spruce-lichen woodland, but the lichen retains more P than does black spruce (Moore 1983). Adding P to black spruce litter does not directly increase soil respiration, however (Moore 1981, Flanagan 1986).

Low soil temperatures and poor litter quality give black spruce the lowest decomposition rates of taiga forest stands (Moore 1981; Van Cleve, Oliver et al. 1983). Taiga spruce stands (black and white) mineralize P (Table 20) at rates 2 to 3 times lower than deciduous stands despite similar pool sizes (Flanagan and Van Cleve 1983). Turnover time for P in black spruce stands (Table 20) is more than 5 times as long as mean P turnover time in deciduous stands (Van Cleve, Oliver et al. 1983).

Black spruce litter resists P mineralization, in part, because insufficient energy may be available to microorganisms responsible for decomposition. Added glucose increased respiration rates of black spruce litter by a factor of 3.8; available P also increased (Flanagan 1986). Low mineralization rates suggest that once transformed to organic form, P is effectively retained in BSWs. A black spruce bog in Minnesota annually retained 60% of DRP and 61% of the largely organic remaining P fractions in runoff (Verry and Timmons 1982).

Phosphorus release by disturbances of black spruce ecosystems also demonstrates significant storage in biomass: available P in organic horizons of burned, nonpermafrost black spruce plots (3.259 to 5.160 $kg \cdot ha^{-1}$) greatly exceeded a control (0.763 $kg \cdot ha^{-1}$) (Viereck et al. 1979); mined bogs discharged greater concentrations of total dissolved P (TDP) than did undisturbed bogs (Moore 1987); and logged black spruce stands on mineral soils showed increased TP and PO_4-P in runoff (Nicolson 1988). Timber removal followed by burning or removing 50% or 100% of the forest floor did not consistently affect PO_4-P in the soil solution, although the highest concentration (~140 $\mu g \cdot L^{-1}$) occurred in one scorched plot in the year of disturbance, and removal of the forest floor tended to depress PO_4-P (Van Cleve and Dyrness 1983*b*).

Functional Summary

Black spruce wetlands perform the nutrient-transformation function for N and P, tending to make inorganic forms less available, and are sinks for nutrient elements contained in accumulating organic matter. Mineralization of organic N to easily-assimilated NH_4-N dominates N transformations in BSWs, although at lower rates than occur in nonwetland communities, and is followed by much smaller moss- and lichen-associated cyanobacterial fixation in ombrotrophic wetlands and by sweetgale- and alder-associated symbiont fixation of unknown magnitude in minerotrophic wetlands. Nitrification appears largely absent, but denitrification may occur at low levels in minerotrophic BSWs where bacterial denitrifiers are more abundant than in ombrotrophic wetlands. Microbes responsible for nitrification and denitrification are present in BSWs and can respond to addition of appropriate substrates.

Adsorption of PO_4-P to Fe-rich peats and uptake by living organisms appear to dominate P transformations in BSWs, where shrubs cycle a disproportionately large share of P. Mineralization of organic P to PO_4-P occurs in BSWs but at much lower rates than in deciduous forests. Chemical precipitation of PO_4-P probably is limited by the acidity and anaerobic conditions characteristic of ombrotrophic BSWs but could tie up P in minerotrophic wetlands with higher pH and potentially more aerobic conditions.

Accumulating organic matter generally accompanies transformations that immobilize nutrients in BSWs. Wetlands exhibiting a predominance of production over decomposition (e.g., those with thick moss layers or substantial litter accumulation) may indicate transformations that reduce nutrient availability. Highly oxidized surfaces may indicate reduced capability for nutrient immobilization.

Ombrotrophy may indicate N fixation by cyanobacteria associated with mosses, particularly *Sphagnum* spp., and the lichens *Nephroma* spp. and *Peltigera* spp., and also may indicate modest rates of P adsorption and nutrient uptake. Iron-rich peats in ombrotrophic BSWs indicate potential P adsorption, but at lower rates than occur in calcareous (highly minerotrophic) wetlands. The vegetation of

ombrotrophic BSWs indicates nutrient transformation through organismal uptake, although at lower rates than found in minerotrophic wetlands.

Minerotrophy may indicate high rates of nutrient mineralization and organismal uptake of nutrients; denitrification; and, in some cases, N fixation by symbionts of alder and sweetgale, P precipitation, or high rates of P adsorption in BSWs. Minerotrophic wetlands have higher pH values, higher base element status, more easily decomposed vegetation (e.g., sedges), vegetation adapted to high nutrient uptake, and thus shorter turnover times for nutrients than do ombrotrophic wetlands. Denitrification, to the small extent that it occurs in taiga BSWs, is favored by pH > 5.5. Transformation of P by chemical precipitation is unlikely in ombrotrophic BSWs and anaerobic conditions but could occur in minerotrophic BSWs, particularly if well aerated. Minerotrophic BSWs containing marl may indicate high rates of P adsorption because peat of calcareous fens apparently adsorbs more P than does bog peat.

Functional Sensitivity to Impacts

The nutrient-transformation function of BSWs is sensitive to placement of fill, which buries the vegetation, soil, water, and associated microbes responsible for nutrient transformations. Transformations occur at specific rates, which may be expressed on a unit-area basis. The impacts of fill placement on nutrient transformation in BSWs thus are at least proportional to the area filled. Fill that changes wetland chemistry, residence times for nutrients or water, or biota necessarily has nonlinear impacts that may be greater than indicated by the area of wetland loss.

Establishing dense vegetation, including N-fixing species, on fill surfaces could mitigate some fill-induced impacts by assimilating N and P in overland flow or atmospheric deposition and by fixing atmospheric N but is unlikely to be consistent with purposes for placing fills. Mineralization of nutrients and adsorption of P would occur only if substantial amounts of organic matter were spread or developed on a fill surface. Nitrification, an aerobic process, might occur on a revegetated fill, but denitrification, an anaerobic process, probably would not.

The nutrient-transformation function of BSWs is less sensitive to drainage than to placement of fill but lower water tables and increased aeration of substrates would alter nutrient transformations. Assuming vegetation were left intact, increased rates of primary production and nutrient uptake by plants and increased abundance of lichens supporting N-fixing phycobionts might occur following drainage. Increased production likely would be accompanied by larger increases in decomposition, net loss of organic matter, and increased mineralization of nutrients.

Acid-inhibited nitrification, denitrification, and chemical precipitation of P probably would be little affected by drainage of ombrotrophic BSWs, but nitrification and P precipitation could increase in drained minerotrophic wetlands due to more oxidizing conditions, at least until drained surfaces became ombrotrophic and acidic. On-site mitigation of altered patterns of nutrient transformation in drained BSWs does not appear possible without restoring lowered water tables to their original positions.

CONTAMINANT REMOVAL

Wetlands that remove contaminants from the water, a water quality function, can be viewed as toxicant sinks or toxicant reservoirs (Kraus 1988). Contaminants including heavy metals and organic compounds (e.g., pesticides or petroleum hydrocarbons) enter long-term sinks, reside for shorter periods in plant tissues or sediments, or degrade to less toxic forms via processes such as adsorption, precipitation, microbial metabolism, and plant uptake (Kadlec and Kadlec 1979, Sather and Smith 1984:13-14, Elder 1988, Ma and Yan 1989). These processes often reduce contaminant concentrations in wetland outflows. The following discussion addresses the functioning of BSWs with respect to uptake and storage of metals in plant tissues, nutrient immobilization, buffering capacity against atmospheric deposition of acids, and ability to degrade organic contaminants.

Metal Uptake and Storage

Vascular and nonvascular plants assimilate metals (Lee et al. 1984, Kraus 1988, Lan et al. 1992) that enter wetlands by atmospheric deposition, surface or subsurface flow of water, or wastewater discharge. The high surface area-to-mass ratios of mosses make them efficient traps for materials deposited from the atmosphere (Santelmann and Gorham 1988); mosses have been used as biomonitors of metal pollution for

>20 yr (Wegener et al. 1992). Accumulation of elements by mosses occurs by cellular uptake, exchange of ions, and adherence of particulate matter to plant surfaces, with the last mechanism most important for retention of lead (Pb), Cd, Fe, and Al (Malmer 1988). *Sphagnum* mosses accumulate airborne metals, especially Mn, to a greater extent than do *Cladina* (*Cladonia*) lichens in the same bogs (Pakarinen 1981) and may have significant potential for uptake of contaminants in BSWs.

Wet and dry deposition of particulates is the only route for metals to enter undisturbed ombrotrophic BSWs. Metal particulates emanating from human activities, such as smelting of metal ores, deposit in peatlands at varying distances from emission sources and can be detected by analysis of organic soils or *Sphagnum* mosses (Pakarinen 1981, Brown et al. 1987). Concentrations of Al, Fe, zinc (Zn), Cd, Pb, and copper (Cu) increase with age of *Sphagnum* tissues (Malmer 1988), with correlations between Pb, Fe, and Zn or between arsenic, Cd, Pb, and Zn noted in several regions (Pakarinen 1981, Santelmann and Gorham 1988). Mosses in Swedish bogs preferentially retained "Mn>Cu>Al, Fe, Zn, Cd, Pb" relative to atmospheric deposition (Malmer 1988:113), but retention of Zn tends to be low in *Sphagnum* (Glooschenko and Capobianco 1979 *in* Malmer 1988).

Mosses in minerotrophic wetlands can accumulate metals contained in metal-rich groundwater or surface runoff. Metal distributions in minerotrophic mires can vary with depth in response to chemical reduction and binding to peat (e.g., Elomaa 1987). Lee et al. (1984) reported that springs with high Zn and sulfate concentrations and high alkalinity supported mosses with tissue concentrations of Pb, Cd, and Zn ranging from 3 to 5 orders of magnitude over concentrations in springwater emanating from an ore body. Tissue concentrations, caused by ion exchange and entrapment of precipitates, varied by species of moss and by location within moss tissue.

Natural or constructed wetlands containing mosses can treat wastewater containing metals. *Sphagnum* mosses provide a large below-water biomass for entrapment of particulates in wastewater treatment systems (Skousen and Sencindiver 1988); remove Fe, Mn, Al, Cd, nickel (Ni), and Zn by cation exchange (Fennessy and Mitsch 1989, Wieder 1990); and acidify their surroundings to enhance uptake of Pb by some vascular plants, although depressing uptake by others (Vedagiri and Ehrenfeld 1991). The cation exchange capacity of *Sphagnum* peat in one test was 1,320 $\mu Eq \cdot g^{-1}$ (Wieder 1990). *Thiobacillus ferrooxidans* regenerates saturated exchange sites by oxidizing Fe so that it precipitates, freeing the sites to bind additional ions (Fennessy and Mitsch 1989).

Vascular wetland plants also remove metals from water. Roots and rhizomes of emergent vegetation growing in temperate estuarine marshes generally accumulate higher concentrations of Cu, Ni, Cd, and Pb than do stems and leaves (Kraus 1988). Cattails effectively take up Pb and Zn, with higher concentrations occurring in roots than in shoots (Lan et al. 1992), although adsorption and microbial activity, rather than plant uptake, may be the mechanisms responsible for most removal of Fe and Mn from mine wastewater (Fennessy and Mitsch 1989). Macrophytes also probably enhance chemical precipitation of metals and their sorption to sediment by providing organic matter to the system, lowering redox potentials, and providing a substrate for microbial populations (Skousen and Sencindiver 1988, Lan et al. 1992). Vegetation of BSWs is a source of organic matter, should lower redox potentials, and should provide microbial substrates in the same way as does marsh vegetation, implying potential for metal uptake and storage.

Plaque made up of Fe oxides and hydroxides forms on the roots, culms, or rhizomes of emergent vascular plants such as cattails and sedges, where it can coprecipitate and adsorb metals such as Mn, Cu, Zn, and Ni (Crowder et al. 1987). Plaques also form on the roots of plants in acid bogs (Armstrong and Boatman 1967 *in* Crowder et al. 1987), and Fe and Mn oxides occur on the flooded roots of black spruce (Levan and Riha 1986). Plaque formation is inversely related to the peat content and CO_3 concentration of wetland soils, perhaps because peat itself binds metal ions (Crowder et al. 1987). Coprecipitation of toxic metals in Fe plaques might occur in BSWs, although the high organic matter contents of these wetlands presumably would limit plaque formation.

Nutrient Immobilization

The balance between net primary production and decomposition controls peat accumulation in mires

(Clymo 1983, Damman 1987), although decomposition may be the most important factor (Johnson 1987). Accumulation of organic matter in mires removes elements from nutrient cycles as peat depth increases (Moore and Bellamy 1974:86) and the rising boundary of the catotelm imposes anaerobic conditions that essentially halt decomposition (Damman 1987). A Minnesota bog retained 55% of entering waterborne nutrients within soils and vegetation (Verry and Timmons 1982), with an estimated 7 to 12.2 kg $N \cdot ha^{-1} \cdot yr^{-1}$ entering the anaerobic catotelm where it is essentially immobilized (Urban and Eisenreich 1988). Similarly, Alaska's BSWs accumulate organic matter and immobilize nutrients because low soil temperatures, poor litter quality, and anaerobic conditions hinder decomposition and nutrient mineralization. Permafrost enhances nutrient immobilization, even in mineral soils (Van Cleve, Dyrness et al. 1983), as frost tables rise in response to thickening organic mats.

Mires in subarctic and boreal wetland regions trend toward peat plateaus and palsas in the zone of discontinuous permafrost and toward treed bogs in continental nonpermafrost areas, although reversion to earlier developmental stages can occur with disturbance or changing environments (Zoltai, Tarnocai et al. 1988; Zoltai, Taylor et al. 1988). Invading ombrotrophic vegetation often covers fen peats deposited in nonpermafrost environments and induces permafrost formation that thrusts surfaces of palsas and peat plateaus above surrounding fens by formation of ice lenses and volumetric expansion of frozen saturated peat (Zoltai and Tarnocai 1975). Long-term rates of accumulation in deep, compacted peat of Canadian taiga mires range from 28 to 106 $mm \cdot 100\ yr^{-1}$, with an average rate of 50 $mm \cdot 100\ yr^{-1}$ (Zoltai, Taylor et al. 1988). Uncompressed, fibric surface peats naturally accumulate at greater rates: *Sphagnum* hummocks in a forested Minnesota bog thickened by 400 mm in 86 yr (Urban and Eisenreich 1988) and a paludified slope of interior Alaska developed 410 to 710 mm of *Sphagnum* peat in <185 yr (Heilman 1966, 1968).

Regional climatic changes may have little influence on long-term peat formation in basin wetlands (Warner and Kubiw 1987), which develop by ***terrestrialization*** or infilling of aquatic environments with peat (Sjörs 1983) to thicknesses of >6 m (Zoltai, Taylor et al. 1988) over many thousands of years (Table 21). Unidirectional successional sequences are uncommon, however (Heinselman 1963). ***Primary mires***, which occur with the growth of peat-forming vegetation directly on wet mineral soils (Sjörs 1983), appear susceptible to climatic change (Table 21), as do peat plateaus and palsas. Raised permafrost bogs do not grow indefinitely (Tallis 1983): peat accumulation can cease (Table 21) after raised surfaces establish (e.g., Zoltai and Tarnocai 1975), probably because the surfaces dry (Zoltai, Tarnocai et al. 1988), and peat surfaces can subside if permafrost thaws (e.g., Kershaw and Gill 1979). Thawed bogs may exhibit renewed peat

Table 21. Periods of active peat accumulation in several North American and Asian mires.

Wetland Type and Location	Basal Peat Age (yr BP)	Cessation of Active Peat Accumulation (yr BP)	Source
Peat plateau bogs - northwestern Canada	~10,000 to ~6,000	~2,700	Zoltai and Tarnocai (1975)
Kettle bog - Ontario	~8,000	0	Warner and Kubiw (1987)
Primary black spruce/ *Sphagnum* bog - Quebec	~5,200	~1,100	Payette et al. (1986)
Black spruce mire - Alaska	~3,500	~1,400[1]	Hamilton et al. (1983)
Paludified river terrace (treeless) - western Siberia	>5,000	?	Gorozhankina (1991)

1. Renewed peat growth has occurred from ~400 yr BP to the present.

growth in collapse scar fens (Zoltai, Tarnocai et al. 1988), a process that may cause repetitive cycles of mire development on river flats of interior Alaska (Drury1956).

Long-term accumulation produces deep peat soils in lowland depressions (mires) of interior Alaska (e.g., Rieger et al. 1963, Rawlinson and Hardy 1982). Migrating rivers can erode such deposits into aquatic ecosystems where sedimentation can rebury organic material or microbial decomposition can release sequestered nutrients. The time scale for river erosion of peat deposits, on the order of hundreds or thousands of years, makes lowland black spruce mires long-term nutrient sinks.

Fire may limit peat accumulation in nondepressional BSWs, as shown by depth and age of organic material (e.g., Heilman 1968). In Northwest Territories, Canada, fire frequency in upland stands may be twice that of lowland black spruce-*Sphagnum fuscum*-Ericaceae communities (Jasieniuk and Johnson 1982). Viereck (1983) hypothesized that permafrost black spruce forests (i.e., BSWs) might develop into treeless *Sphagnum* mires in the absence of fire.

Moderate to heavy burns release immobilized nutrients, increasing total N, TP, and available P in forest floors (Dyrness et al. 1986). Fire volatilizes N and increases K in streams draining burned stands (Viereck and Schandelmeier 1980:23,35). Rapid reestablishment of vegetation following fire presumably retains most nutrients on site, however (Dyrness et al. 1986). The combined effects of nutrient immobilization by peat accumulation in nondepressional BSWs and release by fire appear to favor immobilization.

Buffering Capacity

Wetlands can buffer excessive acidity or alkalinity. Acidic anthropogenic compounds that adversely affect aquatic ecosystems are the chief concern in this context (e.g., Kortelainen and Mannio 1988). Kessel-Taylor and Anderson (1987) proposed that rich fens should have a high capacity to buffer acid deposition based on their characteristically low acidity (pH > 6), high concentration of cations, high bicarbonate (HCO_3) buffering capacity, and flowing waters; poor fens should show a low capacity based on pH concentrations between 4.5 and 6.0, low alkalinity, and slow-moving or standing water; and bogs should have a moderate capacity based on ample organic acids and Al, which act as buffers and also reduce SO_3. In contrast, Holowaychuk et al. (1986 *in* Kessel-Taylor and Anderson 1987) proposed that poor fens buffer acid deposition better than do bogs, but apparently did not consider buffering by organic acids and Al.

Physical and chemical characteristics of organic horizons of forest soils affect buffering capacities (Mahendrappa 1986). Presumably, these characteristics are influenced by vegetation and are as true of forested wetlands as of other forests. Tissue homogenates of black spruce foliage poorly buffered acids, tamarack moderately buffered acids, and Labrador-tea strongly buffered acids (Pylypec and Redmann 1984). Black spruce and Labrador-tea often occur together, but their combined effect on buffering capacities of BSWs is not clear. Tamarack may enhance potentially poor buffering capacities of weakly minerotrophic BSWs for acid deposition.

Contaminant Degradation

Chemical reactions and microbial activity can degrade contaminants entering wetlands and thus lower contaminant concentrations in wetland discharges. Long contact times between water and wetland substrates and diverse microbial communities favor retention of contaminants by wetlands (Elder 1988) and also should favor contaminant degradation. Contact between contaminants and solid surfaces supporting bacteria and fungi promote chemical and microbial transformations of substances in the water column (Kadlec 1988).

Black spruce wetlands provide significant contact between incoming water and solid substrates. Subsurface flow in ombrotrophic wetlands places entrained contaminants in nearly constant contact with peat surfaces, which, for *Sphagnum* peat, have high cation exchange capacities (Clymo 1983), potentially enhancing binding of certain organic compounds. Minerotrophic peats (e.g., peats derived from cotton grass [Clymo 1983]) may have lower cation exchange capacities than ombrotrophic peats, but weakly minerotrophic wetlands generally have low flows favoring long contact times.

Low temperatures and anaerobic conditions may hinder contaminant degradation in BSWs. Although a BSW immobilized experimental spills of crude oil via the absorptive capacity of the thick organic layer

(Johnson et al. 1980), volatilization of lighter hydrocarbon fractions accounted for most changes in composition of the crude during the first 2 yr following the spills (Jenkins et al. 1978). Initially, populations of heterotrophic bacteria increased, but filamentous fungi decreased (Sparrow et al. 1978). Microbial biomass remained depressed after 10 yr, with large amounts of crude remaining at the spill sites (Sparrow and Sparrow 1988).

Functional Summary

Black spruce wetlands perform the contaminant-removal function by taking up and storing metals, immobilizing nutrients, and, in some cases, buffering inputs of acids. Black spruce wetlands do not effectively degrade hydrocarbons and, by extension, presumably do not effectively degrade other toxic organic compounds. Uptake and storage of metals occur in mosses, particularly *Sphagnum* spp., by cellular uptake, ion exchange, and trapping of particulates. Vascular plants concentrate metals in roots and rhizomes. Coprecipitation of toxic metals during formation of Fe plaques on belowground parts of wetland plants also removes contaminants from circulation.

Black spruce wetlands immobilize nutrients by accumulating organic matter. Moss nutrient pools become unavailable to vascular plants as accumulating peat renders subsurface layers anaerobic and as permafrost tables rise. Peat accumulation can continue for thousands of years in lowland basin mires until river erosion exposes peat to degradation. Frequent fires appear to limit peat accumulation in nondepressional BSWs. Nutrients released but not volatilized by fire largely remain on site and supply rapid re-establishment of vegetative cover.

Highly minerotrophic BSWs should strongly buffer acid deposition, but weakly minerotrophic and ombrotrophic wetlands should have only low to moderate buffering capacities. Minerotrophy, perhaps supplemented by the presence of acid-buffering vegetation such as tamarack and Labrador-tea, thus indicates acid buffering capacity.

Ombrotrophic and minerotrophic BSWs both support plant species and processes potentially capable of metal uptake or storage; therefore, species- or community-based indicators of this function are unlikely. In contrast, visually-apparent, rapidly accumulating organic matter indicates high nutrient immobilization whereas stagnant or highly-oxidized organic matter, such as might occur on ombrotrophic peat plateaus and palsas, indicates little immobilization. Peats of minerotrophic wetlands tend to be more decomposed than peats of ombrotrophic wetlands, perhaps indicating that minerotrophic BSWs are slightly less effective than nonstagnant ombrotrophic BSWs for nutrient immobilization.

Functional Sensitivity to Impacts

The contaminant-removal function of BSWs is sensitive to placement of fill. Fill covers vegetation responsible for metal uptake and storage and immobilization of nutrients and diminishes the surface area of buffering systems. Calcareous fill might buffer acid deposition on fill surfaces, however. Warm, aerobic fill surfaces might degrade organic contaminants more rapidly than cold, anaerobic soils of BSWs, if the contaminants could contact the elevated fill surface.

Re-establishment of wetland vegetation and peat-forming systems on fill surfaces might mitigate diminished wetland capability for contaminant removal but is unlikely to be consistent with the purposes for fill placement. Such created wetlands should incorporate plant species known to take up metals, such as *Sphagnum* mosses or cattails; resist decomposition to enhance nutrient immobilization; and buffer acidity. Calcareous substrates or groundwater inputs might be necessary to enhance acid buffering capacity, as well.

The contaminant-removal function of BSWs is less sensitive to drainage than to fill. Sensitivity should increase with drainage effectiveness. Partial drainage would allow wetland plants capable of taking up and storing metals to persist but would increase the depth and warmth of the aerobic zone, initially increasing decomposition and nutrient mineralization and potentially releasing some stored metals. Thorough drainage (i.e., conversion to upland conditions) would eliminate metal-storing plants such as mosses and cattails and accelerate contaminant release from decomposing organic matter but might mineralize sufficient nutrients to promote microbial degradation of hydrocarbons and other organic contaminants.

Surfaces of partially-drained minerotrophic wetlands eventually may develop ombrotrophic vegetation resistant to decomposition and thus regain some

capacity for storing metals and immobilizing nutrients. Such surfaces should have diminished acid buffering capacities in strongly minerotrophic wetlands but possibly increased capacities in weakly minerotrophic wetlands from increased buffering by Al and organic acids. Partially draining ombrotrophic wetlands should have little effect on their acid buffering capacities.

Restoring water tables of BSWs to pre-disturbance elevations would mitigate the effects of drainage on the contaminant-removal function.

DATA GAPS

Data gaps exist with respect to the water quality functions of Alaska's BSWs. Additional studies of sediment retention, nutrient uptake, nutrient transformation, and contaminant removal under subarctic conditions are warranted.

Sediment Retention

Scientists have measured discharges and concentrations of TSS exiting well-defined watersheds containing BSWs in relatively steep terrain (e.g., Chacho 1990), but these sediment yields derive from a variety of source areas. Direct measurements (e.g., mass balance studies) of sediment retention by individual BSWs, particularly in lowland terrain, are needed but appear not to have been made.

Nutrient Uptake

Detailed ecologic studies have characterized nutrient uptake in largely ombrotrophic black spruce forests and woodlands on Alaska permafrost sites, although these sites have been from the drier end of the wetland spectrum (e.g., Van Cleve, Oliver et al. 1983). Nutrient uptake in the wettest ombrotrophic BSWs (e.g., basin bogs) and in most minerotrophic BSWs has received little study. Minerotrophic BSWs are important because they have higher probabilities of receiving waterborne nutrients than do ombrotrophic wetlands and their vegetation should be adapted for nutrient uptake. Nutrient uptake might best be studied via experimental fertilization or controlled application of high-nutrient wastewater and measurement of changes in tissue nutrient concentrations and quantities, rates of photosynthesis, and biomass. These quantities tell more about the fate of influent nutrients than does the mere difference between influent and effluent nutrient loads.

Nutrient Transformation

Scientists have studied N fixation and mineralization; P uptake, leaching, and mineralization; and the significance of P uptake by shrubs in relation to their biomass in ombrotrophic black spruce stands and bogs, but comparable studies are not available for minerotrophic BSWs. Phosphorus precipitation and adsorption, nitrification, and denitrification have received little study in taiga BSWs, regardless of trophic status. All nutrient transformations for N and P thus require quantification in minerotrophic BSWs, and selected transformations such as nitrification, denitrification, and the relative roles of peat and Fe complexes in P adsorption, also require quantification in ombrotrophic BSWs.

Contaminant Removal

Metal uptake and storage by certain plants is reasonably well-documented for metal-tolerant mosses in bogs and in metal-rich fens associated with ore bodies and for selected vascular plants in marshes, although metals are toxic to many other vascular plants and to algae (J. LaPerriere, Univ. Alaska, pers. commun.). Formation of Fe plaques and coprecipitation and adsorption of toxic metals on belowground parts of marsh plants also have been described. Vascular vegetation of minerotrophic BSWs also may take up metals and form plaques, but this has not been documented and should receive study.

Peat accumulation in taiga mires has received substantial study in Canada but little in Alaska. Studies of nutrients tied up in organic matter of Alaska's ombrotrophic black spruce stands are available, but little information exists for minerotrophic BSWs. Controls on peat accumulation in BSWs, including climatic and microclimatic factors (e.g., Hom 1986), the process of paludification, fire, and the frequency of peat erosion by fluvial processes, deserve further attention. In addition, assumptions used in Canadian reviews to rate the acid buffering capacities of mires should be verified for Alaska's BSWs.

Functional Sensitivity to Impacts

Data gaps exist with respect to the sensitivity of certain water quality functions of BSWs to the impacts of drainage and placement of fill. That fill effectively eliminates the sediment-retention, nutrient-uptake, nutrient-transformation, and con-

taminant-removal functions of covered areas in BSWs is relatively self evident and requires little study. In contrast, although drainage at least temporarily reduces sediment retention in bogs and increases decomposition in mires, scientists have obtained little information about the effects of drainage on the other water quality functions of BSWs.

Drainage presumably increases the availability of nutrients to wetland plants, and drained wetlands may continue to remove contaminants at reduced, but unquantified, levels. Drainage effects on nutrient uptake and transformation in BSWs could be documented by obtaining water and nutrient budgets, net primary production, biomass, and tissue nutrient levels before and after drainage of experimental plots. Effects of drainage on contaminant removal might be documented by comparing drained and undrained BSWs with respect to plant community composition and experimentally-determined capacities of such communities for metals uptake and storage and with respect to decomposition and net primary production and thus capacities to immobilize nutrients by peat accumulation. Finally, experimental acidification of undrained and drained minerotrophic wetlands might be used to verify buffering capacities.

GLOBAL BIOGEOCHEMICAL FUNCTIONS

Nitrogen, sulfur (S), and C participate in global biogeochemical cycles (Mitsch and Gosselink 1993:525-527). Molecules containing these elements not only cycle within wetlands but also pass between wetlands and the atmosphere where some affect global climate. This profile discusses N fixation and denitrification as water quality and ecologic functions, but little information on S cycling in mires or mire-like wetlands appears in the literature and consequently is not addressed herein. Although C cycling and storage might be considered water quality or ecologic functions of wetlands, based on the role of C as a nutrient and the importance of peat accumulation in long-term storage of other nutrients and contaminants, this profile separately addresses C cycling and storage because of their importance to anthropogenic air chemistry and removal of atmospheric C in relation to global warming.

CARBON CYCLING AND STORAGE

Carbon is stored, released, and transformed through primary production, decomposition, and other biologically-mediated processes in global biogeochemical cycles. Wetlands contain ~12% of the global soil pool of organic C (Lugo, Brown et al. 1990) and thus are important for C cycling and storage. At least 500 million ha of global wetlands accumulate C as peat (Maltby 1986:51), many in arctic, subarctic, and boreal portions of North America, Europe, and Asia (Mitsch and Gosselink 1993:368-371). Canada alone has an estimated 111.3 million ha of peatlands (Zoltai 1988), constituting "one of the few terrestrial ecosystems where C is stored for thousands of years" (S. C. Zoltai, Can. For. Serv., pers. commun). Peat therefore acts as a sink for atmospheric C fixed by photosynthesis (Friedman and DeWitt 1979; Malmer 1988; Lugo, Brown et al. 1990).

Carbon transformations occurring in wetlands involve changes in phase, such as release of carbon dioxide (CO_2) and methane (CH_4) to the atmosphere (Mitsch and Gosselink 1993:134-136); shifts in chemical equilibria between dissolved CO_2, HCO_3, and carbonate (CO_3), which make up total inorganic C (Wetzel 1983:202-204); precipitation of CO_3 (Wetzel 1983:205-207); cycling between inorganic and organic C via photosynthesis, respiration, and fermentation; and changes in particle size of organic C. Organic C occurs in dissolved (DOC) and particulate (POC) forms in aquatic systems and the soil solution, although these pools are minor in comparison to soil C (D. K. Swanson, Nat. Resour. Conserv. Serv., pers. commun.).

Two major processes encompass C transformations in wetlands: primary production of biomass and its subsequent decomposition. Photosynthesis transforms inorganic C to carbohydrate, and subsequent metabolic processes, including heterotrophic consumption, incorporate C in other organic compounds. Community respiration and anaerobic decomposition (fermentation) release compounds such as CO_2, lactic acid, and ethanol (Mitsch and Gosselink 1993:135). Excluding imports and exports of organic material, the balance between net primary production and decomposition in a wetland determines whether or not it will function as a sink for C.

Primary Production

Plants assimilate atmospheric or dissolved CO_2 to support photosynthesis, although some submersed species (excluding mosses) can use HCO_3 under appropriate conditions (Wetzel 1983:217). Terminal

portions of *Sphagnum* mosses fix significant quantities of atmospheric C in ombrotrophic mires (Malmer 1988). Black spruce stands occurring on permafrost soils, whether lowland or upland, accumulate more forest floor organic matter than other taiga forest types (Van Cleve, Oliver et al. 1983), storing C in soil (Table 22) and aboveground tree components (Table 23). In one such stand, *Sphagnum subsecundum* allocated 70 to 76% of fixed C to brown tissue over the growing season, and, along with feathermosses and *Polytrichum commune*, stored C in polysaccharides (Skre et al. 1983*a*).

Modeling indicates that taiga uplands of interior Alaska, like other taiga regions, are a sink for CO_2 (Bonan 1990*a,b*). Based on large volumes of stored peat, lowland mires also are C sinks. The mean C content of mineral soils (Table 22) and mean estimated C content of aboveground tree components and forest floors (Table 23) suggest an average of ~137 metric tons C·ha^{-1} in black spruce stands sampled by Van Cleve, Oliver et al. (1983). The largest mineral-soil C content reported for cold black spruce stands (Table 22), combined with the largest C content estimated for tree, root, and forest floor biomass (Table 23), suggest that some permafrost BSWs may store >200 metric tons C·ha^{-1}.

The competitive processes of net primary production and decomposition determine wetland C balance, even with significant annual production of biomass (Figure 9). Only the strings of a Quebec northern ribbed fen accumulated C on an annual basis (Figure 10). The rate of C gain for the fen string compares favorably with other sites from Europe and North America: a range of 40 to 670 kg C·ha^{-1}·yr^{-1} but most frequently 150 to 300 kg C·ha^{-1}·yr^{-1} (Moore 1989). Some fen strings are BSWs.

Decomposition

Decomposition comprises leaching of substances from dead organic matter, physical and biological fragmentation of detritus, and oxidation of particulate organic matter by microorganisms (de la Cruz 1979). Anaerobiosis slows decomposition in BSWs and thus is very important for preserving C (D. K. Swanson, Nat. Resour. Conserv. Serv., pers. commun.). In addition, lack of easily metabolizable

Table 22. Soil carbon contents of representative interior Alaska black spruce stands.

Site Type	Soil Carbon Content (metric tons·ha^{-1})			Source
	Organic Layer	Mineral Soil[2]	Soil Profile	
Permafrost black spruce	70.8[1]	39.8[1]	110.6[1]	Sparrow and Sparrow (1988)
Black spruce	~20 to ~75[1]	73[2,3]	~90 to ~150[4]	Van Cleve, Oliver et al. (1983)
Cold black spruce	NA[5]	≤90	NA	Viereck and Van Cleve (1984)

1. Values are total organic carbon (TOC).
2. Values are total carbon (TC).
3. Mean for multiple stands.
4. Sum of reported range of TOC for organic horizons and reported mean TC for mineral soil.
5. NA = not available.

Table 23. Combined carbon contents of aboveground tree components and forest floors of representative interior Alaska black spruce stands based on biomass.

Site Type	Biomass (metric tons·ha^{-1})	Carbon Content[1] (metric tons·ha^{-1})	Source
Black spruce stands	127[2]	~64	Van Cleve, Oliver et al. (1983)
Black spruce stand	~240[3]	~120	Viereck and Van Cleve (1984)

1. Calculated from biomass assuming a biomass to C conversion factor of ~50% (e.g., Moore 1989).
2. Mean value for multiple stands.
3. Includes root biomass.

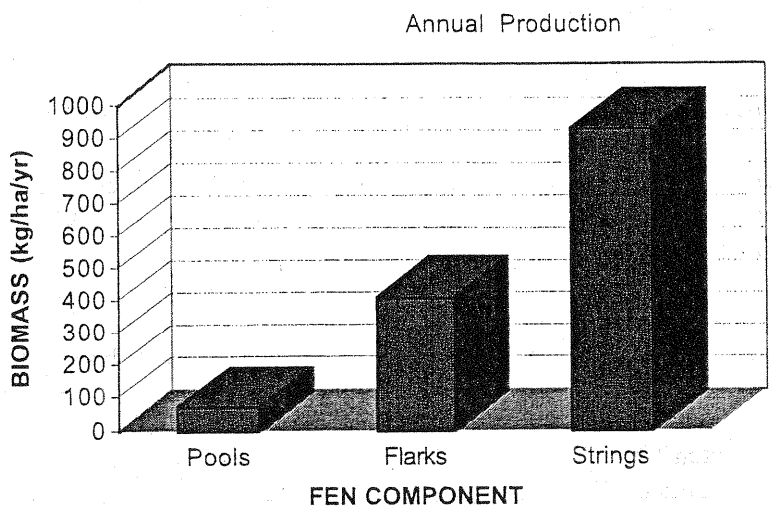

Figure 9. Net primary production for components of a northern ribbed fen in subarctic Quebec (Moore 1989).

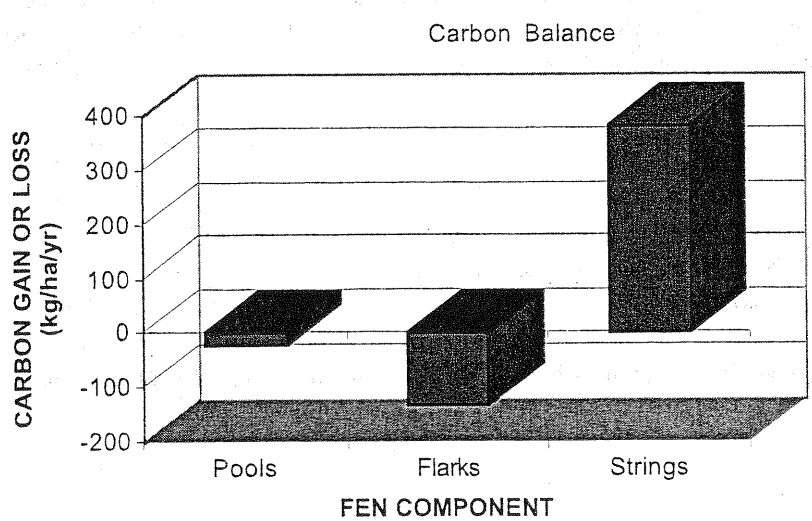

Figure 10. Carbon balance for components of a northern ribbed fen in subarctic Quebec (Moore 1989).

substrates for fungi and other decay microorganisms (Moore 1981, Flanagan 1986) and, more importantly, low soil temperatures slow decomposition in organic horizons of black spruce stands (Moore 1981; Van Cleve, Oliver et al. 1983; Yarie 1983, Van Cleve and Yarie 1986). Where permafrost is present, decomposition of organic matter essentially ceases below the permafrost table.

Black spruce wetlands often store C in forms that resist degradation, even under aerobic processes. Plants can allocate C to growth or to secondary metabolites that function for defense against herbivores (Bryant 1984:7-10, Bryant and Chapin 1986). In ombrotrophic wetlands, slow-growth species such as black spruce have a competitive advantage over deciduous species with high nutrient requirements (Chapin 1986, Brumelis and Carleton 1988). Slow-growth species tend to accumulate C-based antiherbivory compounds (Bryant et al. 1983) that discourage nutrient losses to herbivory but also inhibit decomposition (Bryant and Chapin 1986).

Minerotrophic wetlands might be expected to support easily-degraded, fast-growth plants. Although fens sometimes have more highly degraded peats than do bogs (Clausen and Brooks 1983*b*), this is not necessarily the case (P. H. Glaser, Univ. Minn., pers. commun.). Rates of decomposition vary by type of litter, however, with woody species characteristic of fen strings (e.g., leatherleaf) decomposing slowly and herbaceous species characteristic of pools (e.g., buckbean) decaying quickly (Moore 1989).

Although organic material decomposes slowly in BSWs, some C escapes to the atmosphere. Respiration and fermentation produce CO_2 (Mitsch and Gosselink 1993:134-136), and anaerobic decomposition at low redox potentials produces CH_4 (Lugo, Brown et al. 1990). Carbon dioxide produced within saturated peat exists in solution, but CH_4 apparently also exists in the gaseous phase (Buttler et al. 1991) and lowers peat hydraulic conductivity by occluding pore spaces (Brown and Overend 1993). Methane may be oxidized to CO_2 as it passes through aerobic surficial peats (Mitsch and Gosselink 1986:103, Moore 1989, Fechner and Hemond 1992, Moore et al. 1994).

Water table height is inversely related (linear) to CO_2 evolution (Moore and Knowles 1989) and positively related (logarithmic) to CH_4 evolution (Moore and Knowles 1989). Ratios of CH_4 to CO_2 therefore increase with depth (e.g., Dinel et al. 1988). Strings of a northern ribbed fen evolved predominantly CO_2, pools evolved predominantly CH_4, and flarks (near-surface water table) evolved both gases (Moore 1989). Fen pools can emit much more CH_4 per unit area than nearby peat surfaces (Hamilton et al. 1994, Roulet et al. 1994).

Matthews and Fung (1987) estimated that ~60% of global wetland emission of CH_4 occurs from northern peatlands, although recent estimates (e.g., Roulet et al. 1994) are lower. Soil temperature influences seasonal trends in CH_4 emission (Whalen and Reeburgh 1992, Klinger et al. 1994). Fens emit more CH_4 than do bogs (Svensson and Rosswall 1984, Moore and Knowles 1989, Dise 1992), which emit little (Moore and Knowles 1990, Moore et al. 1990, Brown and Overend 1993, Moore et al. 1994). In Alaska, *Eriophorum vaginatum* tussocks and pond-margin stands of *Carex* spp., settings found in minerotrophic BSWs, produced more CH_4 than did intertussock depressions covered with *Sphagnum* moss or detritus and elevated non-*Sphagnum* moss areas (Whalen and Reeburgh 1992).

Several permafrost black spruce sites in Alaska with seasonally high soil moistures consistently consumed atmospheric CH_4, as well as CH_4 from experimentally enriched atmospheres (Whalen et al. 1991). Warmer, drier soils consumed more CH_4 than cooler, wetter soils (Whalen et al. 1991). It is not clear that these sites were BSWs, but they indicate that drier ombrotrophic BSWs may consume, rather than emit, CH_4.

Oxidation of stored C to CO_2 by fire also is important in interior Alaska where black spruce taiga burns with a cycle of 50 to 200 yr (Viereck and Schandelmeier 1980:12, Dyrness et al. 1989). Fires tend to consume less accumulated organic matter on wetter north-aspect slopes than on drier south-aspect slopes (Van Cleve et al. 1991). Lowland BSWs with high water tables presumably limit release of accumulated C in a similar manner.

Functional Summary

Black spruce wetlands function to cycle and store C, primarily by photosynthesis and decomposition. Photosynthetic fixation of CO_2 (primary production) in BSWs is lower than in nonwetland forests, but rates of decomposition also are low, leading to accu-

mulation of C as organic matter. Decomposition releases stored C as CH_4 and CO_2, and fire releases CO_2 as a combustion product, but saturated conditions in BSWs minimize these losses as compared to nonwetlands. Aerobic surface layers of ombrotrophic BSWs may consume atmospheric CH_4. Black spruce wetlands thus are important sinks for atmospheric C.

Active accumulation of organic matter indicates C storage in BSWs. Highly decomposed organic horizons may indicate a neutral or negative C balance. Wetlands with characteristically high water tables and low redox potentials (often minerotrophic) indicate potential CH_4 emission whereas those with aerobic surface layers (often ombrotrophic) indicate potential CO_2 emission and CH_4 consumption.

Functional Sensitivity to Impacts

The C cycling and storage functions of BSWs is sensitive to placement of fill. Carbon cycling would not occur on a barren fill surface. Establishing dense vegetation on a fill surface could mitigate loss of C fixation by wetland plants. Much fixed C in litter would be lost to decomposition until (and if) coniferous forest and substantial moss cover became established on the fill and soil temperature declined sufficiently for permafrost formation, a process that might take >200 yr in the taiga environment.

The effects of drainage on the C cycling and storage function of BSWs are not clear. Surfaces of minerotrophic wetlands should become ombrotrophic following effective drainage, potentially lowering net primary production but also producing woody litter more resistant to decomposition. Effective drainage should increase decomposition in both ombrotrophic and minerotrophic BSWs and might produce negative C balances. Less effective drainage, however, might allow C storage to continue. Carbon dioxide evolution in drained wetlands should increase at the expense of CH_4 evolution. Fires potentially would consume more accumulated organic matter, with consequent release of stored C, in drained than undrained BSWs.

DATA GAPS

Carbon transformations have been documented in some BSWs of interior Alaska (e.g., Van Cleve, Oliver et al. 1983) and in subarctic Canadian fens (Moore 1989). Carbon fixation has received more attention than decomposition and ombrotrophic woodlands more attention than minerotrophic wetlands. Documentation of net C balance for a variety of BSWs, as influenced by trophic status, community composition, and hydrologic relationships, is warranted given the importance of CO_2 as a greenhouse gas.

ECOLOGIC FUNCTIONS

All wetland functions are, in a holistic sense, ecologic functions because wetland ecosystems encompass all physical, chemical, and biological phenomena (i.e., functions) occurring within ecosystem boundaries. Nevertheless, this report narrowly defines ecologic functions as those primarily derived from biological processes, or from chemical processes mediated by living organisms, but sometimes supplemented by strictly physical or chemical components: nutrient cycling and export, food chain support, and fish and wildlife habitat.

NUTRIENT CYCLING

The nutrient-cycling function of BSWs is closely related to food chain support and nutrient export, as well as to nutrient uptake, transformation, and immobilization discussed in preceding chapters. Nutrients pass through both grazing and detrital food chains in the processes of primary and secondary production and decomposition and thus provide resources to fish and wildlife populations using wetlands and adjacent ecosystems (Sather and Smith 1984:21-39). Nutrients may be retained within a wetland via intrasystem cycling (transformational processes) or exchanged with surrounding ecosystems (Mitsch and Gosselink 1993:115).

Distribution of Nutrients

Biomass of forest floors (~76 metric tons·ha^{-1}) exceeds that of trees (~51 metric tons·ha^{-1}) in black spruce stands of interior Alaska (Van Cleve, Oliver et al. 1983). Element distribution in forested ecosystems generally parallels biomass distribution (Brinson 1990), but forest-floor masses of N, P, K, and Mg exceed those of black spruce trees by factors of ~3 to ~5 despite relatively small between-strata differences in biomass distribution (Van Cleve, Oliver et al. 1983). These findings suggest that nutrients (Ca is an exception) concentrate in the forest floors of BSWs, as has been shown for some bogs (Figure 11).

Cycling Times and Fates of Nutrients

Black spruce wetlands of interior Alaska cycle nutrients slowly (Table 24). Nutrient requirements (N, P, K) for black spruce are ~6 to ~8 times less than those for tree strata of other taiga forest communities, and residence times for these nutrients in the forest floors of black spruce stands exceed those of other taiga communities (pooled) by factors of ~2 to ~3 (Van Cleve, Oliver et al. 1983). Black spruce retains needles for up to 30 yr, which maximizes photosynthate produced for a given nutrient investment (Hom and Oechel 1983). Mosses also tie up nutrients for long periods of time (Oechel and Van Cleve 1986). In contrast, understory shrubs such as Labrador-tea and blueberry rapidly cycle biomass, N, and P in BSWs, perhaps taking up pulses of nutrients that slow-growing black spruce cannot quickly assimilate (Chapin 1983*a*). These nutrients subsequently become available to black spruce through litterfall and decomposition.

Graminoids occurring in BSWs also cycle nutrients. Adaptations for nutrient uptake and plant growth in cold, nutrient-poor environments include higher root surface-to-volume ratios, lower optimum temperatures for root growth, and greater capacities for absorption of P than occur in species and ecotypes from warmer climates (Chapin 1974). In addition, graminoids maintain large belowground nutrient stores and quickly replace aboveground parts lost to fire or grazing (Bryant et al. 1983).

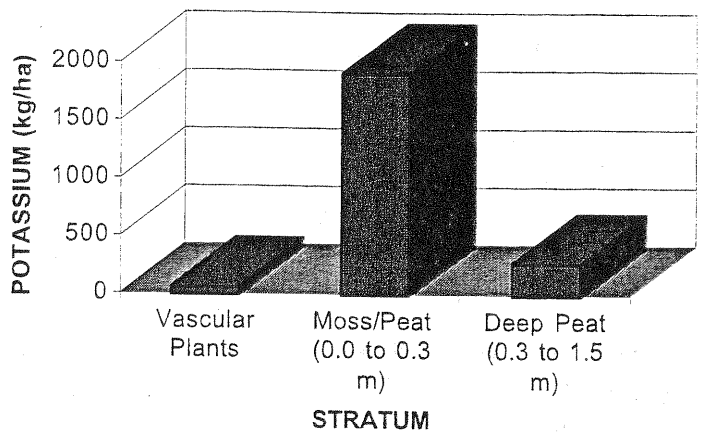

Figure 11. Potassium distribution in a raised bog (Buttleman and Grigal 1985).

Table 24. Contrasting turnover times for nutrient elements in nonpermafrost black spruce stands in Ontario and largely permafrost stands in Alaska.

Site Type and Location	Organic Soil Turnover Time (yr)					Source
	N	P	K	Ca	Mg	
Nonpermafrost black spruce on sand - Ontario	35	2	3	2	3	Gordon (1983)
Nonpermafrost black spruce on peat - Ontario	35	4	6	37	22	Gordon (1983)
Taiga black spruce - Alaska	61	99	74	39	73	Van Cleve, Oliver et al. (1983)

Nutrients can be recycled by respiration and retranslocation, which act rapidly within living tissue, and leaching and litterfall, which act slowly in nonliving tissue (Lugo, Brinson et al. 1990). Decomposition of litterfall mineralizes nutrients, which again become available for uptake by plants. Nitrogen mineralization, for example, dominates N cycling within BSWs (Table 25).

Mire environments inhibit microbiological activity and limit nutrient cycling (Dickinson 1983). Poor litter quality and low soil temperatures also limit decomposition in BSWs of interior Alaska (Brunberg 1983, Flanagan and Van Cleve 1983, Salonius 1983, Flanagan 1986, Van Cleve and Yarie 1986), although mineralization rates in minerotrophic wetlands dominated by graminoids should be higher than in oligotrophic wetlands dominated by mosses. Accumulating peat further removes nutrient elements from biogeochemical circulation (Nikonov and Manakov 1980): >50% of the N input to a Minnesota bog entered the catotelm despite rapid turnover of a small pool of N in the acrotelm (Urban and Eisenreich 1988).

Table 25. Nitrogen mineralization and fixation in a Minnesota bog and Alaska black spruce stands.

Site Type and Location	N Mineralization (kg $N \cdot ha^{-1} \cdot yr^{-1}$)	N Fixation (kg $N \cdot ha^{-1} \cdot yr^{-1}$)	Source
Black spruce bog - Minnesota	43 to 59	0.5 to 0.7	Urban and Eisenreich (1988)
Black spruce stands - Alaska	11 to 18	0.9 to 1.4	Flanagan and Van Cleve (1983), Billington and Alexander (1983)

Functional Summary

Black spruce wetlands, like all ecosystems, cycle nutrients, but the magnitude of this function is low in comparison to more productive communities. Nutrient cycling in BSWs involves only a small proportion of total nutrient pools because decomposition of organic matter is limited. Minerotrophic wetlands, with higher rates of decomposition, likely cycle more nutrients than do ombrotrophic wetlands but are unlikely to approach the nutrient-cycling capabilities of upland deciduous forests in interior Alaska.

Minerotrophy, evidenced by circumneutral pH, vegetation with an important component of easily decomposed graminoid plants, and high Ca and Mg concentrations, may be an indicator of greater than average nutrient cycling in BSWs.

Functional Sensitivity to Impacts

The nutrient-cycling function of BSWs is sensitive to placement of fill. Wetland areas covered by barren fill would not cycle nutrients through plant uptake or remove waterborne nutrients from the water column through adsorptive processes involving organic matter. Buried organic material would become anaerobic, greatly decreasing nutrient mineralization.

Nutrient cycling could be established on fill surfaces covered by dense vegetation and, if established as an upland deciduous forest community, could exceed that of the buried wetland. Creation of a warm upland forest stand is an unlikely objective for fill placement; establishment of grass cover is more likely (e.g., a golf course). Vegetated fill surfaces in most cases would not fully offset the nutrient-cycling losses caused by fill placement.

Nutrients will cycle in drained BSWs, but rates of nutrient-cycling likely will differ from those of comparable undrained wetlands. Drainage should warm soils, as occurred in a drained fen (Lieffers and Rothwell 1987), and increase aeration of the organic layer, mineralization of nutrients, and plant production, all of which suggest enhanced nutrient cycling. On the other hand, drained minerotrophic BSWs may become ombrotrophic, which would favor mosses and woody vegetation resistant to decomposition, as shown for fen strings (Moore 1989). Such changes suggest decreased nutrient mineralization.

Perhaps the only predictions possible with regard to nutrient cycling and drainage of BSWs are that increased decomposition coupled with increased net primary production indicate increased nutrient cycling whereas decreased decomposition coupled with decreased net primary production indicate decreased nutrient cycling. Situations where drainage changes decomposition and net primary production in opposite directions are equivocal. Manipulating the balance of decomposition and production in drained wetlands to simulate predrainage states might mitigate impacts on nutrient cycling.

NUTRIENT EXPORT

Wetlands can export nutrients to adjacent or downstream ecosystems (Adamus and Stockwell 1983:29), a form of food chain support often associated with coastal wetlands (Sather and Smith 1984:25). In some cases, exported nutrients add to the productivity of recipient ecosystems, such as estuaries, which may harbor species of particular biological and economic significance, such as commercial fishes (de la Cruz 1979, Adamus and Stockwell 1983:29-37, Mitsch and Gosselink 1984:120-121, Sather and Smith 1984:25-27). Black spruce wetlands are low-energy environments with only modest potentials for exporting waterborne nutrients. The following section discusses N, P, and C export in Alaska's BSWs.

Nitrogen

Nitrogen export from wetlands is a function of runoff discharge and N concentration. Black spruce wetlands accumulate organic matter and are nutrient sinks in which mineralization and immobilization dominate N cycling. Rapid accumulation of organic matter reduces the residence time of peat in the acrotelm where mineralization can occur (Damman 1987) and therefore may reduce N concentration in peat water (Table 26). Nitrogen export from peat-forming wetlands to aquatic systems should be small in relation to the pool of N in organic matter, particularly in northern taiga where runoff and mineralization rates are low.

A Minnesota bog receiving 0.80 m of precipitation·yr^{-1} exported 50% of N input, yielding 6.374 kg N·ha^{-1}·yr^{-1} in streamflow, mainly as organic N (5.388 kg·ha^{-1}·yr^{-1}) (Verry and Timmons 1982). Export of inorganic N from the bog is comparable to that from natural and agricultural soils of low productivity (Wetzel 1983:283). Although N-export rates are not available for BSWs of interior Alaska, these sites receive only 0.25 m to 0.50 m of precipitation (Watson 1959 *in* Wahrhaftig 1965), which should reduce N export in comparison to sites in wetter regions. Fens export more N than do bogs in Minnesota (Clausen and Brooks 1983*b*) suggesting that minerotrophic BSWs may export more N than ombrotrophic BSWs.

Phosphorus

Phosphorus export from wetlands, like that of N, is a function of runoff discharge and element concentration. Phosphorus occurs in higher concentrations in stagnant peat than in rapidly accumulating peat (Damman 1987), and runoff concentrations from peatlands are small (Table 27). Black spruce wetlands accumulate organic matter and are sinks for P, which implies that exports should be small in relation to P inputs and stored P.

Minerotrophic BSWs potentially export more P than do ombrotrophic wetlands because fens generally have greater flows. An 18-ha Ontario marsh, in some respects similar to a fen, that received surface flow from groundwater discharge and from a developed 130-ha watershed (Gehrels and Mulamoottil

Table 26. Nitrogen export in runoff from bogs and tundra peatland.

Site Type and Location	Nitrogen Concentration in Runoff ($mg \cdot L^{-1}$)			Source
	NH_4-N	NO_3-N	Organic N	
Undisturbed bogs - Minnesota	0.1	0.06	1.4	Clausen and Brooks (1983a)
Undisturbed bogs - Quebec	0.07	NA[1]	NA	Moore (1987)
Tundra beaded stream - Alaska	0.013	0.006	NA	Oswood et al. (1989)

1. NA = not available.

Table 27. Phosphorus concentrations in runoff from northern peatlands.

Site Type and Location	Phosphorus Concentration in Runoff ($\mu g \cdot L^{-1}$)			Source
	TDP	TP	PO_4-P	
Undisturbed bogs - Quebec	28	NA[1]	NA	Moore (1987)
Peatland lakes - Labrador	NA	19	NA	Engstrom (1984)
Tundra stream - Alaska	NA	NA	13	Oswood et al. (1989)
Bogs - Minnesota	NA	60	NA	Clausen and Brooks (1983b)
Fens - Minnesota	NA	80	NA	Clausen and Brooks (1983b)

1. NA = not available.

1990) exported P in surface water and groundwater (Figure 12). The marsh, a strong sink for TP and a weak source of PO_4-P, exported ~1.9 kg TP·ha^{-1}·yr^{-1} in surface water (Gehrels and Mulamoottil 1990). In contrast, a Minnesota bog exported only 0.460 kg TP·ha^{-1}·yr^{-1} (0.308 kg organic P·ha^{-1}·yr^{-1} and 0.154 kg PO_4-P·ha^{-1}·yr^{-1}) in streamflow and retained 61% of P input (Verry and Timmons 1982). The rate of P export from the Minnesota bog is roughly comparable to that from natural and agricultural soils of medium productivity (Wetzel 1983:283).

Particulate and Dissolved Organic Carbon

Wetlands export organic C in particulate and dissolved forms (Crow and Macdonald 1979; Lugo, Brown et al. 1990). For example, the DOC content of several streams flowing through temperate marshes doubled (Wetzel and Otsuki 1974 *in* Wetzel 1983). Dissolved organic C is a constituent of dissolved organic matter (DOM), which is made up of dissolved nonhumic and dissolved and colloidal humic substances; DOC is the predominant form of organic C in freshwater systems, often occurring at 6 to 10 times the concentration of POC (Wetzel 1983:667,676). Wetlands may have slightly lower ratios of DOC to POC, on the order of 3 to 6 (Lugo, Brown et al. 1990), than typical of lakes and streams.

Humic and fulvic acids (Figure 13); chemical oxygen demand (COD), e.g., 389 kg COD·ha^{-1}·yr^{-1} for a Minnesota bog (Verry and Timmons 1982); and DOC and TOC concentrations (Table 28) in peatland runoff demonstrate C export, as do measures of and unit-area C yields on the same order as those for southern freshwater swamps (Table 29). A clearwater lake surrounded by mineral soils showed only 7.18 mg DOC·L^{-1} (Bourbonniere 1989), but typical values for peatland runoff are ~3 to ~6 times higher (Table 28). Moore (1988) characterized C-export rates from Quebec mires (Table 29) as relatively high.

Peat carbon supports aquatic food webs in the Arctic (Schell 1983), suggesting a similar function of organic C in taiga aquatic systems. The mire-draining Bigoray River of Alberta supported 112 species of chironomids in a reach of only 150 m, a species richness attributed to an abundance of micro-

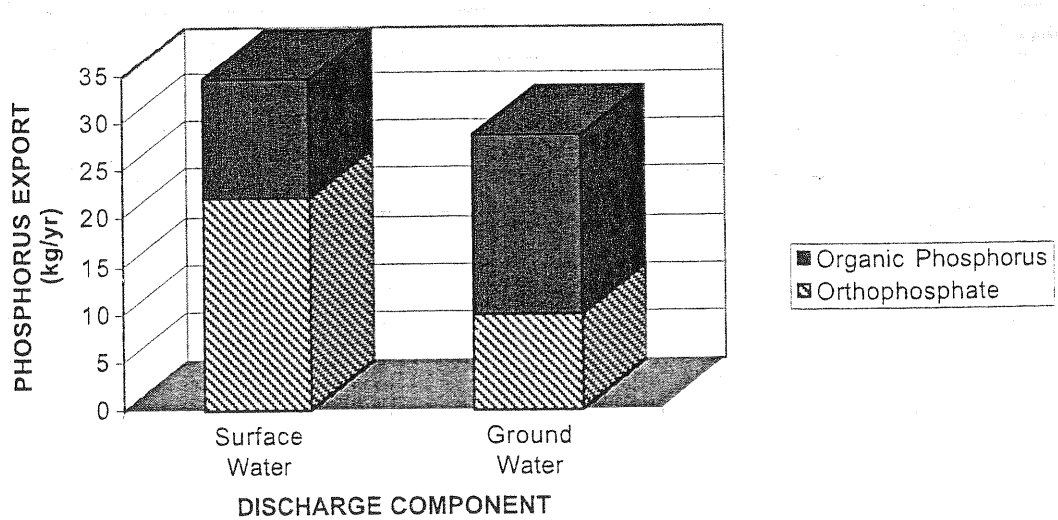

Figure 12. Phosphorus exports from an organic-substrate cattail marsh, Ontario (Gerhrels and Mulamoottil 1990).

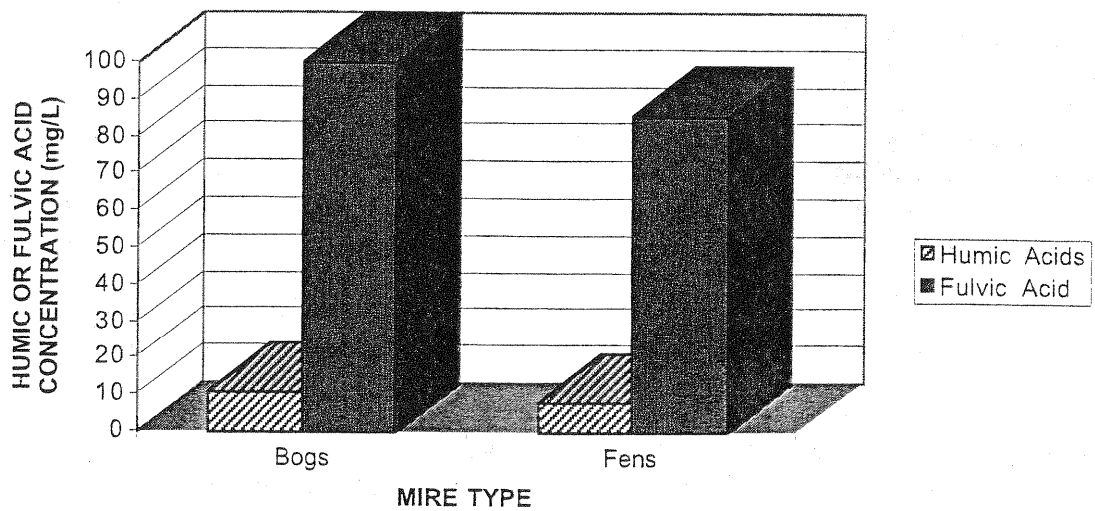

Figure 13. Humic and fulvic acid concentrations in runoff from Minnesota mires (Clausen and Brooks 1983b).

Table 28. Carbon concentrations in runoff from northern peatlands.

Site Type and Location	Carbon Concentration in Mire Runoff ($mg \cdot L^{-1}$)		Source
	DOC	TOC	
Subarctic mires	19.3	NA[1]	Moore (1988)
Headwater lakes in peatland watersheds - Finland	NA	10.9 (mean), 33.9 (max)	Kortelainen and Mannio (1988)
Bogs (upper pore water) - Nova Scotia and Quebec	38.5	NA	Bourbonniere (1987, 1989)
Bogs (upper pore water) - Nova Scotia and Quebec	47.1	NA	Bourbonniere (1987, 1989)
Bogs (natural streams) - Nova Scotia and Quebec	34.5	NA	Bourbonniere (1987, 1989)
Bogs (drainage ditches) - Nova Scotia and Quebec	29.0	NA	Bourbonniere (1987, 1989)
Undisturbed bogs - Quebec	33.7	NA	Moore (1987)
Mires - Quebec	19.3	NA	Moore (1988)
Tundra beaded stream - Alaska	NA	~10	Oswood et al. (1989)
Colville River (spring flows) - Alaska	NA	19.3	Schell and Ziemann (1983)

1. NA = not available.

Table 29. Carbon export rates for swamps and peatlands.

Site Type and Location	Unit-Area Carbon Export (kg C·ha^{-1}·yr^{-1})		Source
	TOC	DOC	
Freshwater swamps - southern USA	20 to 100	NA[1]	Mitsch and Gosselink (1986:120-121)
Tundra and taiga regions	23	NA	Lugo, Brown et al. (1990).
Boreal fens - Quebec	NA	13 to 33	Moore (1988)
Boreal bog - Quebec	NA	48	Moore (1988)
Undisturbed subarctic mires	NA	10 to 50	Moore (1987*b in* Moore 1989)

1. NA = not available.

habitats, including organic matter in bottom sediments (Boerger 1981). LaPerriere (1983) found a significant positive relationship between concentration (number·volume^{-1}) of invertebrate drift and alkalinity in 13 interior Alaska streams but no significant relationship between alkalinity and chlorophyll *a*. She hypothesized that these findings could be explained if anions of organic acids provided noncarbonate alkalinity, DOC flocculated to form POC, and heterotrophic degradation of POC supported an invertebrate community, although P. H. Glaser (Univ. Minn., pers. commun.) questions anions of organic acids as sources of noncarbonate alkalinity.

Ecologic studies relating fish use to organic C in brownwater taiga systems are virtually absent, but brownwater streams draining BSWs of interior Alaska sometimes support high fish densities, perhaps related to wetland C export acting through food chains or elevated water temperatures. Arctic grayling (*Thymallus arcticus*) spawn and rear at high density in brownwater systems (e.g., Shaw Creek, Tanana River drainage), although clearwater systems provide overwintering and adult feeding habitat; longnose sucker (*Catostomus catostomus*), lake chub (*Couesius plumbeus*), northern pike (*Esox lucius*), and (at least occasionally) rearing coho salmon (*Oncorhynchus kisutch*) also occur at high densities in brownwater systems (W. P. Ridder, Alaska Dep. Fish Game, pers. commun.). Brownwater systems draining to the Tanana River of interior Alaska appear to support high densities of longnose sucker (A. G. Ott, Alaska Dep. Fish Game, pers. commun.).

Functional Summary

Black spruce wetlands with outflows perform the nutrient-export function, but the magnitude of such export is small. Nitrogen and P exports from BSWs to streams and lakes probably are insufficient to alter their generally oligotrophic status, but exported C may support detrital food chains in taiga brownwater streams. Minerotrophic BSWs may export more N and P than do ombrotrophic wetlands. Conversely, ombrotrophic BSWs may export more C than do minerotrophic wetlands, based on data from bogs and fens.

Discharge of water from a BSW indicates some nutrient export. Water stained by DOM specifically indicates C export. Wetland surfaces showing high degrees of decomposition and little accumulation of organic matter (i.e., stagnant peat growth) may indicate greater nutrient export than wetland surfaces showing rapid peat accumulation. In the unlikely event that a BSW exported substantial quantities of N and P, downstream eutrophication clearly associated with wetland discharge might be an indicator of such export.

Functional Sensitivity to Impacts

The nutrient-export function of BSWs is sensitive to placement of fill, although the effects are ambiguous for N and P. Fill would bury sources (e.g., peat, decomposing litter) of C and reduce or eliminate mineralization of N and P in BSWs, but minerotrophic wetlands might continue to export some nutrients by groundwater flow through buried peat. Fill surfaces composed of topsoil or organic matter with high nutrient contents might export more

N and P than an undisturbed BSW. Similarly, uses of fill surfaces that included application of fertilizers or other anthropogenic sources of N and P potentially would increase nutrient export. Flows emanating from fill surfaces and the concentrations of nutrients in those flows might be adjusted to match natural conditions to mitigate impacts of fill on the nutrient-export function of BSWs. Such adjustments are unlikely to be compatible with the purposes for which fills are placed, however.

Drainage of BSWs can, at least temporarily, increase nutrient exports through enhanced aerobic decomposition of peat, although the magnitude of increased nutrient export may be small. Mineralized nutrients and TOC should readily move through drainage ditches to receiving waters. Ditching temporarily increased DOC in bog runoff to 55 mg $C \cdot L^{-1}$ before dropping back to 35 to 43 mg $C \cdot L^{-1}$ at a Quebec site (Moore 1987), and peat mining significantly increased levels of NH_4-N and organic N in bog runoff (Clausen and Brooks 1983*a*). Mitigating the effects of drainage on the nutrient-export function of BSWs appears unlikely.

FOOD CHAIN SUPPORT

Food chain support includes, or is closely related to, primary production and the previously discussed functions of nutrient cycling and nutrient export. Photosynthesis supports secondary production, either directly through the grazing pathway or indirectly through the detrital pathway (Crow and Macdonald 1979, Sather and Smith 1984:21-39). Highly productive (eutrophic) wetlands provide more support to food chains than do upland ecosystems or nutrient-poor (oligotrophic) wetlands (Richardson 1979, Adamus and Stockwell 1983:31, Mitsch and Gosselink 1986:121-123).

Primary Production

Photosynthesis produces carbohydrates (gross primary production) that, if unrespired, accumulate as plant biomass (net primary production), which supports food chains. State factors - topography, time, climate, biota, and soil parent material - condition ecosystem controls to limit net primary production (Van Cleve et al. 1991). Cold, wet taiga sites, such as BSWs, are less productive than warm sites (Van Cleve and Yarie 1986), and fens are more productive than bogs (Boelter and Verry 1977), although biomass may be similar in each (Swanson and Grigal 1991). Vegetation and nutrient availability even may vary within bogs because drainageways and peripheral portions receive greater masses of nutrients than do internal portions (Damman 1987; Zoltai, Tarnocai et al. 1988).

Low temperatures limit photosynthesis and growth in trees. For taiga hardwoods, total root respiration increases with increasing soil temperature; significant growth respiration of roots occurs at 5°C for American green alder, at 15°C and 25°C for balsam poplar, and at all three temperatures for quaking aspen (Lawrence and Oechel 1983*a*). American green alder is the only taiga hardwood that photosynthesizes optimally at the low soil temperatures (Figure 14) characteristic of BSWs.

Cold, wet soils limit black spruce production, as well. Johnson and Vogel (1966) estimated aboveground tree production of black spruce stands in the Yukon Flats at only 310 kg (dry weight)$\cdot ha^{-1} \cdot yr^{-1}$ over the life of the stands, ~30% of paper birch production in the same area. In another study, black spruce production averaged <25% that of taiga hardwoods (Figure 15), with individual black spruce stands producing as little as 570 $kg \cdot ha^{-1} \cdot yr^{-1}$ (Viereck et al. 1983).

Shrubs, herbs, and nonvascular plants also contribute to community production in BSWs, as does the growth of belowground plant structures. Several understory shrubs, for example, contributed 190 $kg \cdot ha^{-1} \cdot yr^{-1}$ to production in a black spruce stand with total vascular plant production of 1,210 $kg \cdot ha^{-1} \cdot yr^{-1}$ (Chapin 1983*a*). Belowground production is difficult to measure, but fine root growth in hummocks and upper portions of hollows in an open Swedish bog respectively produced 510 and 860 $kg \cdot ha^{-1} \cdot yr^{-1}$ as compared to production of 830 and 610 $kg \cdot ha^{-1} \cdot yr^{-1}$ for aboveground vascular plants (Backéus 1990). Comparable values might be expected in BSWs.

Cold, wet, low-nutrient sites can produce more moss than warmer sites (Skre and Oechel 1979), perhaps aided by the long photoperiod of subarctic summer (Li and Glime 1991). Moss in one wetland black spruce stand showed net primary production of 1,257 $kg \cdot ha^{-1} \cdot yr^{-1}$, a level comparable to black spruce (Oechel and Van Cleve 1986). Optimum moisture content (dry weight basis) for photosynthesis in *Sphagnum subsecundum* occurred at 725%, and the moss reached the photosynthetic compensation point

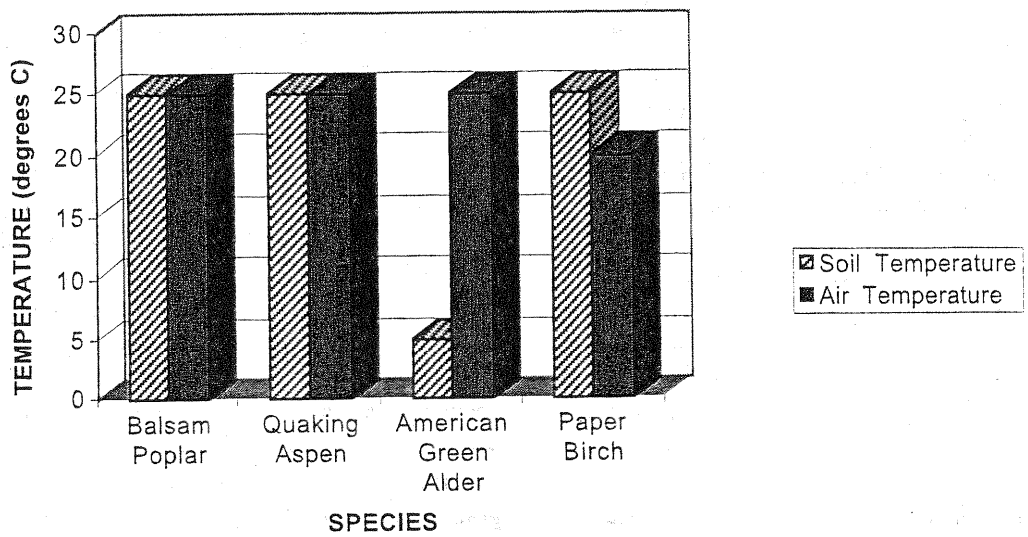

Figure 14. Soil and air temperatures at which maximum photosynthetic rates occurred in seedlings of taiga hardwoods (Lawrence and Oechel 1983b).

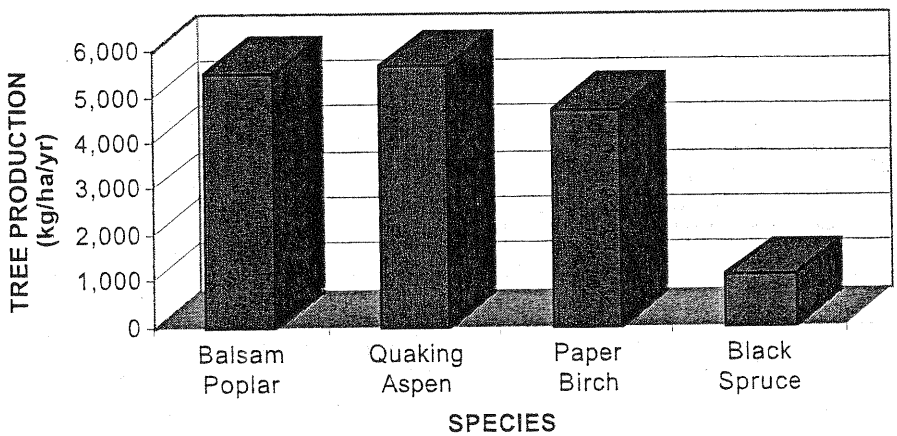

Figure 15. Annual production of taiga trees near Fairbanks, Alaska (Viereck et al. 1983).

after desiccation to 62% moisture (Skre and Oechel 1981). Nevertheless, leaf water content in several moss species can fall from near optimum to below the photosynthetic compensation point in periods as short as 3 days and frequently can be below this point in July (Skre et al. 1983*b*). Among hummock and hollow mosses occurring together, *Sphagnum angustifolium* (a hollow species) had significantly greater growth rates under high moisture conditions than did *S. magellanicum* and *S. fuscum* (hummock species), although the situation reversed during a dry year, when all three species showed less growth (Luken 1985). Low light intensities and lack of moisture also limit photosynthetic rates in *Polytrichum commune* and the feathermosses *Hylocomium splendens* and *Pleurozium schreberi* (Hom 1986).

Community primary production in Alaska's BSWs may reach or exceed 2,000 $kg \cdot ha^{-1} \cdot yr^{-1}$, based on combined aboveground production by black spruce, shrubs, and mosses and belowground production found in similar wetlands. This value is near the lower end of the range of productivities for northern hemisphere mires and far below the productivities of riverine forests (Table 30).

Food Chains

The net primary production of BSWs enters two trophic pathways: grazing (includes browsing) and detrital. Herbivores direct energy contained in living plant tissues to the grazing pathway. Plant species have evolved mechanisms, such as production of antiherbivory compounds, to reduce the impact of grazing on their ability to grow and reproduce.

Nutrient-poor sites such as bogs support stress-adapted, slow-growing, evergreen woody plants (e.g., black spruce and Labrador-tea) known to be unpalatable to vertebrate herbivores and often containing antimicrobial resins that interfere with cecal and rumen digestive functions (Bryant and Kuropat 1980, Bryant 1984:22). Browsing on more palatable early successional species may even favor eventual dominance by less palatable slow-growing evergreen vegetation (Bryant and Chapin 1986). Plants occurring in mature ombrotrophic BSWs thus contain antiherbivory compounds, which should reduce the proportion of community production entering the grazing pathway. The palatability of fast-growing deciduous vegetation in high-nutrient environments (Bryant and Chapin 1986) should act to enhance the relative difference in potential food chain support between BSWs and well-drained uplands.

Nutrient-poor wetlands generally support few herbivorous species, particularly large vertebrates (Mason and Standen 1983, Speight and Blackith 1983). Nevertheless, moose (*Alces alces*), barren-ground caribou (*Rangifer tarandus granti*), snowshoe hare (*Lepus americanus*), spruce grouse (*Dendragapus canadensis*), fruit- and seed-eating songbirds, and rodents potentially feed in BSWs.

Table 30. Comparative production of selected wetland communities and community components.

Site Type and Location	Community Component	Production ($kg \cdot ha^{-1} \cdot yr^{-1}$)	Source
Patterned fen - Quebec	Flark pools	70	Moore (1989)
Patterned fen - Quebec	Strings	930	Moore (1989)
Muskeg - Manitoba	Trees	720	Reader and Stewart (1972 *in* Brown 1990)
Bog forest - Manitoba	Trees	3,030	Reader and Stewart (1972 *in* Brown 1990)
Shrub fen - Michigan	Entire community	3,400	Richardson (1979)
Mires - northern hemisphere	Entire community	3,000 to 10,000	Bradbury and Grace (1983)
Riverine forests	Entire community	6,850 to 21,360	Brinson (1990)

With the exception of spruce grouse and snowshoe hare, which sometimes feed on black spruce, boreal vertebrate herbivores neither consume appreciable quantities of black spruce (Ellison 1976, Wolff 1978*a*, Bryant and Kuropat 1980) nor consume mosses, the two major producers of biomass in ombrotrophic BSWs. Vertebrate herbivores do consume shrubs, herbs, lichens, fruits, and seeds (including those of black spruce) occurring in BSWs, however (e.g. Skoog 1968:137-147, Coady 1982, Gasaway et al. 1983:23-24).

Invertebrate herbivores occupying BSWs also direct primary production to the grazing food chain. Black spruce stands of interior Alaska support many taxa of herbivorous arthropods (Figure 16). The trophic structure of their arthropod faunas should broadly resemble those of BSWs.

Fens often support greater numbers of vertebrates (in particular, herbivores) than do bogs (Speight and Blackith 1983), perhaps because fens have more nutrients and often support graminoid vegetation. Graminoids, although sometimes containing antiherbivory compounds in low-nutrient environments, have adapted to disturbance by maintaining belowground reserves of C and producing nutritious shoots in response to grazing (Bryant et al. 1983). Barren-ground caribou, moose, rodents, and birds (e.g., waterfowl) consume vegetation characteristic of fens (e.g., Coady 1982, White et al. 1975, Lacki et al. 1990). Thus, herbivores may consume a greater proportion of available biomass in minerotrophic than in ombrotrophic BSWs.

The detrital pathway accounts for most energy flow in ecosystems (Krebs 1972:497), and respiration by decomposer organisms greatly exceeds that by herbivores in bogs (Mitsch and Gosselink 1993:404-407). Tundra peatland communities, known to share many similarities with those of the taiga (Kummerow et al. 1983), support few herbivorous taxa (Batzli et al. 1980) and directly contribute ~80% of their primary production to the detrital pathway in the form of dead (unconsumed) vegetation (MacLean 1980). Black spruce wetlands may contribute a similar proportion of their primary production to the detrital pathway, but relative vertebrate biomasses supported by grazing and detrital

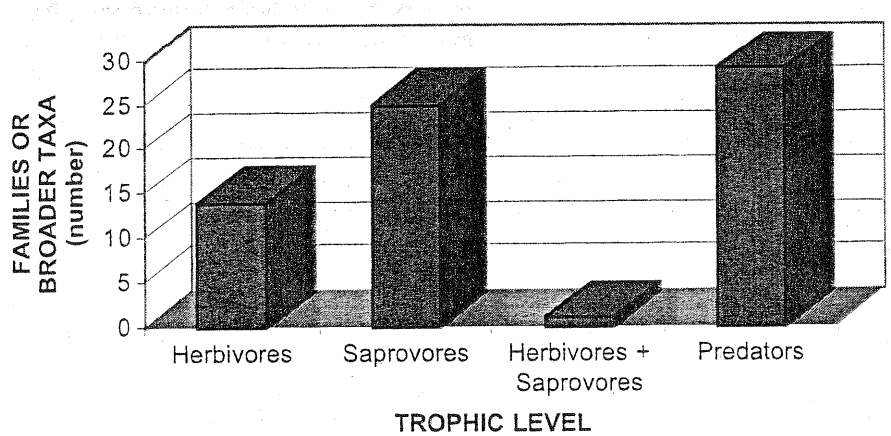

Figure 16. Distribution of aboveground arthropod taxa among trophic levels in black spruce stands of interior Alaska (Werner 1983).

pathways in BSWs apparently have not been documented. The detritus-based food chain may be important to taiga birds, however (P. D. Martin, U.S. Fish Wildl. Serv., pers. commun.).

Organic layer respiration by microbes, invertebrate ***microbivores*** (organisms feeding on algae, bacteria, or fungi [MacLean 1980]), and invertebrate ***saprovores*** (organisms directly consuming decaying organic matter) indicates energy flow in the detrital pathway. In tundra systems, microbivores account for a greater proportion of soil faunal biomass than do saprovores, but the reverse is true in many forest ecosystems (MacLean 1980). Over two seasons, the organic layer of a black spruce stand (probably nonwetland) respired 1,345 and 1,358 g $CO_2 \cdot m^{-2}$, generally slightly less than those of comparable aspen, birch, and white spruce stands (Schlentner and Van Cleve 1985).

The degree of similarity between the soil invertebrate faunas of European blanket bogs and Alaskan tundra (Table 31) suggest a similar fauna for BSWs. Some soil invertebrates of BSWs, as well as arthropod saprovores and predators in aboveground vegetation (Figure 16), should be vulnerable to vertebrate predation and thus support higher trophic levels of detrital food chains. At least ten species of insectivorous and partially insectivorous birds (Gabrielson and Lincoln 1959) are present in BSWs, as are small mammals (e.g., shrews) that feed on invertebrates.

The margins of taiga ponds occurring within BSWs may provide warm littoral microenvironments conducive to decomposition and support of detrital food chains, including a wide variety of insectivorous birds (P. D. Martin, U.S. Fish Wildl. Serv., pers. commun.), but energy flows in these environments apparently have received little or no study. Annual rates of primary and secondary production in BSWs may be less important to birds than are brief pulses of production occurring during the nesting season (P. D. Martin, U.S. Fish Wildl. Serv., pers. commun.). Although more energy flows to invertebrate carnivores than to vertebrate carnivores (primarily insectivorous birds) in Alaskan tundra systems (MacLean 1980), relative energy flows in BSWs are unknown.

Functional Summary

Black spruce wetlands support grazing and detrital food chains, which merge at higher trophic levels. Ombrotrophic to weakly minerotrophic BSWs have low net primary production (i.e., potential energy available to consumers) and unpalatable plants resistant to decomposition, which should reduce energy flow in grazing and detrital pathways. In contrast, moderately to strongly minerotrophic BSWs have elevated base element concentrations and moderate pH values that favor enhanced net primary production by graminoid vegetation adapted to grazing. Such vegetation potentially decomposes more quickly than ericaceous vegetation of ombrotrophic wetlands and probably increases energy flow in grazing and detrital pathways. Although the food-chain support function of BSWs, measured by community production, is lower than that of well-drained taiga uplands, it is essential to organisms limited to wetland environments. In addition, BSWs cover immense areas of interior Alaska and, in aggregate, substantially contribute to energy flow in taiga landscapes.

Minerotrophy may indicate the magnitude of the food chain-support function of BSWs and can be determined by analysis of hydrology, water chemistry (conductivity, alkalinity, pH), or vegetation

Table 31. Common soil invertebrates found in European blanket bogs and Alaska tundra.

Site Type and Location	Oligochaeta (Enchytraeidae)	Diptera (Tipulidae)	Acari	Nematoda	Collembola	Source
Blanket bogs - United Kingdom	Yes	Yes	Yes	Yes	Yes	Mason and Standen (1983)
Tundra - Alaska	Yes	Yes	Yes	Yes	Yes	MacLean (1980)

(Swanson and Grigal 1989). Observation of animal use (e.g., browsed shrubs, fecal pellets, tracks, bird calls, visual sitings) or the presence of preferred food items for herbivores also indicate food chain support. In those few cases where rates of net primary production are known, higher production indicates greater food chain-support function, all other factors being equal.

Functional Sensitivity to Impacts

The food chain-support function of BSWs is sensitive to placement of fill, which eliminates primary production and thus the grazing pathway of energy flow. Buried organic matter generally will not provide energy to the detrital pathway even if anaerobic fermentation continues beneath fill surfaces. Barren fill eliminates energy flow to higher trophic levels.

Re-establishment of vegetative cover, particularly that emulating the undisturbed wetland, could mitigate the effects of fill placement on food chains but is unlikely to be compatible with fill purposes. For "out-of-kind" revegetation, plant species should be chosen for palatability to nonwetland herbivores. Addition of organic material to fill surfaces would provide a source of nutrients via mineralization and might enhance establishment of detrital food chains.

The food chain-support function of BSWs is much less sensitive to drainage than to fill placement. Drainage may increase net primary production, particularly that of trees. Drained minerotrophic wetlands can become ombrotrophic, community production decline, and species composition change to favor unpalatable evergreen trees and shrubs, potentially reducing energy flow in the grazing pathway. Increased decomposition in drained BSWs would increase energy flow through the detrital pathway, perhaps offsetting declines in the grazing pathway. Despite these somewhat unpredictable changes, the basic processes of primary production, herbivory, decomposition, and predation can proceed in a drained wetland.

Habitat manipulation might be used to mitigate shifts in dominance by plant species and potential losses in productivity in drained BSWs. Controlled burning, for example, could prevent shifts from graminoids to woody vegetation. Nutrient release by fire potentially would increase net primary production in drained forested wetlands, possibly enhancing food chain support.

HABITAT

Wetlands provide habitat for plants and animals, including fish and wildlife species of socioeconomic and ecologic significance (Weller 1979, Adamus and Stockwell 1983:38-45, Sather and Smith 1984:40, Mitsch and Gosselink 1986:393-399). Although often associated with waterfowl and furbearers such as beaver and muskrat (Mitsch and Gosselink 1986:394-395), wetlands also support other biologically-important species such as nongame birds (Kroodsma 1979), invertebrates and cold-blooded vertebrates (Sather and Smith 1984:43-44), threatened and endangered species (Mitsch and Gosselink 1986:398), and terrestrial mammals such as moose that use wetlands on a seasonal basis (Weller 1979).

Birds

Avian habitats do not necessarily coincide with subdivisions of the environment (e.g., BSWs, specific plant communities) defined by humans. Waterfowl, for example, use temporarily flooded palustrine wetlands when ponds and lakes are still frozen in early spring (P. D. Martin, U.S. Fish Wildl. Serv., pers. commun.) but may shift preferences during nesting, brood rearing, and foraging. Defining the boundaries of BSWs with respect to avian habitats is difficult and somewhat arbitrary, particularly when considering included or adjacent waterbodies (e.g., patterned fens, bog or fen lakes, thermokarst ponds) whose hydrology, chemistry, and productivity may be influenced by such wetlands.

This profile discusses habitat use by waterbirds and shorebirds that occupy included or adjacent waterbodies as well as habitat use by birds directly occupying black spruce communities. Appendix D interprets community descriptions in avian surveys with respect to BSWs or habitats sharing common characteristics with BSWs. Taxonomic binomials for avian species appear in Tables 32 through 35.

Waterbird use of mires, or waterbodies having characteristics indicative of mires (e.g., floating peat mats, common mire plants), provides evidence for potential association with BSWs (Table 32). Species recorded as breeding on, or adjacent to, taiga mire waterbodies in Alaska include Pacific loon, tundra and trumpeter swans, green-winged teal, mallard, northern pintail, northern shoveler, American wigeon, greater and lesser scaup, white-winged scoter, mew and Bonaparte's gulls, and arctic tern. Al-

though not recorded as breeders, common loon, horned and red-necked grebes, lesser Canada goose, ring-necked duck, common and Barrow's goldeneyes, bufflehead, and glaucous-winged and herring gulls also occurred on mire waterbodies and are moderately probable to be associated with BSWs. Other waterbirds using taiga ponds, lakes, and marshes (Table 32) may or may not be associated with BSWs.

Birds of prey directly use BSWs for hunting and sometimes nesting (Table 33). Black spruce wetlands present a range of structural and trophic characteristics that offer potential habitat to most avian predators occupying taiga landscapes. The northern harrier, northern hawk owl, great gray owl, short-eared owl, and boreal owl have a high probability of nesting in BSWs. The American peregrine falcon and great horned owl nest elsewhere but are highly likely to hunt in (or above) BSWs. These wetlands are moderately probable hunting habitat for the bald eagle, sharp-shinned hawk, northern goshawk, red-tailed hawk, rough-legged hawk, American kestrel, and merlin.

Among nonpasserine birds of Alaska taiga other than waterbirds and raptors (Table 34), the spruce grouse, sandhill crane, greater and lesser yellowlegs, solitary sandpiper, Hudsonian godwit, least sandpiper, short-billed dowitcher, common snipe, red-necked phalarope, three-toed woodpecker, black-backed woodpecker, and northern flicker have a high probability of nesting in BSWs. Sharp-tailed grouse and upland sandpipers have a moderate probability of nesting in BSWs. Willow ptarmigan and ruffed grouse are moderately likely to forage in such wetlands but do not nest in them.

A significant number of Alaska's taiga passerines (Table 35) have a high probability of nesting in BSWs: olive-sided flycatcher; western wood-pee-wee; alder flycatcher; tree swallow; gray jay; boreal chickadee; ruby-crowned kinglet; gray-cheeked and Swainson's thrushes; American robin; varied thrush; Bohemian waxwing; orange-crowned, yellow-rumped, and blackpoll warblers; American tree, chipping, savannah, fox, song, Lincoln's, and white-crowned sparrows; dark-eyed junco; rusty blackbird; pine grosbeak; white-winged crossbill; and common redpoll. Violet-green and bank swallows and the common raven nest elsewhere but are highly likely to forage in BSWs. Species with a moderate probability of nesting in BSWs are northern shrike, Wilson's warbler, and golden-crowned sparrow. Cliff swallows and black-capped chickadees are moderately likely to forage in these wetlands.

Although many avian species use BSWs, or some subset thereof, the magnitude of such use is a function of species distribution and abundance and strength of species association with such wetlands. The probabilities presented in Tables 32 through 35 show that BSWs provide habitat for a substantial number of avian species. These probabilities do not take bird abundance and distribution into account and thus do not necessarily reflect the constellation of birds likely to be encountered in the average BSW. For example, the Hudsonian godwit is strongly associated with BSWs (P.D. Martin, U.S. Fish Wildl. Serv., pers. commun.) but is rare in Alaska taiga; therefore a given BSW has a low probability of use by godwits.

Several investigators have structured their avian surveys to identify birds commonly found in habitats that can be interpreted with respect to BSWs. Table 36 lists birds regularly found in, and dependent upon, BSWs. Species occurring at low densities, such as widely spaced predators, or species associated with a wide variety of plant communities appear in Tables 32 through 35 but may not appear in Table 36.

Dark-eyed juncos frequently are the most abundant breeders in BSWs of interior Alaska (Spindler 1976, Spindler and Kessel 1980). White-crowned sparrow, common snipe, yellow-rumped warbler, lesser yellowlegs, ruby-crowned kinglet, gray-cheeked thrush, American robin, Swainson's thrush, gray jay, Bohemian waxwing, and savannah sparrow are among the consistently occurring species in these wetlands (Table 36).

Mammals

Black spruce forest and woodland covers much of interior and southern Alaska below treeline. Species of mammals occupying black spruce forest, post-fire seres sharing structural characteristics with shrubby wetlands, and some palustrine emergent wetlands potentially occur in BSWs as well. Taxonomic binomials for common names of mammals appear in Tables 37 through 39.

Small insectivorous and herbivorous mammals are among the most characteristic mammals of

BSWs (Table 37). The common, pygmy, dusky, and northern water shrews; red squirrel; meadow jumping mouse; northern red-backed, tundra, meadow, and yellow-cheeked voles; northern bog lemming; porcupine; and snowshoe hare all are highly probable to breed and forage in BSWs. Species with a moderate probability of breeding and foraging in BSWs are beaver, brown lemming, and muskrat. In the case of beaver and muskrat, however, the association may be largely coincidental (D.K. Swanson, Nat. Resour. Conserv. Serv., pers. commun.). Little brown bats are moderately likely to forage over BSWs.

Carnivores (Table 38) feed on the insectivores and small herbivorous mammals occurring in these wetlands. Lynx, wolverine, marten, ermine, least weasel, mink, and black bear are highly probable to breed and forage in BSWs, and coyote, wolf, red fox, and brown bear are highly probable to forage in such wetlands but may den elsewhere. Other carnivores are unlikely to use BSWs.

Of Alaska's two large indigenous taiga herbivores (Table 39), the moose is highly likely to breed and forage in some types of BSWs and the caribou is highly likely to use BSWs as winter range. Characteristic black spruce communities of interior Alaska (Foote 1983) contain little moose browse; thus, unbroken expanses of mature black spruce forest, including treed wetlands, provide poor habitat for moose. The moose habitat function of BSWs depends, in part, on community composition, structure, successional state, and diversity, factors poorly defined by "BSW." The value of BSWs as winter range for caribou largely is a function of the presence of preferred lichens and herbaceous vegetation, but black spruce helps maintain low-density snow conditions favorable for caribou feeding.

The probabilities presented in Tables 37 through 39 are those that a species at least occasionally uses BSWs but are not the probability that a species will be found in a given BSW. Small mammals and furbearers are the really characteristic species of BSWs. Table 40 presents those species judged to be consistently present in most BSWs, although the frequency with which they are encountered varies with their typical areal density.

Amphibians

The environmental conditions of interior Alaska are hostile to reptiles and amphibians (e.g., Hodge 1976:17-19). Only a single species, the wood frog (*Rana sylvatica*), represents these ***ectothermic*** vertebrate classes in the Interior (Kessel 1965, Hodge 1976:54-56). Wood frogs are distributed across boreal North America from Alaska, where their range extends northward to the Brooks Range (Hock 1956 *in* Hadley 1969:1), to Labrador and south along the Appalachian Mountains (Conant 1958: 303,352). The wood frog's life cycle presents three potential opportunities for using BSW habitats: breeding, foraging, and hibernation.

Wood frogs breed and deposit egg masses in clumps in warm microenvironments within breeding ponds (Seale 1982). In Alaska, synchronous breeding occurs as soon as air temperature rises above 0°C, surficial soils thaw, and open water develops (Kessel 1965, Kirton 1974:36, Waldman 1982). Communal aggregates of egg masses exhibit elevated internal temperatures as compared to surrounding water (Herreid and Kinney 1967, Seale 1982, Waldman 1982), which causes central (warmer) egg masses to hatch more successfully than peripheral masses (Waldman 1982). Warm microenvironments also increase fertilization rates (Herreid and Kinney 1967) and, in bogs, increase hatching success (Karns 1992). The thermal characteristics of highly-colored, solar-heated ponds or drainages in ombrotrophic wetlands would seem to favor wood frog reproduction but are offset by low pH (Table 41). Bogs are suboptimal breeding habitat as compared to poor fens and fens.

Wood frogs occupy moist wooded areas, often far from water (Conant 1958:303, pers. observ.). Post-breeding habitat use of terrestrial areas by wood frogs apparently has not been studied in interior Alaska, although frogs occurred in a birch-aspen woodland prior to entering hibernation (Kirton 1974:2-4). For frogs breeding in bogs and fens, at least transitory use of terrestrial mire habitats must occur during movements from hibernacula to breeding sites and from breeding sites to terrestrial foraging areas. Similar use of BSWs is likely.

Wood frogs overwinter in leaf litter by supercooling and tolerating extracellular freezing (Storey and Storey 1984). In interior Alaska, Kirton (1974:3-31) located frog hibernacula near waterbodies (mean distance = 8.2 m). Overwinter survival of juvenile frogs was greater in dry than in damp hibernacula.

Table 32. Use of aquatic habitats potentially associated with black spruce wetlands (BSW) by waterbirds (loons, grebes, waterfowl, gulls, and terns) in Alaska.

Species	Abundance in Alaska Taiga (Common, Uncommon, Rare, Casual/ Accidental)	Habitat Use (Breeding or Potentially Breeding = B, Generally Occurring or Unspecified Use = O) and Preference When Tested (Selected = [+], Neutral = [0], Avoided = [-])			Probability Species Uses Aquatic Habitats Associated with BSW (Low = L, Medium = M, High = H)
		Mire Lakes and Ponds	Freshwater Marsh and Open Water	Tundra or Taiga Lakes and Ponds	
Red-Throated Loon (*Gavia stellata*)	U[7,15]			O[1,2], B[3,7,8]: [+] small ponds[8]	L: few data, low density
Pacific Loon (*Gavia pacifica*)	C[7], U[15] near upper Susitna	B[4,5]: [0] only use larger waterbodies[5]	B[5]: [0] herb marsh, [+] sedge marsh	O[1,2], B[7,15]	H: larger waterbodies
Common Loon (*Gavia immer*)	C[7], U[15] near upper Susitna	O[6]: [+] low pH and conductivity	B[17]	O[1,2,10], B[3,5,7,15]	M: few data
Pied-Billed Grebe (*Podilymbus podiceps*)	A[7] in southcoastal only	O[6]: [+] bogs	O[6], B[17]		L: accidental occurrence
Horned Grebe (*Podiceps auritus*)	C[7], U[15] near upper Susitna	O[4,5,9,16]: [-] only use larger waterbodies[5]	B[5,17]	O[11,12], B[3,5,7,10,15,16]	M: minerotrophic waterbodies
Red-Necked Grebe (*Podiceps grisegena*)	C[7], U[15] near upper Susitna	O[4]	O[4,5], B[17]	O[11,12], B[3,5,7,10,15,16]	M: minerotrophic waterbodies
Tundra Swan (*Cygnus columbianus*)	U[7]	B[13]: taiga-tundra ecotone[13] with mire vegetation[14]		O[15], B[7]	H: in forest-tundra
Trumpeter Swan (*Cygnus buccinator*)	C[15]	B[21]: lakes with fen vegetation[19,20,21] in needleleaf forest[18]		O[3,10]: [+] low Ca lakes[3] B[3,5,7,13,15]	H: in major breeding areas
Greater White-Fronted Goose (*Anser albifrons*)	U[7,19]			O[3]: [+] low Ca lakes B[3,5,7,19]	L
Lesser Canada Goose (*Branta canadensis parvipes*)	C[7]	O[4]		O[3,10,19]: [+] low Ca lakes[3], uses "muskeg"[19] B[3,5,7]	M

Table 32 (Cont'd). Use of aquatic habitats potentially associated with black spruce wetlands (BSW) by waterbirds (loons, grebes, waterfowl, gulls, and terns) in Alaska.

Species	Abundance in Alaska Taiga (Common, Uncommon, Rare, Casual/ Accidental)	Habitat Use (Breeding or Potentially Breeding = B, Generally Occurring or Unspecified Use = O) and Preference When Tested (Selected = [+], Neutral = [0], Avoided = [-])			Probability Species Uses Aquatic Habitats Associated with BSW (Low = L, Medium = M, High = H)
		Mire Lakes and Ponds	Freshwater Marsh and Open Water	Tundra or Taiga Lakes and Ponds	
Green-Winged Teal (*Anas crecca*)	C[7], U[15] near upper Susitna	B[3,4,5,16]: [0] thaw ponds and larger waterbodies[5]	B[5,17]: [0] herb and sedge marshes[5]	B[3,5,7,10,11,15,16,22,23]	H: broad trophic tolerance
Mallard (*Anas platyrhynchos*)	C[7], U[15] near upper Susitna	B[3,4,5]: [-] only use larger waterbodies[5]	B[5,17]: [0] herb marsh, [+] sedge marsh[5]	B[3,5,7,10,11,15,22,23]	H: minerotrophic waterbodies
Gadwall (*Anas strepera*)	R[7]		B[7,17]	O[3,15]	L: low density
Northern Pintail (*Anas acuta*)	C[7], U[15] near upper Susitna	B[3,4,5,16]: [-] only use larger waterbodies[5]	B[5,17]: [0] herb and sedge marshes[5]	B[3,5,7,10,11,15,22,23]	H: minerotrophic waterbodies
Blue-Winged Teal (*Anas discors*)	R[7,24]		B[17]	B[3,5,7]	L: low density
Northern Shoveler (*Anas clypeata*)	C[7], U[15] near upper Susitna	B[3,4,5]: [-] only use larger waterbodies[5]	B[5,17]: [0] herb and sedge marshes[5]	B[3,5,7,10,11,15,22,23]	H: minerotrophic waterbodies
American Wigeon (*Anas americana*)	C[7,15]	B[3,4,5]: [0] thaw ponds, [-] larger waterbodies[5]	B[5,17]: [+] herb and sedge marshes[5]	B[3,5,7,10,11,15,22,23]	H: broad trophic tolerance
Canvasback (*Aythya valisineria*)	U[7]		B[5,17]: [-] herb marsh, [0] sedge marsh[5]	B[3,5,7]	L: low density
Redhead (*Aythya americana*)	R[7]		B[17]	B[3,5,7]	L: low density
Ring-Necked Duck (*Aythya collaris*)	U[7]	O[5,17]: bogs[17]	O[5], B[17]	B[3,5,7,10,23]	M: low density
Greater Scaup (*Aythya marila*)	C[7,15]	O[4], B[3,5]: [-] thaw ponds and larger waterbodies[5]	B[5,17]: [+] herb and sedge marshes[5]	B[3,5,7,10?,15,23?]	H: minerotrophic waterbodies
Lesser Scaup (*Aythya affinis*)	C[7,15]	B[3,5]: [-] thaw ponds and larger waterbodies[5]	B[5,17]: [+] herb and sedge marshes[5]	B[3,5,7,10?,15,23]	H: minerotrophic waterbodies

Table 32 (Cont'd). Use of aquatic habitats potentially associated with black spruce wetlands (BSW) by waterbirds (loons, grebes, waterfowl, gulls, and terns) in Alaska.

Species	Abundance in Alaska Taiga (Common, Uncommon, Rare, Casual/ Accidental)	Habitat Use (Breeding or Potentially Breeding = B, Generally Occurring or Unspecified Use = O) and Preference When Tested (Selected = [+], Neutral = [0], Avoided = [-])			Probability Species Uses Aquatic Habitats Associated with BSW (Low = L, Medium = M, High = H)
		Mire Lakes and Ponds	Freshwater Marsh and Open Water	Tundra or Taiga Lakes and Ponds	
Common Goldeneye (*Bucephala clangula*)	C[7], U[15] near upper Susitna	O[5]: only use larger waterbodies[5]	O[5], B[17]	B[3,5,7,10,15]	M: cavity nester[7]
Barrow's Goldeneye (*Bucephala islandica*)	C[7], U[15] near upper Susitna	O[5]: only use larger waterbodies[5]	B[17]	B[3,5,7,15]	M: cavity nester[7]
Bufflehead (*Bucephala albeola*)	C[7]	O[4,5]: only use larger waterbodies[5]	B[5,17]	B[3,5,7]	M: cavity nester[7]
Oldsquaw (*Clangula hyemalis*)	C[7,15]			O[10], B[3,5,7,15]	L
White-Winged Scoter (*Melanitta fusca*)	C[7]	B[5]: [-] only use larger waterbodies, [0] by post-breeders[5]	B[5,17]: [-] herb marsh, [0] sedge marsh[5]	B[3,5,7]	H: minerotrophic waterbodies
Surf Scoter (*Melanitta perspicillata*)	C[7], U[15] near upper Susitna		O[5], B[17]	B[3,5,7,15]	L: few data
Black Scoter (*Melanitta nigra*)	A[7], C[15] near upper Susitna			B[7,15]	L: few data, limited distribution
Common Merganser (*Mergus merganser*)	R[7], U[15] near upper Susitna			B[7]	L: few data, not abundant
Red-Breasted Merganser (*Mergus serrator*)	R[7], U[15] near upper Susitna		O[5]	O[10,15], B[3,7]	L: few data, low density
Glaucous-Winged Gull (*Larus glaucescens*)	R[7]	O[4]			M: low density

Table 32 (Cont'd). Use of aquatic habitats potentially associated with black spruce wetlands (BSW) by waterbirds (loons, grebes, waterfowl, gulls, and terns) in Alaska.

Species	Abundance in Alaska Taiga (Common, Uncommon, Rare, Casual/ Accidental)	Habitat Use (Breeding or Potentially Breeding = B, Generally Occurring or Unspecified Use = O) and Preference When Tested (Selected = [+], Neutral = [0], Avoided = [-])			Probability Species Uses Aquatic Habitats Associated with BSW (Low = L, Medium = M, High = H)
		Mire Lakes and Ponds	Freshwater Marsh and Open Water	Tundra or Taiga Lakes and Ponds	
Herring Gull (*Larus argentatus*)	U[7]	O[4]	B[6]		M: nests on gravel bars[28]
Mew Gull (*Larus canus*)	C[7,15]	B[4,16,25]		B[7,10,11,15,25]	H: ground and tree (spruce) nester[26,28]
Bonaparte's Gull (*Larus philadelphia*)	U[7,15]	B[4]		O[27], B[7,10,11,15]	H: nests in low conifers[7,15,26]
Arctic Tern (*Sterna paradisaea*)	U[7], C[15] near upper Susitna	B[4]	B[7]	O[10], B[15]	H: low density

1. Gabrielson and Lincoln (1959)
2. Lanctot and Quang (1992)
3. Heglund (1988)
4. Hogan and Tande (1983)
5. Heglund (1992)
6. Gibbs et al. (1991)
7. Armstrong (1990)
8. Davis (1972 *in* Johnson and Herter 1989)
9. Gillespie and Kendeigh (1982)
10. Martin et al. (1995)
11. West and DeWolfe (1974)
12. Manuwal (1978)
13. Wilk (1993)
14. Talbot et al. (1986)
15. Kessel et al. (1982)
16. Spindler (1976)
17. Erskine (1977)
18. U.S. Fish Wildl. Serv. (1987)
19. Bellrose (1980)
20. McKelvey et al. (1983)
21. Hansen et al. (1971)
22. Spindler and Kessel (1980)
23. Murphy et al. (1984)
24. Kessel and Springer (1966)
25. Burger and Gochfeld (1988)
26. Murie (1963)
27. White and Haugh (1969)
28. J. Wright, Alaska Dep. Fish Game, pers. commun.

Table 33. Use of black spruce wetlands (BSW) in Alaska by raptorial birds (hawks, eagles, harriers, ospreys, falcons, and owls).

Species	Abundance in Alaska Taiga (Common, Uncommon, Rare, Casual/ Accidental)	Habitat Use (Breeding or Potentially Breeding = B, Foraging = F, Generally Occurring or Unspecified Use = O) and Preference When Tested (Selected = [+], Neutral = [0], Avoided=[-])					Prey Occurs in BSW (Insects = I, Fish = F, Birds = B, Mamm. = M)	Probability Species Uses BSW (Low = L, Medium = M, High = H)
		Nonwetlands or Mixed Wetlands and Nonwetlands			Wetlands			
		Shrub	Mixed Taiga Landscape	Black Spruce	Mires	Other		
Osprey (*Pandion haliaetus*)	R[1]: locally abundant[2]		B[1,2]: shorelines (primarily lakes[2])		O[21]: [-] "bogs"		F[1]	L: hunting, near nests
Bald Eagle (*Haliaeetus leucocephalus*)	U[1,16], C[1] in southcoastal		B[1,16]: large trees, cliffs on rivers and shorelines		O[18,21]: [-] "bogs"[21]		F[1]: largely scavenger[1]	M: foraging, near nests
Northern Harrier (*Circus cyaneus*)	U[1,16]: abundant migrant[7,23]	O[7]	B[1,3,16,22]: nests on ground in open country, wetlands, meadows, moorland and heath (Europe), scrub woodland	B[3]	O[12,21]: black spruce[12], [+] "bogs"[21] B[11,15,18,22,24]: fens[15], bogs[11,22,24]	O[16,21]: BSW[16], [+] shrub swamps[21] B[3,22]: emergent	B,M[22,25]: hunts near ground[10,22]	H: hunting, breeding, sparsely treed BSW
Sharp-Shinned Hawk (*Accipiter striatus*)	C[1], U[16] near upper Susitna	F[14]	B[1,3,11,13,14,15,16]: nests near open areas in mixed, coniferous, and deciduous forest	B[11]	O[12]: black spruce			M: hunting, scrub- shrub BSW
Northern Goshawk (*Accipiter gentilis*)	U[1,16]: numbers follow prey density[2]		O[5,6,7], F[3,10]: woodlands, edges, willow, alder B[1,8,16]: often nest in birch in mixed, deciduous, and coniferous forest	O[9]	F[3]: "bogs"	O[4]: forested wetlands (Europe)	B,M[3,9,10,11]	M: hunting habitat, scrub-shrub and forested BSW
Swainson's Hawk (*Buteo swainsoni*)	R[1]: very rare (Taylor Highway)[20]		O[17,20]: scattered woodland and dwarf forest near treeline[20]					L: few data

Table 33 (Cont'd). Use of black spruce wetlands (BSW) in Alaska by raptorial birds (hawks, eagles, harriers, ospreys, falcons, and owls).

Species	Abundance in Alaska Taiga (Common, Uncommon, Rare, Casual/ Accidental)	Habitat Use (Breeding or Potentially Breeding = B, Foraging = F, Generally Occurring or Unspecified Use = O) and Preference When Tested (Selected = [+], Neutral = [0], Avoided=[-])					Prey Occurs in BSW (Insects = I, Fish = F, Birds = B, Mamm. = M)	Probability Species Uses BSW (Low = L, Medium = M, High = H)
		Nonwetlands or Mixed Wetlands and Nonwetlands			Wetlands			
		Shrub	Mixed Taiga Landscape	Black Spruce	Mires	Other		
Red-Tailed Hawk (*Buteo jamaicensis*)	C[1]: relatively abundant[2] U[16] near upper Susitna		F[1,17]: generalist, dense spruce, open areas B[1,15,16,17]: tree and cliff nester, mixed and coniferous forest	F[17]	O[18]		B,M[10,17,19]	M: hunting habitat, scrub-shrub and forested BSW
Rough-Legged Hawk (*Buteo lagopus*)	U[1]: common migrant		F[17]: clearings B[1,10,17,19]: cliff and tree nester, alpine tundra and western taiga		F[17]: open "bogs"		B,M[10,17,19]	M: hunting, sparsely treed BSW
American Kestrel (*Falco sparverius*)	C[1]		O[5,26], B[1,2,10,15,17]: cavity nester, open woodlands, edges, burns, openings, and meadows	O[12]				M: hunting, sparsely treed BSW
Merlin (*Falco columbarius*)	U[1,16]		O[27], B[1,2,15,16,17]: conifers, scattered woodland and dwarf forest, edges, burns, openings	O[1,28]				M: hunting, sparsely treed BSW
American peregrine falcon (*Falco peregrinus anatum*)	C[2] in preferred nesting habitat		F[2,17]: lakes, streams, all taiga bird habitats[2] B[1,2,29]: cliffs along rivers		B[17]: bog hummocks (Finland)		B[30,31,54]: lesser yellowlegs, gray jays are major summer prey	H: hunting, all BSW
Great Horned Owl (*Bubo virginianus*)	C[1], U[16] near upper Susitna	F[33]	O[12,26], F[33], B[1,2,7,15,32,33]: cliffs and old stick nests, coniferous and deciduous forest, edges, scrub-shrub, habitat generalist		B[24]: bogs	F[33]: emergent	B[10,35], M[10,34,35,36]	H: hunting, all BSW
Northern Hawk Owl (*Surnia ulula*)	C[1], U[16] near upper Susitna	F[35], O[26]	O[5,7,39], B[1,10,15,16,32,33,35,37,38]: snag nester, open mixed or coniferous forest near marshes or clearings, low scrub	B[10,33,35]	F[35,39]: *Sphagnum*[35], black spruce[39]	O[27]: BSW	I,B,M[10,33,35,39]	H: hunting, breeding, all BSW

Table 33 (Cont'd). Use of black spruce wetlands (BSW) in Alaska by raptorial birds (hawks, eagles, harriers, ospreys, falcons, and owls).

Species	Abundance in Alaska Taiga (Common, Uncommon, Rare, Casual/ Accidental)	Habitat Use (Breeding or Potentially Breeding = B, Foraging = F, Generally Occurring or Unspecified Use = O) and Preference When Tested (Selected = [+], Neutral = [0], Avoided=[-])					Prey Occurs in BSW (Insects = I, Fish = F, Birds = B, Mamm. = M)	Probability Species Uses BSW (Low = L, Medium = M, High = H)
		Nonwetlands or Mixed Wetlands and Nonwetlands			Wetlands			
		Shrub	Mixed Taiga Landscape	Black Spruce	Mires	Other		
Great Gray Owl (*Strix nebulosa*)	R[1]		O[7,42]: poplar, white spruce along watercourses in wetland landscape[42] F[41]: [-] dense shrubs B[1,15,33]: nests on stubs or in raven nests, coniferous and deciduous forest near "muskeg", bogs, edges	F[40,41]: [-] pure stands[41]	F[41]: [+] mixed grass and moss ground cover B[24,40]: bogs[24], black spruce and/or tamarack[40] (may include meadows[45])		B,M[38,40,42,43,44]: rodent specialist	H: hunting, sparsely treed BSW with graminoids
Short-Eared Owl (*Asio flammeus*)	C[1], U[16] near upper Susitna	O[16]	O[5,7], B[1,10,35]: ground nester in open habitats, wetlands, similar to northern harrier	B[1]	B[15,18,33,47]: shrub[15], "bogs"[33,47]	F[10,35,50], B[46]: sedge meadow	M[33,35, 46,48,49]	H: hunting, breeding, sparsely treed BSW
Boreal Owl (*Aegolius funereus*)	C[1], R[16] near upper Susitna		O[6,7], B[1,2,15,33,37]: cavity nester, mixed, coniferous, and deciduous forest near openings, woodlands, meadows	B[2,35]	B[51]: bogs (Norway)	B[2]: BSW	I[10], B[10,53], M[2,10,52,53]	H: hunting, breeding, all BSW

1. Armstrong (1990)
2. J. Wright, Alaska Dep. Fish Game, pers. commun.
3. Palmer (1988*a*)
4. Wiegers (1990)
5. West and DeWolfe (1974)
6. Kron (1975)
7. Cooper et al. (1991)
8. McGowan (1975)
9. Zachel (1985)
10. Gabrielson and Lincoln (1959)
11. Bent (1937)
12. Carbyn (1971)
13. Clarke (1982)
14. Clarke (1984)
15. Erskine (1977)
16. Kessel et al. (1982)
17. Palmer (1988*b*)
18. Hogan and Tande (1983)
19. Mindell and Dotson (1982)
20. D.D. Gibson, Univ. Alaska Mus., pers. commun.
21. Gibbs et al. (1991)
22. Watson (1977)
23. C. McIntyre, Natl. Park Serv., pers. commun.
24. Larsen (1982)
25. Hamerstrom (1986)
26. Spindler and Kessel (1980)
27. Gillespie and Kendeigh (1982)
28. Murie (1963)
29. Ambrose et al. (1988)
30. White (1982)
31. Ambrose (1982)
32. Clark et al. (1987)
33. Johnsgard (1988)
34. White and Haugh (1969)
35. Bent (1938)
36. Houston (1987)
37. Meehan and Ritchie (1982)
38. Jones (1987)
39. Kertell (1982)
40. Nero (1980)
41. Servos (1987)
42. Osborne (1987)
43. Korpimäki (1986)
44. Duncan (1987)
45. Spreyer (1987)
46. Clark (1975)
47. Roberts and Bowman (1986)
48. Baker and Brooks (1981)
49. Village (1987)
50. Lein and Boxall (1979)
51. Hayward et al. (1993)
52. Korpimäki (1987)
53. Korpimäki and Norrdahl (1989)
54. Hunter et al. (1988)

Table 34. Use of black spruce wetlands (BSW) in Alaska by nonpasserine birds other than waterbirds and raptors (see preceding tables).

Species	Abundance in Alaska Taiga (Common, Uncommon, Rare, Casual/ Accidental)	Habitat Use (Breeding or Potentially Breeding = B, Foraging = F, Generally Occurring or Unspecified Use = O) and Preference When Tested (Selected = [+], Neutral = [0], Avoided = [-])					Food Occurs in BSW (Insects = I, Fish = F, Plants = P)	Probability Species Uses BSW (Low = L, Medium = M, High = H)
		Nonwetlands or Mixed Wetlands and Nonwetlands			Wetlands			
		Shrub	Mixed Taiga Landscape	Black Spruce	Mires	Other		
Spruce Grouse (*Dendragapus canadensis*)	C[1,16]		B[1,2,16,17]: ground nester, mixed and coniferous forest, edges, burns, blueberry barrens, clearings	O[4,5] B[1,17]	B[1,7]: "bogs"	O[3,6]: BSW	I,P[2,8,9,10,11,12]: spruce needles[11], blueberries[12]	H: nesting foraging, brood habitat, all BSW
Willow Ptarmigan (*Lagopus lagopus*)	C[1,16]	O[12] B[16]	O[6,14], F[2,12,13,15,17]: use treeline habitats, burns, and "muskeg" in fall and winter B[1,12]: ground nester, wet willow shrub in tundra	F[1]		O[16]: BSW	P[9,12,15]: willows, shrub birches	M: foraging, shrubby BSW within winter range
Rock Ptarmigan (*Lagopus mutus*)	C[1,16]	B[16]	F[1,12]: use shrubby taiga openings on hills in winter, sometimes sympatric with willow ptarmigan B[1]: ground nester in tundra				P[9,12]: willows, shrub birches	L: foraging, shrubby BSW within winter range
White-Tailed Ptarmigan (*Lagopus leucurus*)	U[1,16]		O[6], F[2,8,12]: some use taiga in winter but many remain above treeline B[1]: ground nester in upland tundra				P[9]: alder, shrub birches	L: rare foraging, shrubby BSW within winter range
Ruffed Grouse (*Bonasa umbellus*)	C[1]: limited distribution[12]		O[2,6,18]: may use conifers for cover[2] B[1,2,17]: dry slopes in deciduous woodlands, willow, alder	O[5]	B[7]: bogs		P[9]: willows, aspen, paper birch	M: limited foraging, cover, all BSW within distribution
Sharp-Tailed Grouse (*Tympanuchus phasianellus*)	U[1]: limited distribution[12]	O[1,2,6,8,12]	B[1,2,8,12]: coniferous forest, scrub woodlands, treeline, burns, edges, openings	B[1,2,8,12]	B[1,2,8,12]: "bogs"		I,P[8,12]: paper birch, aspen, seeds, berries	M: nesting, foraging, open BSW within distribution

Table 34 (Cont'd). Use of black spruce wetlands (BSW) in Alaska by nonpasserine birds other than waterbirds and raptors (see preceding tables).

Species	Abundance in Alaska Taiga (Common, Uncommon, Rare, Casual/ Accidental)	Habitat Use (Breeding or Potentially Breeding = B, Foraging = F, Generally Occurring or Unspecified Use = O) and Preference When Tested (Selected = [+], Neutral = [0], Avoided = [-])					Food Occurs in BSW (Insects = I, Fish = F, Plants = P)	Probability Species Uses BSW (Low = L, Medium = M, High = H)
		Nonwetlands or Mixed Wetlands and Nonwetlands			Wetlands			
		Shrub	Mixed Taiga Landscape	Black Spruce	Mires	Other		
Sandhill Crane (*Grus canadensis*)	C[1]: 150,000 to 200,000 migrants[6,21]	O[5,21]	O[18], B[1,8,19,20]: lowland tundra, scattered taiga nesting in a mosaic of treed and treeless wetlands, grassy meadows	B[20]	O[21], B[2,23]: "bogs"[2], shrub[23]	O[19]: emergent		H: nesting, foraging, roosting, sparsely treed BSW
Semipalmated Plover (*Charadrius semipalmatus*)	C[1], U[16] near upper Susitna		B[1,16]: gravel bars, beaches, moss		B[22]			L: nesting, foraging, sparsely treed BSW with shorelines
Killdeer (*Charadrius vociferus*)	R[1]		B[1]: gravel shores, grasslands		B[22]	O[1]: emergent		L: nesting, foraging, graminoid BSW
Greater Yellowlegs (*Tringa melanoleuca*)	R[1], U[16] near upper Susitna, C[1] in southcoastal		F[16]: shorelines	B[1]	B[2,17,22]: shrub, fens[17]	B[1,3,16]: BSW[3], emergent[1], meadow[16]		H: nesting, foraging, sparsely treed BSW
Lesser Yellowlegs (*Tringa flavipes*)	C[1]	B[4,24]	O[23]: ponds and lakes B[24]: mixed forest	O[23] B[1,24]	B[4,17,22,23]: shrub, fens[17], black spruce[4,23]	B[1,3,5,24]: emergent[1,24], BSW[3,5]		H: nesting, foraging, sparsely treed BSW
Solitary Sandpiper (*Tringa solitaria*)	U[1,16]	B[23]	O[24]: mixed forest[24] B[1,16]: lakes and ponds, scattered woodland, edges	O[5] B[1,23]	B[17,22,23]: black spruce[23], shrub, fens[17]	O[5], B[1,3]: emergent[1], BSW[3]		H: nesting, foraging, sparsely treed BSW
Spotted Sandpiper (*Actitis macularia*)	C[1,16]		B[16,17,19]: fluviatile shorelines		B[22,25]: [-] "bogs"[25]	O[25]: emergent		L: nesting, foraging, sparsely treed BSW with fluviatile shorelines

Table 34 (Cont'd). Use of black spruce wetlands (BSW) in Alaska by nonpasserine birds other than waterbirds and raptors (see preceding tables).

Species	Abundance in Alaska Taiga (Common, Uncommon, Rare, Casual/ Accidental)	Habitat Use (Breeding or Potentially Breeding = B, Foraging = F, Generally Occurring or Unspecified Use = O) and Preference When Tested (Selected = [+], Neutral = [0], Avoided = [-])					Food Occurs in BSW (Insects = I, Fish = F, Plants = P)	Probability Species Uses BSW (Low = L, Medium = M, High = H)
		Nonwetlands or Mixed Wetlands and Nonwetlands			Wetlands			
		Shrub	Mixed Taiga Landscape	Black Spruce	Mires	Other		
Upland Sandpiper (*Bartramia longicauda*)	U[1], R[16] near upper Susitna	O[20]	B[1,16,17,20]: sparsely vegetated uplands, dwarf shrub near scattered spruce, perch in spruce	B[16]		O[20]: treeline BSW[20]		M: nesting, foraging, sparsely treed BSW near treeline
Whimbrel (*Numenius phaeopus*)	C[1], U[16] near upper Susitna		B[1,16,19]: tundra nester		O[22], B[26]: black spruce-tamarack (Manitoba)			L (Alaska): migration foraging, sparsely treed BSW
Hudsonian Godwit (*Limosa haemastica*)	A[1]: rare or uncommon regular migrant[19,20] U[1] in southcoastal		B[1]: wetlands		O[22], B[1,2]: "bogs"	B[1]: wet tundra, emergent		H: nesting, foraging, sparsely treed BSW
Western Sandpiper (*Calidris mauri*)	A[1], U[1] southcoastal (coastal migrant[20])				B[22]: atypical, usually nest in dry tundra[1,19]			L: migration foraging, sparsely treed BSW near coast
Least Sandpiper (*Calidris minutilla*)	U[1], C[1] in southcoastal		F[1,20]: migrants use pond edges B[16,20,28]: tundra and taiga nesting but distribution poorly known, tussock-heath meadows	B[1]	B[17,22,27]: fens[17], treeless "bogs"[27]	B[1,16]: emergent		H: nesting, foraging, sparsely treed BSW
Baird's Sandpiper (*Calidris bairdii*)	U[1,16]		F[1,20]: migrants use ponds and lakes B[1]: dry tundra					L: migration foraging, BSW with ponds

Table 34 (Cont'd). Use of black spruce wetlands (BSW) in Alaska by nonpasserine birds other than waterbirds and raptors (see preceding tables).

Species	Abundance in Alaska Taiga (Common, Uncommon, Rare, Casual/ Accidental)	Habitat Use (Breeding or Potentially Breeding = B, Foraging = F, Generally Occurring or Unspecified Use = O) and Preference When Tested (Selected = [+], Neutral = [0], Avoided = [-])					Food Occurs in BSW (Insects = I, Fish = F, Plants = P)	Probability Species Uses BSW (Low = L, Medium = M, High = H)
		Nonwetlands or Mixed Wetlands and Nonwetlands			Wetlands			
		Shrub	Mixed Taiga Landscape	Black Spruce	Mires	Other		
Pectoral Sandpiper (*Calidris melanotus*)	U[1]		F[1,20]: migrants use grassy edges of ponds and lakes[1,20]		O[22]	O[1]: emergent B[1]: wet tundra		L: migration foraging, BSW with ponds
Short-Billed Dowitcher (*Limnodromus griseus*)	A[1] limited distribution C[1] in southcoastal		B[1]: nesting locations poorly known	B[1]	B[2,17,22]: fens[17]	O[3]: BSW		H: nesting, foraging, sparsely treed BSW
Long-Billed Dowitcher (*Limnodromus scolopaceus*)	U[1]		F[1,20]: migrants use ponds and lakes[1,20]			B[1]: wet tundra		L: migration foraging, BSW with ponds
Common Snipe (*Gallinago gallinago*)	C[1,16]	B[24]		B[1,4,5,24]	B[17,22,23]: fens[17], shrub[17,23], black spruce[23]	B[1,3,5,16,24]: emergent[1,16,24], BSW[3,5,16]		H: nesting, foraging, sparsely treed BSW
Red-Necked Phalarope (*Phalaropus lobatus*)	C[1,16]		F[20]: ponds, open water B[1,19,20]: ground nester in tundra and taiga		O[22]	O[16]: meadow ponds[16] B[1,3,20]: BSW[3,20], emergent[1]		H: nesting, BSW near ponds
Belted Kingfisher (*Ceryle alcyon*)	C[1], U[16] near upper Susitna		O[1,2,6,17,18,19]: perch in trees along shores of fish-bearing waters B[19]: nests in bank burrows		O[22,25]: [-] "bogs"[25]		F,I,P[1,8]: also take birds, mammals	L: foraging, BSW with fish-bearing waterbodies
Downy Woodpecker (*Picoides pubescens*)	U[1,16] or C[19]		B[8,16,17,19,29,31]: open woodland, mixed and deciduous forest, riparian willow and alder					L: foraging, open BSW

Table 34 (Cont'd). Use of black spruce wetlands (BSW) in Alaska by nonpasserine birds other than waterbirds and raptors (see preceding tables).

Species	Abundance in Alaska Taiga (Common, Uncommon, Rare, Casual/ Accidental)	Habitat Use (Breeding or Potentially Breeding = B, Foraging = F, Generally Occurring or Unspecified Use = O) and Preference When Tested (Selected = [+], Neutral = [0], Avoided = [-])					Food Occurs in BSW (Insects = I, Fish = F, Plants = P)	Probability Species Uses BSW (Low = L, Medium = M, High = H)
		Nonwetlands or Mixed Wetlands and Nonwetlands			Wetlands			
		Shrub	Mixed Taiga Landscape	Black Spruce	Mires	Other		
Hairy Woodpecker (*Picoides villosus*)	U[1,16] or C[19]		O[6,18], B[2,6,16,17,19]: mature mixed and deciduous forest, woodland		O[30]: black spruce			L: foraging, closed BSW
Three-Toed Woodpecker (*Picoides tridactylus*)	U[1,16]		O[8,14], B[1,2,16]: mixed and coniferous forest, woodlands, burns	O[4,5] B[17]	O[23]: black spruce (winter)	O[6,16]: BSW B[3]: BSW		H: nesting, foraging, all BSW
Black-Backed Woodpecker (*Picoides arcticus*)	R[1]		O[31], B[1,16,17]: mixed and coniferous forest	O[8,29]		O[29]: BSW		H: nesting, foraging, closed? BSW
Northern Flicker (*Colaptes auratus*)	C[1], U[16] near upper Susitna	B[5]	O[6,18,31], B[1,2,17,29]: burns with snags, open coniferous and deciduous forest, open woodlands, edges	O[4]	O[22] B[23]: black spruce, shrub	O[3,6]: BSW		H: nesting, foraging, all BSW

1. Armstrong (1990)
2. Godfrey (1979)
3. Gillespie and Kendeigh (1982)
4. Carbyn (1971)
5. Spindler and Kessel (1980)
6. Cooper et al. (1991)
7. Larsen (1982)
8. Gabrielson and Lincoln (1959)
9. Bryant and Kuropat (1980)
10. Ellison (1989)
11. Ellison (1976)
12. Weeden and Ellison (1968)
13. Gruys (1993)
14. Kron (1975)
15. Viereck and Schandelmeier (1980)
16. Kessel et al. (1982)
17. Erskine (1977)
18. West and DeWolfe (1974)
19. J. Wright, Alaska Dep. Fish Game, pers. commun.
20. P.D. Martin, U.S. Fish Wildl. Serv., pers. commun.
21. Kessel (1984)
22. Hogan and Tande (1983)
23. Spindler (1976)
24. Martin et al. (1995)
25. Gibbs et al. (1991)
26. Skeel (1983)
27. D.D. Gibson, Univ. Alaska Mus., pers. commun. to P.D. Martin, U.S. Fish Wildl. Serv.
28. Kessel and Schaller (1960)
29. Bent (1939)
30. Ewert (1982)
31. Murie (1963)

Table 35. Use of black spruce wetlands (BSW) in Alaska by passerine birds.

Species	Abundance in Alaska Taiga (Common, Uncommon, Rare, Casual/ Accidental)	Habitat Use (Breeding or Potentially Breeding = B, Foraging = F, Generally Occurring or Unspecified Use = O)					Probability Species Uses BSW (Low = L, Medium = M, High = H)
		Nonwetlands or Mixed Wetlands and Nonwetlands			Wetlands		
		Shrub	Mixed Taiga Landscape	Black Spruce	Mires	Other	
Olive-Sided Flycatcher (*Contopus borealis*)	U[1,12]		O[6,9], B[1,6,11,12,13]: open mixed and coniferous forest, scattered woodland and dwarf forest, burns	O[5,8]	O[2,7]: "bogs" B[10,16]: black spruce[16]	B[5]: BSW	H: nesting, foraging, open BSW
Western Wood-Peewee (*Contopus sordidulus*)	U[1], R[12] near upper Susitna		O[9], B[1,2,6,8,11,12,13]: open mixed, coniferous, and deciduous forest, edges		O[10]	O[6]: BSW B[13]: BSW	H: nesting, foraging, open BSW
Alder Flycatcher (*Empidonax alnorum*)	C[1], U[12] near upper Susitna	O[9], B[5,15]	B[1,11,12,13,14]: alder and willow thickets, perch and sing in conifers	B[15]	B[2,8,10,11,16]: "bogs"[2,8], shrub[11,16]	O[5]: BSW B[3,15]: BSW[3], emergent[15]	H: nesting, foraging, all BSW
Hammond's Flycatcher (*Empidonax hammondii*)	C[1]	O[5]	O[9,17], B[1,2,11]: riparian deciduous forest, open conifers, mature mixed and coniferous forest				L: foraging, shrubby BSW
Tree Swallow (*Tachycineta bicolor*)	C[1,12]		O[6], F[1,11,12]: over water or moist ground, successional shrubs, edges B[8]: tree cavity nester	O[4] B[16]	O[1,2]: "bogs" B[10,16,19]: black spruce[16], shrub[19]	O[1,2,3]: BSW[3], marsh, meadow[1,2] F[18]: low pH	H: nesting, foraging, all BSW
Violet-Green Swallow (*Tachycineta thalassina*)	C[1,12]	O[5]	O[6,14], F[1,2,8,11]: over open terrain, water, forest canopy, and edges B[13]: cliffs, block fields, crevices, other cavities		B[10,16]: shrub[16]		H: foraging, all BSW near nesting habitat
Bank Swallow (*Riparia riparia*)	C[1], U[12] near upper Susitna	O[5]	O[9], F[2,11,17]: over water, open land, and edges extending >5 km from nest B[8,11,12,13]: earth cavities along banks		O[10]	O[3,6]: BSW	H: foraging, sparsely treed BSW extending >5 km from nesting habitat

Table 35 (Cont'd). Use of black spruce wetlands (BSW) in Alaska by passerine birds.

Species	Abundance in Alaska Taiga (Common, Uncommon, Rare, Casual/ Accidental)	Habitat Use (Breeding or Potentially Breeding = B, Foraging = F, Generally Occurring or Unspecified Use = O)					Probability Species Uses BSW (Low = L, Medium = M, High = H)
		Nonwetlands or Mixed Wetlands and Nonwetlands			Wetlands		
		Shrub	Mixed Taiga Landscape	Black Spruce	Mires	Other	
Cliff Swallow (*Hirundo pyrrhonota*)	C[1], U[12] near upper Susitna	O[5]	O[6], F[1,2,12,17]: over open land and water closer to nest than bank swallow B[8,11]: mud nests on cliffs		O[10]	F[1,2]: marsh	M: foraging, sparsely treed BSW near nesting cliffs
Gray Jay (*Perisoreus canadensis*)	C[1,12]	O[5]	O[9,20], B[1,8,11,12]: mixed and coniferous forest, woodlands, forest openings, treeline	O[4] B[11]	O[2,10,16]: black spruce (winter)[16], "bogs"[2] B[4,7,16]: black spruce[4,16], bogs[7]	O[12]: BSW B[3,5,6]: BSW	H: nesting, foraging, all BSW
Black-Billed Magpie (*Pica pica*)	C[1]: southern Interior only U[12] near upper Susitna		O[6,25]: ground forager in dry mixed stands[25] B[1,2,11,12,13,25]: nest in larger deciduous trees, scattered woodland and dwarf forest, mixed riparian stands, treeline, shrub thickets, edges	B[13]	O[10]		L: foraging, open BSW within species distribution
Common Raven (*Corvus corax*)	C[1,12]		O[6,9,20], F[1,2,11,12]: scavenger and predator, uses most habitats, prefers shorelines and coniferous forest B[8]: cliff, tree nester		O[10]	O[12]: BSW	H: foraging, all BSW
Black-Capped Chickadee (*Parus atricapillus*)	C[1], U[12] near upper Susitna		O[6,9,20], F[1,11]: openings, edges, shrubs B[1,11,12]: cavity nester, deciduous and coniferous forest		O[10,16]: black spruce (winter)[16]		M: foraging, shrubby BSW
Boreal Chickadee (*Parus hudsonicus*)	C[1,12]		O[6,9,20], F[1,2,8]: willow, alder B[1,2,8,12,13,15]: cavity nester, mixed, deciduous, and coniferous forest	O[5] B[4,11]	O[10,16]: black spruce (winter)[16] B[7]: bogs	O[6]: BSW B[3,12]: BSW	H: nesting, foraging, all BSW

Table 35 (Cont'd). Use of black spruce wetlands (BSW) in Alaska by passerine birds.

Species	Abundance in Alaska Taiga (Common, Uncommon, Rare, Casual/ Accidental)	Habitat Use (Breeding or Potentially Breeding = B, Foraging = F, Generally Occurring or Unspecified Use = O)					Probability Species Uses BSW (Low = L, Medium = M, High = H)
		Nonwetlands or Mixed Wetlands and Nonwetlands			Wetlands		
		Shrub	Mixed Taiga Landscape	Black Spruce	Mires	Other	
Ruby-Crowned Kinglet (*Regulus calendula*)	C[13], U[12] near upper Susitna	O[5]	O[1,6], F[1]: shrubs B[1,2,11,12,13]: nests in conifers, mixed and coniferous forest	B[2,4,15]	B[10,16]: black spruce[16]	B[3,5,12]: BSW	H: nesting, foraging, all BSW
Mountain Bluebird (*Sialia currucoides*)	R[1]		O[6,8,17,21], B[1,2,11,13]: cavity nester, open woodland, meadows, burns, openings, edges				L: foraging, sparsely treed BSW
Gray-Cheeked Thrush (*Catharus minimus*)	C[1,12]	B[5]	O[9], B[1,2,8,11,12,13,14]: mixed and coniferous forest, scattered woodland and dwarf forest, treeline, burns, shrubs	B[3,5,15]	B[16]: black spruce	B[5,6,12]: BSW	H: nesting, foraging, all BSW
Swainson's Thrush (*Catharus ustulatus*)	C[1,12]: abundant[13]	B[5,15]	O[9], B[1,2,8,11,12,13,15]: mixed, coniferous, and deciduous forest, tall shrubs, at lower elevations than gray-cheeked thrush	B[4,5,11,15]	B[4,7,10,16]: bogs[7], shrub[16], black spruce[4]	O[12]: BSW B[5,6]: BSW	H: nesting and foraging, all BSW
Hermit Thrush (*Catharus guttatus*)	C[1,12] (absent from northern interior[24])		O[6], B[1,2,5,6,8,11,12,13,22]: mixed and deciduous forest, young or open coniferous forest, edges, tall shrubs, prefer deciduous habitats in central Alaska but use BSW in Canada	B[11]	B[4,7,10,11]: bogs[7], black spruce[4,11]	B[3]: BSW	L (Alaska)[13,22]: foraging, shrubby BSW
American Robin (*Turdus migratorius*)	C[1,12]	B[5]	O[9], B[1,2,11,12,13]: mixed and deciduous woodlands, scattered woodland and dwarf forest, shrubs, openings, edges	O[1] B[4,5,15]	B[10,16]: black spruce, shrub[16]	B[3,5,6,12]: BSW	H: nesting, foraging, all BSW
Varied Thrush (*Ixoreus naevius*)	C[1,12]		O[9], B[1,2,8,12,13]: shaded areas, damp mixed, coniferous, and deciduous forest, prefers conifers for nesting	B[1,2,8]		O[5,12]: BSW B[6]: BSW	H: nesting, foraging, open to closed BSW

Table 35 (Cont'd). Use of black spruce wetlands (BSW) in Alaska by passerine birds.

Species	Abundance in Alaska Taiga (Common, Uncommon, Rare, Casual/ Accidental)	Habitat Use (Breeding or Potentially Breeding = B, Foraging = F, Generally Occurring or Unspecified Use = O)					Probability Species Uses BSW (Low = L, Medium = M, High = H)
		Nonwetlands or Mixed Wetlands and Nonwetlands			Wetlands		
		Shrub	Mixed Taiga Landscape	Black Spruce	Mires	Other	
Bohemian Waxwing (*Bombycilla garrulus*)	C[1], U[12] near upper Susitna	B[5,6]	O[9], F[11]: successional stands B[1,2,8,11,13]: scattered woodland and dwarf forest	O[17] B[1,2,4,5,8,13]	B[10,16]: black spruce, shrub[16]	O[6,12]: BSW B[5]: BSW	H: nesting, foraging, open BSW
Northern Shrike (*Lanius excubitor*)	U[1,12]		O[6,20], F[2,8]: preys on insects, birds, rodents B[1,2,8,11,12,13]: nests in conifers or tall shrubs in mixed and coniferous forest, scattered woodland and dwarf forest, edges			O[10]	M: nesting, foraging, all BSW
Orange-Crowned Warbler (*Vermivora celata*)	C[1], U[12] near upper Susitna	B[5,15]	O[6,9], B[2,11,12,13,22]: shrubs, deciduous forest, scattered woodland and dwarf forest	B[15]	B[10,16]: shrub[16]	O[12]: BSW B[3,5,15]: BSW[3,5], emergent[15]	H: nesting, foraging, shrubby BSW
Yellow Warbler (*Dendroica petechia*)	C[1]	B[3,5,15]	O[6,9,17], B[2,11,13]: riparian shrub, scattered woodland and dwarf forest		B[2,8]: "bog"-margin tall shrub	B[15]: emergent[15]	L: nesting, foraging, shrubby BSW
Yellow-Rumped Warbler (*Dendroica coronata*)	C[1,12]		O[9], B[1,2,8,12,13]: nests in conifers in open mixed, coniferous, and deciduous forest, scattered woodland and dwarf forest, tall shrub	B[4,5,11]	B[4,7,10,11,16]: bog[7], black spruce[4,11,16]	B[3,5,6,11,12]: BSW	H: nesting, foraging, open BSW
Townsend's Warbler (*Dendroica townsendi*)	C[1]		O[5,6,9,21]: spruce-birch[5], aspen[21] B[1,2,5,8,13,24]: nests in conifers, mixed and coniferous forest, sings from large spruce				L: foraging, mixed BSW
Blackpoll Warbler (*Dendroica striata*)	U[1], C[12] near upper Susitna		O[9], B[1,2,8,11,12,13]: mixed, deciduous, and coniferous forest, scattered woodland and dwarf forest, willow, alder	B[4,15]	O[10], B[7,29]: bogs[7]	B[3,12]: BSW	H: nesting, foraging, open to closed BSW

Table 35 (Cont'd). Use of black spruce wetlands (BSW) in Alaska by passerine birds.

Species	Abundance in Alaska Taiga (Common, Uncommon, Rare, Casual/ Accidental)	Habitat Use (Breeding or Potentially Breeding = B, Foraging = F, Generally Occurring or Unspecified Use = O)					Probability Species Uses BSW (Low = L, Medium = M, High = H)
		Nonwetlands or Mixed Wetlands and Nonwetlands			Wetlands		
		Shrub	Mixed Taiga Landscape	Black Spruce	Mires	Other	
Northern Waterthrush (*Seiurus noveboracensis*)	C[1,12]		O[6,9], B[1,2,8,11,12,13]: tall shrub riparian, mixed and deciduous forest edges, treeline		B[2,8]: "bog"-margin tall shrub	B[3]: BSW	L: foraging, shrubby BSW
Wilson's Warbler (*Wilsonia pusilla*)	C[1,12]	B[12]	O[9], B[2,8,13]: mixed woodlands, tall and medium shrub thickets, treeline		B[2,8]: shrubs near "bogs"	B[3]: BSW	M: nesting, foraging, shrubby BSW
American Tree Sparrow (*Spizella arborea*)	C[1,12]	B[3,5,12]	B[1,2,8,11,12,13]: stunted spruce, low to tall shrub thickets, treeline		B[2,8,10,16]: shrub[16], shrubs near "bogs"[2,8]	O[5]: BSW B[3,12]: BSW	H: nesting, foraging, shrubby BSW
Chipping Sparrow (*Spizella passerina*)	U[1]: limited distribution (upper Tanana)		O[9], B[1,2,11,13]: coniferous and deciduous forest, scattered woodlands and dwarf forest, treeline, thickets, openings, edges, grass meadows	B[4,11]	B[4,11,19]: black spruce	B[11]: BSW	H: nesting, foraging, open BSW
Savannah Sparrow (*Passerculus sandwichensis*)	C[1,12]	B[3,5,6,12]	O[9], B[1,11,12,13]: ground nester, meadows, low shrub with graminoid ground cover, scattered woodland and dwarf forest, treeline	O[5]	B[2,11,16]: "bogs"[2], black spruce, shrub[16], graminoid[11]	O[5]: BSW B[2,3,6,10,12]: BSW[3,6,12]; emergent[2]	H: nesting, foraging, open graminoid BSW
Fox Sparrow (*Passerella iliaca*)	C[1,12]	O[5,12] B[15]	O[9], B[1,2,8,11,12,13]: ground nester, medium and tall shrub, scattered woodland and dwarf forest, mixed forest, treeline	O[5]	B[16]: black spruce	O[3,12]: BSW	H: nesting, foraging, shrubby BSW
Song Sparrow (*Melospiza melodia*)	C[1] in southcoastal	B[4]	B[1,2,8,11,13]: beaches, shrubby successional forest, low riparian shrub, forest edges and openings		B[4,10,11,19]: black spruce[4,19], shrub[11,19]		H: nesting, foraging, shrubby BSW within species distribution

Table 35 (Cont'd). Use of black spruce wetlands (BSW) in Alaska by passerine birds.

Species	Abundance in Alaska Taiga (Common, Uncommon, Rare, Casual/ Accidental)	Habitat Use (Breeding or Potentially Breeding = B, Foraging = F, Generally Occurring or Unspecified Use = O)					Probability Species Uses BSW (Low = L, Medium = M, High = H)
		Nonwetlands or Mixed Wetlands and Nonwetlands			Wetlands		
		Shrub	Mixed Taiga Landscape	Black Spruce	Mires	Other	
Lincoln's Sparrow (*Melospiza lincolnii*)	C[1], U[12] near upper Susitna	O[12] B[5,6,15]	O[9], B[1,2,8,11,13,22]: moist meadows, low to tall riparian shrub, scattered woodland and dwarf forest, low spruces	O[5] B[2,4,8,15]	B[2,8,10,11,16,19]: "bogs"[2,8], black spruce[16,19], shrub[11,16]	O[13,22]: BSW B[1,2,8,15]: emergent	H: nesting, foraging, open BSW
Golden-Crowned Sparrow (*Zonotrichia atricapilla*)	U[1,12], C[1] in southcoastal		B[1,11,12,13]: ground nester, low shrub, scattered woodland and dwarf forest primarily near treeline		B[10]		M: nesting, foraging, shrubby BSW near treeline
White-Crowned Sparrow (*Zonotrichia leucophrys*)	C[1,12]	B[3,5,6,12,15]	O[9], B[1,2,8,11,12,13]: ground nester, low to tall shrub, scattered woodland and dwarf forest, edges, treeline	B[5,15]	B[10,16]: black spruce, shrub[16]	B[3,5,6,12,15]: BSW[3,5,6,12], emergent[15]	H: nesting, foraging, open BSW
Dark-Eyed Junco (*Junco hyemalis*)	C[1,12]	B[5]	O[9], B[1,2,8,11,12,13]: young to mature mixed, coniferous, and deciduous forest, openings, edges, scattered woodland and dwarf forest, tall shrub, treeline	B[1,2,3,4,5,8,15]	B[4,7,10,11,16]: black spruce[4,11,16], shrub[16]	B[3,4,5,6,11,12,15]: BSW[3,4,5,6,11,12], emergent[15]	H: nesting, foraging, all BSW
Rusty Blackbird (*Euphagus carolinus*)	U[1], R[12] near upper Susitna	B[3,5,6]	O[9], B[1,2,8,11,13]: wet woods, riparian shrub, scattered woodland and dwarf forest, shrubby successional forest	O[5] B[2,8]	B[2,8,10,11,16]: black spruce[11,16], shrub[16], "bogs"[2,8]	O[12]: BSW B[2,3,8,13]: BSW[3], emergent[2,8,13]	H: nesting, foraging, shrubby BSW near water
Pine Grosbeak (*Pinicola enucleator*)	U[1,12]	O[5]	O[9], B[1,2,8,11,13]: nests in conifers, open coniferous and mixed forest, edges, scattered woodland and dwarf forest	O[4]	B[16]: black spruce	B[3,6]: BSW	H: nesting, foraging, open BSW
White-Winged Crossbill (*Loxia leucoptera*)	U[1] (irregular nomad[13]), C[12] near upper Susitna		O[20], B[1,2,8,11,13]: nests in conifers, open coniferous and mixed forest, edges, openings, scattered woodland and dwarf forest	O[5] B[4]	O[4], B[10]	O[12]: BSW B[6]: BSW	H: nesting, foraging, open BSW

Table 35 (Cont'd). Use of black spruce wetlands (BSW) in Alaska by passerine birds.

Species	Abundance in Alaska Taiga (Common, Uncommon, Rare, Casual/ Accidental)	Habitat Use (Breeding or Potentially Breeding = B, Foraging = F, Generally Occurring or Unspecified Use = O)					Probability Species Uses BSW (Low = L, Medium = M, High = H)
		Nonwetlands or Mixed Wetlands and Nonwetlands			Wetlands		
		Shrub	Mixed Taiga Landscape	Black Spruce	Mires	Other	
Common Redpoll (*Carduelis flammea*)	C[1,12]: abundant[12]	O[6] B[5,12]	O[9,20], B[2,11,12,13]: low to tall thickets, all forest habitats including scattered woodland and dwarf forest, treeline	B[5]	B[16]: black spruce, shrub	O[6]: BSW B[3,5,10,12]: BSW[3,5,12]	H: nesting, foraging, all BSW
Hoary Redpoll (*Carduelis hornemanni*)	R[1] in summer but C[1] in winter and spring[1,8,21]		O[20]: often occur with common redpoll in winter[21] F[13]: paper birch primary winter food B[1,13,16]: primarily tundra nester, low/medium shrub, mixed woodland				L: winter foraging, shrubby BSW
Pine Siskin (*Carduelis pinus*)	R[1] (irregular near upper Susitna[12]), C[1] in southcoastal		O[5,6,21]: tall spruce F[1]: deciduous trees and ground when not nesting B[1,2,8,11,13]: nests in conifers, coniferous and mixed forest, treeline		B[10]		L: foraging, forested BSW

1. Armstrong (1990)
2. Godfrey (1979)
3. Gillespie and Kendeigh (1982)
4. Carbyn (1971)
5. Spindler and Kessel (1980)
6. Cooper et al. (1991)
7. Larsen (1982)
8. Gabrielson and Lincoln (1959)
9. West and DeWolfe (1974)
10. Hogan and Tande (1983)
11. Erskine (1977)
12. Kessel et al. (1982)
13. J. Wright, Alaska Dep. Fish Game, pers. commun.
14. Murie (1963)
15. Martin et al. (1995)
16. Spindler (1976)
17. White and Haugh (1969)
18. Blancher and McNichol (1991)
19. Ewert (1982)
20. Kron (1975)
21. Kessel and Springer (1966)
22. P.D. Martin, U.S. Fish Wildl. Serv., pers. commun.
23. Walley (1989)
24. D.K. Swanson, Nat. Resour. Conserv. Serv., pers. commun.
25. R. Sinnott, Alaska Dep. Fish Game, pers. commun.

Table 36. Frequently occurring avian species in Alaskan and Canadian black spruce forests and wetlands (all waterbirds except gulls, all raptors, and species not occurring in interior Alaska are excluded).

Species (number of times species reported for nine sites or site types)	Black Spruce Forest - Upper Tanana Valley, Alaska[1]	Common Species in Canadian Black Spruce Forest[2]	Black Spruce Mire - Fairbanks, Alaska[3]	Black Spruce Bog - Upper Tanana Valley, Alaska[1]	Black Spruce Dwarf Forest - Upper Susitna Valley, Alaska[4]	Common Species in Canadian Open Black Spruce Bogs[2]	Tussock-Low Shrub Mire - Fairbanks, Alaska[1]	Common Species in Canadian Open Shrub-Sedge Bogs[2]	Common Species in Canadian Fens[2]
Dark-Eyed Junco (7)	X	X	X	X	X	X	X		
Common Snipe (7)	X		X	X	X		X	X	X
Yellow-Rumped Warbler (6)	X	X	X	X	X	X			
Lesser Yellowlegs (5)	X		X	X				X	X
Ruby-Crowned Kinglet (5)	X	X	X	X	X				
Gray-Cheeked Thrush (5)	X	X	X	X	X				
American Robin (5)	X		X	X	X		X		
White-Crowned Sparrow (5)	X		X	X	X		X		
Common Redpoll (5)	X		X	X	X		X		
Gray Jay (4)	X	X	X	X					
Swainson's Thrush (4)	X	X		X			X		
Bohemian Waxwing (4)	X		X	X			X		
Savannah Sparrow (4)			X		X		X	X	
Solitary Sandpiper (3)			X					X	X
Boreal Chickadee (3)	X	X			X				
Lincoln's Sparrow (3)			X				X	X	
Rusty Blackbird (3)			X			X	X		
Spruce Grouse (2)	X	X							
Sandhill Crane (2)							X		X
Greater Yellowlegs (2)								X	X
Three-Toed Woodpecker (2)	X	X							
Northern Flicker (2)			X				X		
Olive-Sided Flycatcher (2)			X	X					
Alder Flycatcher (2)							X	X	
Hermit Thrush (2)		X				X			
Orange-Crowned Warbler (2)				X			X		
Blackpoll Warbler (2)		X			X				

Table 36 (Cont'd). Frequently occurring avian species in Alaskan and Canadian black spruce forests and wetlands (all waterbirds except gulls, all raptors, and species not occurring in interior Alaska are excluded).

Species (number of times species reported for nine sites or site types)	Black Spruce Forest - Upper Tanana Valley, Alaska[1]	Common Species in Canadian Black Spruce Forest[2]	Black Spruce Mire - Fairbanks, Alaska[3]	Black Spruce Bog - Upper Tanana Valley, Alaska[1]	Black Spruce Dwarf Forest - Upper Susitna Valley, Alaska[4]	Common Species in Canadian Open Black Spruce Bogs[2]	Tussock-Low Shrub Mire - Fairbanks, Alaska[1]	Common Species in Canadian Open Shrub-Sedge Bogs[2]	Common Species in Canadian Fens[2]
American Tree Sparrow (2)					X		X		
Chipping Sparrow (2)		X				X			
Fox Sparrow (2)			X		X				
Bonaparte's Gull (1)									X
Mew Gull (1)			X						
Least Sandpiper (1)									X
Short-Billed Dowitcher (1)									X
Tree Swallow (1)			X						
Violet-Green Swallow (1)							X		
Song Sparrow (1)								X	
Pine Grosbeak (1)			X						

1. Spindler and Kessel (1980)
2. Erskine (1977)
3. Spindler (1976)
4. Kessel et al. (1982)

Table 37. Use of black spruce wetlands (BSW) in Alaska by insectivores, chiropterans, rodents, and lagomorphs. Other habitat abbreviations are Mixed Taiga Landscape (MTL), Black Spruce Forest (BSF), Mire (M), Bog (B), Fen (F), Swamp (S), and Emergent (E).

Species[8]	Alaska Distribution (Arctic/Western = A, Interior = I, Southern = S) and General Habitat Preferences	Habitats Where Observed or Captured	Prey or Food Potentially Occurs in BSW	Probability Species Uses BSW
Common Shrew (*Sorex cinereus*)	I, S[1]: occurs in talus slopes, forests, open country, brushland, wet mossy areas, marshes, moist areas[1,2,3,61]	MTL[4], BSF[5,61], B[6]: heath-moss BSW[61]: mature moss/shrub F[7], S[7]: black spruce-tamarack	Shrews feed on invertebrates, often in moist habitats[9]	H: breeding, foraging, all BSW
Pygmy Shrew (*Sorex hoyi*)	I, S (limited distribution)[1]: forested and open areas[2]; prefers drier habitats than other shrews[1] but uses bogs and marshes[9]; moisture preference may change from wet in spring to drier in summer[11]	BSF[61], S[7,11], E[7,11], B[7,11]: heath-moss[7], alpine[11] F[7]: willow/alder (birch)	Shrews feed on invertebrates, often in moist habitats[9]	H: breeding, foraging, BSW with mixed moisture conditions
Dusky Shrew (*Sorex monticolus*)	I, S[1]: moist environments[1], marshes, coniferous forests, heather[2]	MTL[3]: moist grass, deep moss, dwarf alder BSF[61], BSW[61]: mature moss/shrub E[7], F[7]: willow-alder (birch)	Shrews feed on invertebrates, often in moist habitats[9]	H: breeding, foraging, all BSW
Northern Water Shrew (*Sorex palustris*)	S (Cook Inlet area, may penetrate Copper River basin from Canada)[1,10]: damp riparian areas[1], "bogs"[2,6]; prefers moss near flowing water[10]; greatest densities occur in riparian marsh and shrub and in willow/graminoid communities[7,10]	B[7]: sedge-moss, heath-moss S[7]: black spruce-tamarack	Shrews feed on invertebrates, often in moist habitats[9]	H: breeding, foraging, riparian BSW
Tundra Shrew (*Sorex tundrensis*)	A[1]: wet or dry tundra[1], species sometimes lumped with taiga populations as the arctic shrew (*S. arcticus*)[1,2,3,9]		Shrews feed on invertebrates, often in moist habitats[9]	L: foraging, sparsely treed BSW
Little Brown Bat (*Myotis lucifiga*)	I (southern), S[1,3]: hunts over water, riparian zones along rivers, and forested areas between roosts and primary feeding area[12,13,14]; nursery colonies often close to riparian zones[14]		Feeds on aquatic insects (especially chironomids), moths, and beetles[12,13]	M: foraging over BSW near rivers within species distribution
Red Squirrel (*Tamiasciurus hudsonicus*)	I, S[1,15]: coniferous or mixed forest, swamps[1,2,16]	BSF[17,18,19,20,21]	Prefers white spruce seed[20,21], but black spruce more dependably produces cones; squirrels in black spruce feed nearly exclusively on black spruce seeds[21]	H: breeding, foraging, well-treed BSW

Table 37 (Cont'd). Use of black spruce wetlands (BSW) in Alaska by insectivores, chiropterans, rodents, and lagomorphs. Other habitat abbreviations are Mixed Taiga Landscape (MTL), Black Spruce Forest (BSF), Mire (M), Bog (B), Fen (F), Swamp (S), and Emergent (E).

Species[8]	Alaska Distribution (Arctic/Western = A, Interior = I, Southern = S) and General Habitat Preferences	Habitats Where Observed or Captured	Prey or Food Potentially Occurs in BSW	Probability Species Uses BSW
Northern Flying Squirrel (*Glaucomys sabrinus*)	I (central), S (Cook Inlet)[1]: prefers conifers; use mixed, coniferous, and deciduous forest[22]; nest in cavities, witches' broom, or balls of plant material ("drays") in foliage near red squirrel middens; prefer spruce ≥8 m for gliding	MTL[23]: white spruce-paper birch	Prefers fungi and lichens[22] raided from red squirrel middens[23] but also eats bark, fruit, berries, and insects[9]; spruce cones not selected over alternatives[24]	L: breeding, foraging, forested (trees ≥6 m) BSW
Beaver (*Castor canadensis*)	I, S[1,25]: uses waterbodies in proximity to preferred forage (aquatic vegetation, deciduous trees and shrubs)[9,25,26,27,28], including riparian sedge-willow mats, thaw lakes with peat and sedge mats near birch stands, and kettle lakes with pond lily (*Nuphar* spp.) in black spruce/*Sphagnum*[27]		Pond lily and buckbean can support beavers where other foods are scarce[26,27]; spruce needles sometimes consumed[26] but cuttings in caches may not be eaten[27]	M: breeding, foraging, BSW with deep ponds or flowing water and deciduous component, pond lily, or buckbean
Meadow Jumping Mouse (*Zapus hudsonius*)	I (southern), S[1]: occupies meadows but has broad habitat preferences[2] including grass, marsh, and open woods[1]; thick riparian or pond-edge vegetation, thick herbaceous cover in forests[9,48]; avoids sparse cover[48]	BSF[38]: burned and unburned stands MTL[4]: surrounding a lake		H: breeding, foraging, graminoid BSW within species distribution
Northern Red-Backed Vole (*Clethrionomys rutilus*)	A, I, S[1]: some consider southern red-backed vole (*C. gapperi*) conspecific with *C. rutilus*[3,29]; *C. gapperi* uses muskeg, sedge marsh, "bog"[29]; *C. rutilus* occupies many habitats[30] from dry tundra to bog mat with greatest density in dwarf shrub, alder, and vegetated talus[3]; thick moss favorable for overwintering[34]	MTL[30,31,32,33,39]: shrub tundra, successional deciduous forest, white spruce, black spruce, balsam poplar BSF[61], M[39], BSW[39,61]: mature moss/shrub (abundant)[61]	Berries[61]	H: breeding, foraging, all BSW
Bering Collared Lemming (*Dicrostonyx rubricatus*)	A[1]: arctic and alpine tundra	E[3]: low, moist or wet cotton grass meadows in mountain valley bottoms		L: breeding, foraging, graminoid BSW near tundra
Brown Lemming (*Lemmus trimucronatus*)	A, I, S[1]: damp arctic tundra and drier alpine tundra[2,3,9]	BSW[31]: post-fire stand	Consumes graminoids (e.g., *Carex*, *Eriophorum*) and mosses other than *Sphagnum*[47]	M: breeding, foraging, graminoid or post-fire BSW

Table 37 (Cont'd). Use of black spruce wetlands (BSW) in Alaska by insectivores, chiropterans, rodents, and lagomorphs. Other habitat abbreviations are Mixed Taiga Landscape (MTL), Black Spruce Forest (BSF), Mire (M), Bog (B), Fen (F), Swamp (S), and Emergent (E).

Species[8]	Alaska Distribution (Arctic/Western = A, Interior = I, Southern = S) and General Habitat Preferences	Habitats Where Observed or Captured	Prey or Food Potentially Occurs in BSW	Probability Species Uses BSW
Long-Tailed Vole (*Microtus longicaudus*)	I (eastern)[40]: occupies a variety of habitats, some of which are dry, rocky, or grassy areas far from water[1,3,35]; low, wet, spruce woodland[3]; grassy areas in forest[9], riparian areas, marshes, willow-alder stands, white spruce forest[40]	MTL[3]: rocky mountainsides primary habitat in Yukon		L: breeding, foraging, grassy BSW within species distribution
Singing Vole (*Microtus miurus*)	A, I (mountainous areas)[1,35]: occupies alpine tundra[9]			L: BSW near treeline
Tundra Vole (*Microtus oeconomus*)	A, I, S[1]: moist and wet tundra[2,9], sedge meadow, bogs, and *Sphagnum*[3], alpine tundra, subalpine shrub tundra, marsh[30]; high niche overlap with meadow voles[30]	BSW[31]: wet post-fire stand BSF[37]: post-fire stand		H: breeding, foraging, graminoid or shrubby BSW
Meadow Vole (*Microtus pennsylvanicus*)	A (part), I, S[1]: moist or wet grassy meadows and shrublands near waterbodies, including marsh, bog mats, swamps, and forested areas[1,2,3,6,9,35]; moist grassland optimum habitats[36]	MTL[4,30]: shrub birch[30] BSF[31,37,38]: post-fire stands E[30,39]: marsh[30], bluejoint meadow[39]		H: breeding, foraging, graminoid or shrubby BSW
Yellow-Cheeked Vole (*Microtus xanthognathus*)	I[1]: black spruce forest, bog, forest-tundra, runways in tree or shrub communities, sedges, grassy taiga, post-fire successional stands, graminoid lakeshores, and riparian areas[1,2,4,9,35,41,42,43,61]	MTL[3,61]: *Sphagnum* riparian area in an old burn[3] E[39]: bluejoint meadow BSF[4,61], BSW[61]: mature moss/shrub	Horsetail (*Equisetum* spp.) or fireweed (*Epilobium* spp.) rhizomes for winter food and heavy moss over deadfall for easy burrowing are key factors in habitat selection[37]; graminoids, forbs[61]	H: breeding, foraging, BSW with abundant rhizomes and good burrowing conditions
Muskrat (*Ondatra zibethicus*)	I, S[1]: waterbodies and marshes[2] deep enough for overwintering[9] but can occur >3 km from water[1]; usually present at beaver colonies[26]	B[44]: Wisconsin	Eats cattails, bulrush, pondweed (*Potamageton* spp.), horsetail, and aquatic invertebrates[9,45,46]	M: breeding, foraging, minerotrophic BSW with sufficient water depth for overwintering
Northern Bog Lemming (*Synaptomys borealis*)	I, S[1]: wet environments, alpine and subalpine meadows, muskeg, *Sphagnum* bogs, ericaceous vegetation, sedge meadows, and marshes[1,2,3,6]; construct nests in *Sphagnum* mounds or graminoid tussocks[9]	BSF[5]: upland stand MTL[4]: surrounding a lake BSW[31]: post-fire stand		H: breeding, foraging, all BSW

Table 37 (Cont'd). Use of black spruce wetlands (BSW) in Alaska by insectivores, chiropterans, rodents, and lagomorphs. Other habitat abbreviations are Mixed Taiga Landscape (MTL), Black Spruce Forest (BSF), Mire (M), Bog (B), Fen (F), Swamp (S), and Emergent (E).

Species[8]	Alaska Distribution (Arctic/Western = A, Interior = I, Southern = S) and General Habitat Preferences	Habitats Where Observed or Captured	Prey or Food Potentially Occurs in BSW	Probability Species Uses BSW
Porcupine (*Erethizon dorsatum*)	A (some), I, S[1]: conifer, aspen, and mixed forests; brushlands, open tundra, and riparian corridors[1,2,9,49,50]		Feeds on shrubs and trees, including spruce, and herbaceous vegetation, including sedges and aquatic plants[50]	H: breeding, foraging, all BSW
Snowshoe Hare (*Lepus americanus*)	A, I, S[1]: mixed and coniferous forests, swamps, thickets[1,2,6,9,51]; prefers brushy understory for winter food and cover, overstory may be scattered or absent[52]; uses most available habitats during cyclic population highs but only dense cover during lows[53,54,55]; uses opens stands in summer but dense cover in winter[53]; hares have poor survival in open habitats, black spruce and shrub thickets protect hares from predators[52,53,54,56]	B[52,57]: black spruce[52], bog margins[57] BSF[58]: stable hare habitat MTL[57,58]: alder thickets[58] forest openings[57]	Food includes blueberry, Labrador-tea, willows, paper birch, black spruce, and alder[59,60]; black spruce is not preferred but is most abundant food in hare habitat and about half of winter hare diet[59]	H: breeding, foraging, cover, all BSW (preferred type varies by season and cyclic population level)

1. Manville and Young (1965)
2. Burt and Grossenheider (1964)
3. Youngman (1975)
4. Douglass (1977)
5. Martell (1984)
6. Larsen (1982)
7. Wrigley et al. (1979)
8. Jarrell et al. (1994)
9. Nowak and Paradiso (1983)
10. Beneski and Stinson (1987)
11. Long (1974)
12. Fenton and Barclay (1980)
13. Humphrey (1982)
14. B. Lawhead, ABR, Inc., pers. commun.
15. Flyger and Gates (1982)
16. Larsen (1982)
17. Prévost et al. (1988)
18. Wood (1967)
19. Modaferri (1972)
20. Nodler (1973)
21. Kelly (1978)
22. Wells-Gosling and Heaney (1984)
23. Mowrey and Zasada (1984)
24. Brink (1964)
25. Hill (1982)
26. Hakala (1952)
27. Dennington and Johnson (1974)
28. Jenkins and Busher (1979)
29. Merritt (1981)
30. Krebs and Wingate (1985)
31. West (1982)
32. Whitney and Feist (1984)
33. Gilbert and Krebs (1991)
34. West (1977)
35. Johnson and Johnson (1982)
36. Reich (1981)
37. Wolff and Lidicker (1980)
38. Martell (1984)
39. Osborne (1987)
40. Smolen and Keller (1987)
41. Lensink (1954)
42. Douglass and Douglass (1977)
43. Wolff and Lidicker (1981)
44. Jackson (1914 *in* Larsen 1982)
45. Willner et al. (1980)
46. Perry (1982)
47. Batzli and Pitelka (1983)
48. Whitaker (1972)
49. Woods (1973)
50. Dodge (1982)
51. Bittner and Rongstad (1982)
52. Keith et al. (1984)
53. Wolff et al. (1979)
54. Wolff (1980)
55. Boutin et al. (1985)
56. Parker (1984, 1986)
57. Keith (n.d.)
58. Fox and Bryant (1984)
59. Wolff (1978*a*)
60. Trapp (1962)
61. Swanson (1996)

Table 38. Use of black spruce wetlands (BSW) in Alaska by carnivores. Other habitat abbreviations are Mixed Taiga Landscape (MTL), Black Spruce Forest (BSF), Mire (M), Bog (B), Fen (F), Swamp (S), and Emergent (E).

Species[56]	Alaska Distribution (Arctic/Western = A, Interior = I, Southern = S) and General Habitat Preferences	Habitats Where Observed or Captured	Prey or Food Potentially Occurs in BSW	Probability Species Uses BSW
Arctic Fox (*Alopex lagopus*)	A, S (some)[1]: arctic and alpine tundra in coastal areas[4]; regular inland migrations, reported from Eurasia, do not occur in Alaska[7], but records exist from inland tundra[5,8] and taiga locations[1,6]	MTL[1,6]: Kenai Peninsula, Manitoba[6], southern foothills of Brooks Range[1]	Foxes moving inland feed on lemmings[4]	L: foraging, sparsely treed BSW near coastal tundra
Coyote (*Canis latrans*)	A (some), I, S[1,9,10]: broad ecological tolerances[1], prefer grassland, brush, and broken forests[4];		Consume lagomorphs, rodents, ungulates, birds, invertebrates, fruit, and carrion[4,9,11,12]	H: foraging, all BSW
Wolf (*Canis lupus*)	A, I, S[1]: distribution follows prey availability rather than specific habitat characteristics[14], occupies most natural habitats, including mires, in the absence of human persecution and habitat modification[13,14]	M[4]: Minnesota	Primarily prey on ungulates, including moose, caribou, and muskox (*Ovibos moschatus*), but some consistently take beaver[4,13]	H: foraging, all BSW
Red Fox (*Vulpes vulpes*)	A, I, S[1,3]: broad tolerances, prefers habitat mosaics, ecotones, and other areas of habitat diversity[2,3,4]	E[1]	Consume small mammals (snowshoe hare, red squirrel, ground squirrel, lemmings, voles), birds (ptarmigan, passerines), insects, and fruits[3,4,5]	H: foraging, all BSW
Lynx (*Lynx canadensis*)	A (some), I, S[1]: taiga forests and openings, swamps, black spruce "bogs," brushland, marsh, and shrub barrens[1,2,15,16]; avoid post-fire successional stands for ≥15 yr following fire but abundant where post-fire successional stands are mixed with stands of mature spruce[17]		Primarily prey on snowshoe hares[16], generally occur wherever hares are found[1]; also eat squirrels, shrews, voles, birds, beaver, moose, caribou, muskrat, and fish (includes carrion)[15,15,16,44]	H: breeding, foraging, all BSW
River Otter (*Lontra canadensis*)	A (some), I, S[1]: freshwater streams and lakes, estuaries, and littoral marine waters[4,18]; select watersheds containing abundant active or abandoned beaver ponds, avoided headwater areas (Maine)[19]; use forested, scrub-shrub, and other wetlands (Massachusetts)[20]		Primarily consume fish but also take crustaceans, aquatic insects, and amphibians, as well as occasional birds and small mammals[18]	L: foraging, BSW bordering fish-bearing waterbodies
Wolverine (*Gulo gulo*)	A, I, S[1,21]: forest, mountains, and tundra[1,4]; and favors marshy areas[22]; prefer spruce to alpine tundra in winter[23]	MTL[23]: mixed spruces	Feed on moose (mainly carrion), caribou (mainly carrion), lagomorphs, beaver, marmots, red squirrel, ground squirrels, small rodents, ptarmigan, waterfowl, eggs, carrion, and berries[3,4,22,23,24]	H: breeding, foraging, all BSW

Table 38 (Cont'd). Use of black spruce wetlands (BSW) in Alaska by carnivores. Other habitat abbreviations are Mixed Taiga Landscape (MTL), Black Spruce Forest (BSF), Mire (M), Bog (B), Fen (F), Swamp (S), and Emergent (E).

Species[56]	Alaska Distribution (Arctic/Western = A, Interior = I, Southern = S) and General Habitat Preferences	Habitats Where Observed or Captured	Prey or Food Potentially Occurs in BSW	Probability Species Uses BSW
Marten (*Martes americana*)	I, S[1]: mature mixed or coniferous forest[1,2,25]; winter den sites often in red squirrel middens in stands containing white spruce[27]; avoids some clearcuts[28,29] but uses burns (use higher in younger seres) in a landscape of black spruce forest, treeless bogs, and wet meadows[30,32]; uses spruce forests and woodlands more frequently and shrub habitats less frequently than expected; significantly more snow digging and tracks in black spruce woodland than expected[26]		Consume voles (often red-backed)[26,33,34], snowshoe hares when abundant[35], bog lemmings, red squirrels, arctic ground squirrels, northern flying squirrels[26], fruits, birds [26,31], and insects[31]	H: breeding, foraging, all BSW
Ermine (*Mustela erminea*)	A, I, S[1,36]: forest and shrub habitats[2], open tundra[4]; prefers successional sites and ecotones, scrub, riparian habitats, marshes, and alpine meadows; distribution follows prey[37]	BSF[38]: post-fire sere	Prey primarily rodents and lagomorphs[37]; other items include fish, amphibians, birds, insects, and small amounts of vegetation[36,37]	H: breeding, foraging, all BSW
Least Weasel (*Mustela nivalis*)	A, I, S (some)[1]: meadows, emergent wetlands, scrub-shrub, riparian areas, and woodland[2,36,39]; habitats resemble those used by ermine[4]; local distribution follows prey[39]		Primarily prey on red-backed and meadow voles and lemmings, but males take hares when rodent abundance low[36,39]	H: breeding, foraging, all BSW
Mink (*Mustela vison*)	A (most), I, S[1]: wetlands including bogs, swamps, marshes, and margins of waterbodies but also occurs in forests[1,4,40,41]; shorelines of large waterbodies and interconnected waterbody complexes and beaver/muskrat trails[40,42,43]	M[43], BSW[43]	Consume voles, brown and bog lemmings, snowshoe hare, muskrat, red squirrel, birds (including waterfowl and willow ptarmigan), eggs, fish, and frogs[2,4,40,42,43]	H: breeding, foraging, BSW bordering lakes, rivers, streams, sloughs
Black Bear (*Ursus americanus*)	A (some), I, S[1]: forests, swamps, and mountains with thick understory vegetation and abundant food; occasionally use tundra[1,4,45]; spruce forest (white and black) used in proportion to availability, birch-aspen and willow-alder used more than expected, and heath and marsh used less than expected; den in spruce, willow-alder, birch-aspen, and heath but significantly favor willow-birch and tend to avoid heath[47]	BSW[46]: with bog blueberry	Consume more plants than animals: shoots of herbaceous plants, buckbean, fruits and berries, fish, invertebrates, rodents, snowshoe hares, moose calves, birds, eggs, and carrion[4,45,46,48]	H: breeding, foraging, all BSW but favor well-treed BSW and BSW with abundant fruits and berries

Table 38 (Cont'd). Use of black spruce wetlands (BSW) in Alaska by carnivores. Other habitat abbreviations are Mixed Taiga Landscape (MTL), Black Spruce Forest (BSF), Mire (M), Bog (B), Fen (F), Swamp (S), and Emergent (E).

Species[56]	Alaska Distribution (Arctic/Western = A, Interior = I, Southern = S) and General Habitat Preferences	Habitats Where Observed or Captured	Prey or Food Potentially Occurs in BSW	Probability Species Uses BSW
Brown Bear (*Ursus arctos*)	A, I, S[49]: broad habitat tolerances, prefers open terrain including tundra and coastal areas, swamps, streams, forests[1,4]; in an area of north-aspect slopes supporting black spruce, females prefer habitats above treeline, but males significantly prefer elevations below treeline[50]; heavy predation on moose calves suggests that brown bears are present in wetland habitats such as the Tanana Flats[55]; bears seasonally seek bog blueberry in cotton grass tussocks and black spruce woodland[52]	MTL[52]: low forested flats along Kantishna River	Consume graminoids, common horsetail (*Equisetum arvense*), *Hedysarum* spp. roots, bog blueberry, buffaloberry (*Shepherdia canadensis*), calf moose (significant numbers[53,54]) snowshoe hare, and carrion in spring and early summer; forage on *Hedysarum* spp roots, fruits and berries, graminoids, and salmon in late summer and fall[4,49,51,52]	H: foraging, all BSW

1. Manville and Young (1965)
2. Burt and Grossenheider (1964)
3. Samuel and Nelson (1982)
4. Nowak and Paradiso (1983)
5. Eberhardt (1977)
6. Underwood and Mosher (1982)
7. Chesemore (1967)
8. E. Follmann, Univ. Alaska, pers. commun.
9. Bekoff (1977)
10. Bekoff (1982)
11. Post (1976)
12. Harrison (1983)
13. Mech (1974)
14. Paradiso and Nowak (1982)
15. McCord and Cardoza (1982)
16. Tumlison (1987)
17. Stephenson (1984)
18. Toweill and Tabor (1982)
19. Dubuc et al. (1990)
20. Newman and Griffin (1994)
21. Pasitschniak-Arts and Larivière (1995)
22. Wilson (1982)
23. Gardner (1985)
24. Magoun (1985)
25. Strickland et al. (1982)
26. Buskirk (1983)
27. Buskirk (1984)
28. Snyder and Bissonette (1987)
29. Steventon and Major (1982)
30. Magoun and Vernam (1986)
31. Strickland et al. (1982)
32. Paragi et al. (1994)
33. Douglass et al. (1983)
34. Koehler and Hornocker (1977)
35. Raine (1987)
36. Svendsen (1982)
37. King (1983)
38. Wolff and Lidicker (1980)
39. Sheffield and King (1994)
40. Linscombe et al. (1982)
41. Larsen (1982)
42. Arnold and Fritzell (1990)
43. Harbo (1958)
44. Youngman (1975)
45. Pelton (1982)
46. Hatler (1967, 1972)
47. Hechtel (1991)
48. Schwartz and Franzmann (1991)
49. Craighead and Mitchell (1982)
50. T. Boudreau, Alaska Dep. Fish Game, pers. commun.
51. McCarthy (1989)
52. Valkenburg (1976)
53. Gasaway et al. (1992)
54. Ballard et al. (1991)
55. Gasaway et al. (1983)
56. Jarrell et al. (1994)

Table 39. Use of black spruce wetlands (BSW) in Alaska by cervid artiodactyls (moose, caribou).

Species[37]	Alaska Distribution (Arctic/Western = A, Interior = I, Southern = S) and General Habitat Preferences	Prey or Food Potentially Occurs in BSW	Probability Species Uses BSW
Moose (*Alces alces*)	A (most), I, S (most)[1]: taiga, shrub riparian tundra[1,2]; prefer seral communities from fire or alluviation that provide abundant, high-quality forage[3,4,5]; cows select tall cover in spruce and deciduous stands during calving on the Tanana Flats[8]; calve on muskeg hummocks for predator avoidance[2]; proximate coniferous cover increases the value of successional stands to moose[4]; select lowland black spruce during late summer in Minnesota[10]; use black spruce muskeg during late winter in Alberta[11]; some open black spruce has willow component[13,14]; select aquatic-herbaceous habitat during May and June[8]	Forage in riparian willow, treeline resin birch and willow, lowland decadent willow, spruce forest[4,6,7]; fire stimulates willow production in burned black spruce stands[9]; eat forbs and aquatic vegetation in summer[3,10,12], which supply sodium[2]	H: breeding, foraging, open BSW with willows, surrounding ponds with aquatic vegetation, or providing cover next to forage
Barren-Ground Caribou (*Rangifer tarandus granti*)	A, I, S (some)[1,15,16]: tundra and taiga habitats, the latter primarily in winter[17,18]; winter range in open spruce, sometimes with lakes, ponds, and bogs, provides sedges and arboreal and terrestrial lichens[19,20,21]; *Cladina rangiferina* covered 10% to 30% of the nonvascular layer in three apparently hydric and one mesic black spruce "core groups" in the western winter range of the Denali caribou herd[14,22]; woodland caribou (*R.. t. caribou*) sometimes select lowland black spruce habitats, including bog and muskeg, for winter range[23,24], but Canadian barren-ground caribou (*R. t. groenlandicus*) prefer dry spruce-lichen forest[25], a type more abundant in Canada than Alaska[26,27]	Forage on lichens, graminoids, and shrubs in winter[19]; terrestrial lichens often majority of winter diet[15,28,29,30]; energy-rich lichens poor in nutrients, graminoids and evergreen *Equisetum* can be important and may maintain condition during winter[19,28,30,31]; terrestrial lichens favored by caribou occur in many BSW communities[14,32,33]; cotton grass (*Eriophorum* spp.) important spring, summer, and fall[19,22,34,35,36]	H: foraging, open BSW with abundant lichens or sedges, mainly within winter range

1. Manville and Young (1965)
2. Telfer (1984)
3. Franzmann (1981)
4. Coady (1982)
5. Viereck and Schandelmeier (1980)
6. Dyrness et al. (1983)
7. Ballard et al. (1991)
8. Gasaway et al. (1985)
9. Wolff (1978*b*)
10. Peek et al. (1976)
11. Rolley and Keith (1980 *in* Telfer 1984)
12. Nowak and Paradiso (1983)
13. Yarie (1983 *in* Viereck et al. 1992)
14. Heebner (1982)
15. Scotter (1967)
16. Miller (1982)
17. Kelsall (1968)
18. Hemming (1971)
19. Skoog (1968)
20. Durtsche and Hobgood (1990)
21. Davis et al. (1978)
22. Boertje (1981)
23. Fuller and Keith (1981)
24. Schaefer and Pruitt (1991)
25. Kelsall (1968)
26. Viereck (1983)
27. Rowe (1984)
28. Boertje (1984)
29. Duquette (1984)
30. Saperstein (1993)
31. Russell and Martell (1984)
32. Foote (1983)
33. Viereck et al. (1992)
34. White et al. (1975)
35. Bishop and Cameron (1990)
36. Cameron et al. (1992)
37. Jarrell et al. (1994)

Table 40. Mammals most characteristic of black spruce wetlands in Alaska.

Species	Comment
Common Shrew	Use moist forest litter
Dusky Shrew	Use moist forest litter
Red Squirrel	Requires drier, well-treed BSW for ample cone production
Northern Red-Backed Vole	Ombrotrophic (*Sphagnum*) wetlands
Meadow Vole	Minerotrophic (graminoid) wetlands
Yellow-Cheeked Vole	Favors rhizomes for forage and moss or graminoids for burrowing
Snowshoe Hare	Core habitat is black spruce during winter and cyclic population lows
Wolf	Wide-ranging predator uses all habitats but keys on moose and caribou
Red Fox	Preys on small mammals and birds
Lynx	Largely dependent on snowshoe hares and follows hare cycles
Marten	Hunts in trees and on ground for voles, red squirrels, and sometimes hares
Ermine	Preys on rodents and hares
Black Bear	Omnivorous feeder on green vegetation, fruits and berries, and moose calves

Table 41. Wood frog reproduction under ombrotrophic and minerotrophic conditions.

Site Type and Location	pH	Life Stage	Comment	Source
Bogs and Marshes - Nova Scotia	4.3 to 7.8	Eggs, larvae, adults	At least one life stage present	Dale et al. (1985)
Quebec		Eggs	Egg mass density negatively correlated with acidity and TOC, and hatching success positively correlated with pH	Gascon and Planas (1986)
Laboratory	Low	Eggs	Reduced hatching success	Dale et al. (1985), Freda and Dunson (1985:53), Karns (1992)
Pond - Quebec	3.4	Eggs	Some hatched	Gascon and Planas (1986)
Laboratory	3.0	Eggs	100% mortality	Ling et al. (1986)
Labratory - Ontario	4.0	Larvae	95% survival at 3 weeks	Grant and Licht (1993)
Mesocosms - Pennsylvania	4.2, 6.0	Larvae	Increased time (8 days) to metamorphosis at lower pH	Rowe et al. (1992)
Bogs - Minnesota	<4.5	Larvae	Survival to metamorphosis near 0%	Karns (1992)
Poor Fens - Minnesota	4.5 to 5.0	Larvae	Healthy populations	Karns (1992)
Fens - Minnesota	>5.0	Larvae	Healthy populations	Karns (1992)

Black spruce wetlands might not provide favorable environments for frog hibernation, although use of dry microsites (e.g., hummocks) cannot be ruled out. Studies reviewed for this profile suggest that areas of standing water within BSWs, particularly those ≥ 4.5 pH, provide breeding habitat for wood frogs. Use of terrestrial BSW habitats for foraging by adult frogs or for hibernation sites is poorly documented but probable.

Functional Summary

Alaska's BSWs perform the habitat function for a greater number of species than commonly recognized. Although the characteristic and abundant fauna of BSWs comprises relatively few species, many more species derive at least part of their living from these wetlands. Failure to appreciate the importance of BSW habitats may arise from the tendency of researchers and resource managers to focus on studies of habitat "selection" and "avoidance." Although such studies provide useful information, they sometimes draw our attention from the widespread use of habitats that are not "preferred" (Telfer 1984). When integrated over their substantial area within the taiga biome, peat-forming wetlands provide substantial resources for wildlife even when not offering preferred habitats. The importance of BSWs to Alaska's wildlife species perhaps is not surprising given the dominance of black spruce communities in taiga landscapes.

The scale at which habitat is addressed determines inclusion or exclusion of open-water components of BSWs. Most waterbirds associated with BSWs use larger waterbodies (at a scale of, say, 10^2 to 10^3 m) having zones of mire-like vegetation rather than small thaw ponds (at a scale of, say, 10 to 10^2 m), temporarily flooded areas (at a scale of, say, 1 to 10 m), or black spruce itself, although there are exceptions (e.g., green-winged teal, spring migrant waterfowl, mew gulls). Waterbodies within at least weakly minerotrophic BSWs also provide breeding and rearing habitat for the wood frog; unflooded BSWs probably provide foraging habitat for frogs.

Black spruce wetlands directly provide habitat to a large number of avian species, especially passerines, and a smaller number of mammalian species. Excluding waterbirds, however, only about 12 nonraptorial bird species, 7 raptorial bird species, and 13 mammalian species might be judged commonly and consistently present in BSWs. Moose and caribou, although important users of BSWs, do not appear in these totals because other plant communities are their preferred habitats.

Many avian and mammalian species distribute themselves in response to composition of ground, herbaceous, and shrub strata, which affect availability of resources (e.g., cover and food), rather than to overstory vegetation. One factor determining the structure and composition of understory vegetation of BSWs is their degree of minerotrophy. Trophic status might prove a good predictor for presence or absence of selected avian or mammalian species, but such relationships rarely have been tested.

Directly sensing avian and mammalian species or their vocalizations, nests, droppings, tracks, browsed or cropped stems, burrows, or dens best evaluates the habitat function of BSWs. When such observations are not possible or practical, known food or cover preferences of various animal species provide indicators of potential animal habitats. These indicators may be identified in the field or from descriptions of plant communities. Prey distribution (or the habitat of such prey) indicates potential habitat for avian and mammalian predators.

Functional Sensitivity to Impacts

The habitat function of BSWs is sensitive to placement of fill. Barren fill eliminates food and cover of potential use by vertebrates. In the unlikely absence of continuing human activity, barren fill surfaces can provide sites where birds or mammals may rest, observe the landscape for potential predators or prey, or engage in other activities such as ingestion of grit. Species that use fill surfaces are unlikely to be those that originally occupied filled sites, and the resources provided by fill surfaces are unlikely to approach those that were lost to fill placement.

Revegetating fill surfaces might partially mitigate the impact of fill placement on the habitat function. Unless wetlands were created on the fill surface, however, such revegetation would be unlikely to provide habitat for the animal species using the original wetland. Re-establishment of cover structure and food density characteristic of the original BSW would be extremely difficult and unlikely to be compatible with the purpose for which the wetland was filled.

The habitat function of BSWs is less sensitive to

drainage than to fill placement. Drainage likely would change composition and structure of the vegetation, typically increasing dominance by woody vegetation, with concomitant changes in avian and mammalian species occupying the site. In the absence of other disturbance, however, the habitat resources provided by the drained site should approximate in magnitude, if not in kind, those present before drainage.

The impacts of mire drainage on the habitat function would be difficult to mitigate if the objective were to restore pre-drainage avian and mammalian habitats. Habitat manipulation, for instance prescribed fire to prevent invasion of a drained fen by trees, might minimize changes in plant species composition. Although unlikely to be compatible with the purposes for which mires are drained, ponds excavated to, or below, the water table could replace portions of specific (e.g., waterfowl) habitats lost with drainage.

DATA GAPS

Data gaps exist with respect to the ecologic functions of Alaska's BSWs. Additional studies of nutrient cycling and export, food chain support, and habitat are warranted. The following discussion identifies information needs for these functions of BSWs.

Nutrient Cycling

Studies of taiga forest ecosystems have yielded a significant amount of information on nutrient cycling in black spruce forest, including cold, wet stands occurring on permafrost soils. These studies address only a portion of the ecologic communities that lie on a gradient from treed to treeless wetlands, however. Nutrient cycling in black spruce communities characterized as "woodland" and "dwarf tree scrub" by Viereck et al. (1992:24-25) apparently has received little study in Alaska, although some data have been collected in sparsely treed, *Sphagnum*-dominated stands (e.g., Heilman 1966, 1967; Dyrness and Grigal 1979). Although one can infer more rapid nutrient cycling in minerotrophic than in ombrotrophic BSWs, comparative studies on the trophic controls of nutrient cycling in these communities are lacking.

Nutrient Export

The magnitude of nutrient export from BSWs in Alaska and its importance to aquatic systems have received little study. Black spruce wetlands export C, which may support detrital food chains and allow significant production by higher trophic levels in taiga waterbodies, but virtually no studies exist to explore these potential relationships. In addition, C may affect thermal characteristics of brownwater systems so that they offer favorable thermal environments for fish, a problem currently under investigation (J. D. LaPerriere, Alaska Coop. Fish Wildl. Res. Unit, pers. commun.). The role of exported C in brownwater systems demands attention because fish species are highly-valued resources for Alaska residents.

Black spruce wetlands presumably export small amounts of N and P, based on studies elsewhere, but such exports should be quantified for Alaska. Export of P from BSWs, although likely to be small, might control production in some taiga waterbodies because P availability often limits primary production in oligotrophic lakes (Wetzel 1983:286) and tundra ponds (Hobbie 1984:10-22). Nitrogen can be a limiting factor for primary production in aquatic systems where P and C are available in excess of demand (Wetzel 1983:251), but excess P is unlikely in ombrotrophic waterbodies.

Food Chain Support

Significant information on primary production (and thus biomass available for food-chain support) exists for black spruce forests, including cold, wet stands on permafrost soils. Much less is known about primary production in sparsely treed, palustrine scrub-shrub wetlands. Partitioning of energy flows between grazing and detrital food chains in BSWs, the effects of trophic status on such partitioning, and the vertebrate biomasses supported by energy flows have received little study. Black spruce wetlands generally produce less biomass than do warm, well-drained taiga ecosystems, but most taiga vertebrates at least occasionally use black spruce habitats. The food-chain support function of BSWs thus is important to Alaska's fish and wildlife populations.

Habitat

Habitat studies of Alaska birds and mammals often have been autecologic rather than synecologic, at least with respect to wildlife use of BSWs. These

studies rarely, if ever, are framed to reveal the relationships between wildlife species and wetland classes such as bogs or fens. As a result, identifying the habitat functions of BSWs is difficult without species-by-species review of the literature. Further, even autecologic information on birds and nongame mammals of taiga regions is sparse. Soricids and microtines provide examples of taxa for which the literature sometimes gives habitat preferences in only the most general terms. Synecologic studies of vertebrate use of BSWs, particularly studies that differentiate between ombrotrophic and minerotrophic wetlands, as well as vegetation structure and composition, would be most helpful in fully documenting their habitat function.

Functional Sensitivity to Impacts

The sensitivity of nutrient cycling in BSWs to placement of fill seems self-evident (i.e., elimination of cycling) and should require no study. In contrast, the effects of wetland drainage on this function are not clear. The magnitude of nutrient cycling following wetland drainage depends on the balance between production and decomposition. Factors including increased aeration and decomposition of organic soils, altered soil temperature regimes, increased ombrotrophy of surface layers, shifts in species composition, and changes in permafrost tables likely influence outcomes. Accurate predictions about the effect of drainage on nutrient cycling require experimental investigations of the controls on production and decomposition under drained and undrained conditions for both ombrotrophic and minerotrophic BSWs.

Data gaps exist with respect to the impacts of fill placement on nutrient exports from BSWs. Presumably export of C ceases with fill placement. The same is unlikely to be true of N and P if anthropogenic sources are present. Because the natural nutrient-export function of BSWs for N and P is poorly quantified, the effects of fill placement on this function are basically unknown. Several studies have shown small effects of mire drainage on nutrient export in the form of elevated DOC (Bourbonniere 1987), N (Clausen and Brooks 1983*a*), and P (Moore 1987), but similar information is not available for BSWs in Alaska.

Barren fill provides no food-chain support, a self-evident impact that requires no study. In contrast, drainage does not eliminate the food-chain support function of BSWs, and the effects of such drainage are not easily predicted. Data gaps exist regarding the evolution of drained sites, particularly minerotrophic BSWs, under the potentially opposing effects of increased mineralization of nutrients and development of more ombrotrophic vegetation with lowered water tables. Studies should address community composition and production and partitioning of energy flow between grazing and detrital food chains before and after drainage.

The sensitivity of the habitat function of BSWs to barren fill is self-evident, but for fill surfaces supporting re-established vegetation, there is room for research on how such vegetation can be made to provide productive wildlife habitat. Research might target structure and composition of vegetation in relation to species-specific preferences of wildlife, including management techniques for achieving desired endpoints. The effect of drainage on the habitat function of BSWs is not clear. Potential changes in plant species composition as sites become drier but, perhaps, more ombrotrophic, require study. Research on the evolution of drained (but otherwise unaltered) BSWs in relation to wildlife habitat could facilitate prediction of drainage impacts on the habitat function.

SOCIOECONOMIC USES

Sather and Smith (1984:58-68) divide socioeconomic uses of wetlands into consumptive and nonconsumptive components. Consumptive uses include harvest of wetland resources whereas nonconsumptive uses include recreation and aesthetic or cultural appreciation. Adamus and Stockwell (1983:46-47) further divide recreation into active and passive components.

CONSUMPTIVE

Wetlands provide resources of use to humans, either as individuals or collectively. Consumptive uses of these resources thus may take place at a personal or societal level. Subsistence and personal uses of wetland resources include harvests of fuel, food, and other plant and animal materials largely for direct consumption, distribution, or barter. Extraction of economic resources includes logging, mining, fishing, trapping, and guiding for cash sale.

Subsistence and Personal Uses

Subsistence and personal uses of fish and wildlife resources, plants, and fuels from wetlands are closely related to extraction of economic resources but are not pursued in a commercial or recreational context. Alaska Natives are highly dependent upon wetlands for provision of subsistence resources (Ellanna and Wheeler 1989) to support noncash economies. Wild foods supply up to 80% of intake in some native communities in Alaska and Canada (Larson 1991). In interior Alaska, for example, the village of Minto has an annual per capita harvest of more than 450 kg of wild foods (Anonymous 1989). Other Alaska residents harvest wild materials for personal consumption as well: the statewide median harvest is ~113 kg (Anonymous 1989). Black spruce wetlands provide wild resources needed for subsistence and personal uses.

Harvest of animals for subsistence and personal use includes large game, small game, furbearers, waterfowl, and fish (Table 42). With the exception of fish, harvested species directly use BSWs. Even some fish species that enter subsistence harvests may be influenced by BSWs. Coho salmon, for example, rear in areas of groundwater discharge with emergent or shrub vegetation during the freshwater phase of their life cycle (A. G. Ott, Alaska Dep. Fish Game, pers. commun.). Such areas presumably are spring fens. Likewise, forage fish that help support populations of harvested species such as northern pike and burbot (*Lota lota*) inhabit brownwater drainages that receive water from BSWs along the Tanana River (A. G. Ott, Alaska Dep. Fish Game, pers. commun.).

Residents of communities in the upper Tanana Valley of interior Alaska take moose, caribou, and smaller numbers of black and brown bears (Marcotte 1991:59-61). Small game and waterfowl species harvested in this area include snowshoe hare; ruffed, sharp-tailed, and spruce grouse; willow ptarmigan; numerous duck species; several goose species; and sandhill crane (Marcotte 1991:60,63). Finally, red squirrel, muskrat, beaver, least weasel, marten, mink, otter, wolverine, wolf, red fox, and lynx are furbearers taken in the Interior (Andrews 1988: 210-240, Marcotte 1991:62). The importance of furbearer harvest is illustrated by Minto where 49% of the households had a member who trapped in 1983-84 (Andrews 1988:218).

Plant materials potentially harvested in BSWs in-

clude wood, craft materials such as bark or roots, and berries (Andrews 1988:241-260, Marcotte 1991:64-65). Wood may be used as fuel or construction material (Andrews 1988:251-255). Pole-size spruce find many uses in construction (e.g., fish drying racks) in rural communities (Andrews 1988:254-255). Pole-size and slightly larger spruce fuelwood grow in well-treed BSWs in Alaska and may be harvested for personal use. Five upper Tanana communities had an estimated combined harvest of 8,184 cords of wood (Marcotte 1991:71).

Other subsistence uses of wood include basketry incorporating birch bark and spruce roots (Marcotte 1991:65). Harvest of spruce roots takes place "in mossy ground close to river or lake banks where the ground is moist" (Nelson et al. 1982), a description consistent with BSWs; paper birch occasionally occurs in these communities as well. Berries provide an important wild harvest for subsistence and personal use by Alaskans (Table 42).

Extraction of Economic Resources

Humans extract many economic resources from wetlands: timber (Mitsch and Gosselink 1986:397), peat (Maltby 1991), fish, shellfish (Maltby 1986:19-24), and furbearers (Mitsch and Gosselink 1986:394). Economic values have been estimated for wetlands supplying these resources, but many criticisms of these techniques exist in the literature (Sather and Smith 1984:61-62) because wetlands have global life support values (e.g., biogeochemical cycling of elements) independent of economic resource extraction (Maltby 1986:146, Mitsch and Gosselink 1986:405-408). Economists have recently developed novel methods to apply economics to ecosystems (Maxwell and Costanza 1989).

Commercial use of renewable resources directly or indirectly related to BSWs in Alaska includes wood harvest, trapping furbearers, commercial fishing, and guiding sport hunters and fishers. Silversides (1983) has proposed harvest of northern boreal forests for energy feedstocks. Black spruce wetlands could provide such feedstocks because all cellulosic material can be used, regardless of tree size or species, but low biomass production in Alaska BSWs would make them the last choice for harvest. At present, little or no commercial harvest of black spruce occurs in interior Alaska, although some pole-sized material has been salvaged from burned stands for fence posts, furniture manufacture, and similar uses. Van Hees (1990) listed "the dispersed nature of the resource, poor access, and lack of markets" as limiting use of forested wetlands in Alaska.

Commercial trapping largely overlaps trapping for subsistence and personal uses, since trapping can be a source of cash income in subsistence economies. Harvest levels for furbearers fluctuate drastically with fur prices (T. Boudreau, Alaska Dep. Fish Game, pers. commun.); thus, short periods of record (Table 43) may underrepresent sustainable harvest levels. Trapping in the Interior harvests furbearers produced in BSWs.

Commercial fishing, as a component of the seafood industry, the state's largest private employer (Holmes 1990), is extremely important to Alaska's economy. Alaska's salmon harvests had ex-vessel

Table 42. Representative subsistence harvests for several interior Alaska resources directly or indirectly related to black spruce wetlands.

Resource	Per Capita Harvest (kg)	Location	Source
Moose	17 to 92	Several representative interior Alaska villages	Andrews (1988:272), Marcotte (1991:74-82)
Ducks and geese	~11	Minto	Andrews (1988:184-194,267)
Fish	~41	Upper Tanana communities	Marcotte (1991:70)
Fish	567	Hughes	Andrews (1988:271)
Berries	>3	Dot Lake, Tanacross, Minto	Andrews (1988:267), Marcotte (1991:75-77)

Table 43. Mean annual estimated furbearer harvests between 1986 and 1991 in Game Management Unit (GMU) 25 (northeastern Interior), GMU 24 (Koyukuk River), and GMU 21 (mid-Yukon River) (Abbott 1993: 250-253,277-283,291-294).

Species	Harvest (number)		
	GMU 25	GMU 24	GMU 21
Red Fox	233	41	63
Lynx	569	106	38
Mink	87	68	108
Muskrat	836	16	34
Otter	5	13	44
Wolverine	48	48	25
Beaver	314	467	1,059
Marten	3,739	1,760	2,781

values of $478 million, $754 million, and $505 million in 1987, 1988, and 1989, respectively (Savikko and Page 1990:40). In 1989, commercial fishers harvested ~833,000 coho salmon from the Yukon, Kuskokwim, and Copper rivers, which drain the taiga landscapes of interior Alaska (Savikko and Page 1990:33-36). To the extent (perhaps limited) that rearing cohoes use drainages arising in minerotrophic BSWs, commercial fishing represents economic resource extraction of wetland-dependent resources.

Guided hunts for big game and waterfowl and guided fishing contribute to the economy of taiga regions. Big game species using BSWs and targeted by guided hunters include black and brown bears, moose, and caribou. To the extent that hunted populations of big game and waterfowl depend upon wetland habitats, revenues from guiding represent extraction of economic resources from wetlands. Guided fishing is analogous to guided big game hunting and commercial fishing in the sense that populations of targeted species such as coho salmon or northern pike may rear in habitats associated with BSWs. Quantitative information on the proportion of guiding revenues that can be attributed to the extraction of wetland-dependent resources does not exist.

Commercial extraction of nonrenewable resources also occurs in BSWs. Most prominent is mining of peat for fuel and horticultural uses, but materials such as gravel and placer and hard rock minerals may be mined from underlying strata as well. Some might consider peat a renewable resource because organic matter can continue to accumulate if wetland conditions are re-established following mining, but thousands of years would be required for reaccumulation of commercial quantities of peat. Thus, peat is not renewable in periods amenable to human economic or resource planning.

Small-scale peat mining for fuel has occurred in northern Minnesota mires; more recent large-scale proposals have proven infeasible (Glaser 1987:67-68). Alaska's peat resources have been mapped based on the distribution of Histosols and an assumed peat depth of 1.5 m (Rawlinson and Hardy 1982). Huck and Rawlinson (1982) provide more detailed information for southcentral Alaska. Available energy from Alaska's fuel-grade peat is estimated to range from 6.9 to 77.5 quads under various assumptions (e.g., including or excluding frozen peat, ability to reduce ash content) (Rawlinson and Hardy 1982). Significant use of peat for fuel presently does not occur in Alaska, but horticultural peat is mined in or near Alaska's larger population centers. Peat extracts have been proposed as a fermentation substrate for submerged culture of edible mushrooms (Martin 1983), but such use is not known to have occurred in Alaska.

Black spruce wetlands located in floodplains can be a source of alluvial gravel following removal of overlying peat deposits; such gravel pits operate in the Fairbanks area of interior Alaska. In addition, many of Alaska's placer gold mines operate in valley-bottom BSWs. Miners strip peat and mineral soil overburden from underlying gold-bearing alluvial materials. Likewise, Glaser (1987:69-70) describes an ore-bearing greenstone formation occurring under peat and glacial till in northern Minnesota. Hardrock gold ores underlying BSWs currently are being developed for mining near Fairbanks as well. In these cases, extraction of nonrenewable economic resources from BSWs is only coincidental.

Use Summary

Black spruce wetlands provide for consumptive uses. Subsistence, personal, and commercial harvests of wetland-dependent fish, wildlife, and plant resources are the most important consumptive uses of Alaska's BSWs. Such uses predominate throughout the Subarctic (Larson 1991). Consumptive uses of renewable wetland resources may become more important as improved technologies and favorable market conditions develop for biomass conversion and manufacture of wood fiber products. Consumptive uses of nonrenewable resources such as peat, gravel, and placer and hardrock minerals occurring in or beneath BSWs currently are few in Alaska.

The magnitude of consumptive uses of BSWs perhaps is best judged through regional and local socioeconomic studies, including surveys and records of animal, plant, and peat harvests. Less direct methods include documenting occurrence of BSWs within traditional harvest areas for communities, within registered guiding areas targeting wetland-dependent species, or along established traplines. Black spruce wetlands that provide habitats for fish and wildlife species included in subsistence, personal use, and commercial harvests may be assumed to support potential consumptive use. The magnitude of consumptive uses of nonrenewable resources occurring within or beneath BSWs probably can be judged from the records of management or regulatory agencies because such resource extraction normally occurs with government oversight.

Use Sensitivity to Impacts

Consumptive use of wetland-dependent renewable resources is sensitive to placement of fill, as discussed with respect to the food-chain support and habitat functions. Harvests of wetland-dependent fish, wildlife, peat, and plant resources potentially are diminished in proportion to wetland area filled. Placement of fill does not necessarily prevent extraction of nonrenewable resources such as peat or minerals at some future time, but fill removal would render mining more difficult and expensive.

Re-establishment of vegetation on fill surfaces, although unlikely to be compatible with the purposes for which fills are placed, could provide habitat for nonwetland animal species subject to subsistence, personal, and commercial uses. Harvest of such alternative species might mitigate loss of renewable BSW resources. Fully mitigating the effects of fill placement on extraction of nonrenewable resources does not appear feasible, but minimization of fill depths would reduce costs of future fill removal for mining underlying peat or mineral resources.

Consumptive use of renewable resources found in BSWs may be facilitated or hindered by drainage. Drainage can increase timber production (e.g., Dang and Lieffers 1989). In contrast, draining minerotrophic wetlands used by rearing coho salmon could decrease harvest of adult fish. Similar adverse effects might be expected on harvests of other wetland-dependent fish and wildlife species. Black spruce wetlands generally must be drained to extract nonrenewable resources such as peat or underlying minerals and thus drainage can be considered to benefit the consumptive use.

Habitat manipulation designed to maintain populations of fish and wildlife species dependent upon BSWs might mitigate adverse effects of drainage on consumptive use of those populations. Alternatively, species adapted to mesic conditions might provide substitute harvests for subsistence, personal, and commercial uses. Presumably, no mitigation would be required for the generally positive effects of drainage on extraction of fuel, fiber, and minerals from mires.

NONCONSUMPTIVE

Socioeconomic uses of BSWs that do not involve harvest of plants or animals for consumption or sale, and that do not involve extraction of peat, minerals, or other nonrenewable resources, are non-consumptive. As has been pointed out many times by others,

"nonconsumptive" uses of natural resources are rarely without impact; nevertheless, the term conveniently discriminates between those activities that intentionally remove materials from natural systems and those that do not. Nonconsumptive uses of wetlands include active and passive recreation, nature education, appreciation of unique geomorphic features, and preservation of scarce species. Documentation and evaluation of such nonconsumptive uses of wetlands is, in many cases, neither rigorous nor extensive (Sather and Smith 1984:60).

Active Recreation

Active recreation in wetlands includes swimming and boating (Adamus and Stockwell 1983:46). Hiking, mountain biking, skiing, dog sledding, snowmobiling, and similar activities might be added for Alaska's BSWs, which often are more accessible in winter than in summer. Active recreation can be divided into motorized and unmotorized activities. Motorized forms of active recreation in BSWs involve snowmobiles, all-terrain vehicles (ATVs), and airboats (Table 44). Nonmotorized active recreation in BSWs includes hiking, mountain biking, horseback riding, nordic skiing, and dog sledding (Table 45).

Passive Recreation and Use of Heritage Sites

Some socioeconomic uses of wetlands, labeled as passive recreation and use of heritage sites, occur

Table 44. Motorized forms of active recreation that occur in black spruce wetlands (BSWs) in Alaska.

Activity	Season	Comment
Snowmobiles	Winter	Snowmobiles can access most components of the taiga landscape, limited only by dense tree cover, deep snow without trails, or open water; cleared trails, including traplines, allow snowmobiles to use even densely treed wetlands
All-terrain vehicles	Summer, some winter use on trail systems	Provide motorized access to backcountry areas on established trails or cross-country routes that often pass through BSWs, although wettest areas avoided; traffic can degrade permafrost and create the potential for erosion in subarctic wetlands (Racine and Ahlstrand 1991)
Airboats	Summer	Traverse sparsely treed BSWs and treeless fens (Racine and Walters 1991) on the Tanana Flats

Table 45. Nonmotorized forms of active recreation that occur in black spruce wetlands (BSWs) in Alaska.

Activity	Season	Comment
Hiking	Summer, some winter use of trails	Minimize summer use of trails passing through the wettest wetlands because travel can be difficult or uncomfortable; in winter, trails passing through BSWs are used
Mountain biking	Summer, some winter use of trails	Minimize summer use of trails passing through the wettest wetlands because travel can be difficult or uncomfortable; in winter, trails passing through BSWs are used
Horseback riding	Summer, some winter use of trails	Minimize summer use of trails passing through the wettest wetlands because travel can be difficult or uncomfortable; in winter, trails passing through BSWs are used
Nordic skiing	Winter	Nordic skiers often use dedicated ski trails that pass through BSWs as well as using the general trail system used by mushers and snowmobilers
Dog sledding	Winter	Major winter use of most trails; some trails major training routes for competitive mushers, others routes for recreational travel and winter camping; many trails on valley bottoms or flats in BSWs to avoid steep terrain (pers. observ.)

without obvious consumption of wild resources and sometimes without actual entry into the wetlands themselves. Adamus and Stockwell (1983:47) describe passive recreation and uses of heritage sites as "aesthetic enjoyment, nature study, picnicking, education, scientific research, open space, preservation of rare or endemic species, maintenance of the gene pool, protection of archaeologically or geologically unique features, maintenance of historic sites, and an infinite number of other mostly intangible uses." Black spruce wetlands support many of these uses.

Passive recreation encompasses aesthetic enjoyment and open space uses of BSWs. Wetlands occurring in a wilderness setting contribute to landscape diversity and presumably contribute to the aesthetic enjoyment of such landscapes. Although use of mires for open space at least conceptually occurs in wilderness contexts, such use is most apparent in urban and suburban settings where open space is scarce. Many of the remaining open areas in Anchorage and Fairbanks, for example, are BSWs (Municipality of Anchorage 1982; Hogan and Tande 1983; D.K. Swanson, Nat. Resour. Conserv. Serv., pers. commun.).

Although passivity may characterize a few uses of heritage sites, most uses listed by Adamus and Stockwell (1983:47), such as nature study and education, imply some sort of active involvement with wetlands. Black spruce wetlands relatively accessible from roads and trails not only provide open space but also the opportunity for bird watching and nature study, especially if ponds supporting breeding waterfowl and other birds (e.g., Hogan and Tande 1983, Murphy et al. 1984, Martin et al. 1995) occur in association with the wetland. On a more organized basis, BSWs can be sites for nature education, such as occurs on the Creamer's Field Migratory Wildlife Refuge in Fairbanks, and sites for scientific research (e.g., Slack et al. 1980, Siegel and Glaser 1987).

Mire "types" and plant communities sometimes are rare or endangered because of changes brought about by wetland drainage or loss (Lee et al. 1982, Eurola et al. 1991). Minnesota mires support rare plant species (Glaser 1987:42-45), and brownwater streams draining Alberta peatlands contain rare midges (Boerger 1981). In Alaska, BSWs support a number of relatively rare plant species (R. Lipkin, Alaska Nat. Heritage Prog., Univ. Alaska, Anchorage, pers. commun.). Protecting habitats, and consequently gene pools, for rare, threatened, or endangered species constitutes a use of heritage sites.

Black spruce wetlands in the zone of discontinuous permafrost sometimes contain unique geomorphic features such as thermokarst ponds and palsas. Like preserving rare plants and animals, preserving unusual geomorphic features is a use of heritage sites. These features can serve educational and research purposes as well.

Use Summary

Black spruce wetlands provide for non-consumptive uses. Active recreation in BSWs, particularly in winter, appears to constitute their major nonconsumptive use. Dog sledding and snowmobiling predominate, but hiking, mountain biking, horseback riding, nordic skiing, ATV riding, and airboating also occur in BSWs. Less active uses of these wetlands include their provision of open space and landscape diversity, sites for nature study and education, research sites, habitats and maintenance of gene pools for rare species, and unique geomorphic features related to permafrost phenomena.

Nonconsumptive uses of BSWs are best documented through local and regional surveys, studies, or plans related to outdoor recreation, heritage sites, and land use. The current magnitude of many nonconsumptive uses of wetlands depends upon their accessibility and proximity to population centers. For example, established trails through or adjacent to BSWs may indicate their potential for recreational and educational use. Other wetland uses, such as maintaining gene pools of rare species, wilderness, and landscape diversity, may be inversely related to proximity of human populations. The nature of surrounding landscapes and their ecosystems or the uniqueness of BSWs within such landscapes may indicate these uses.

Use Sensitivity to Impacts

The sensitivities of nonconsumptive uses of BSWs vary with respect to fill. Active recreation that incidentally occurs in wetlands (e.g., use of a trail that passes through a bog) often would not be affected by fill. In fact, fill sometimes is placed in wetlands to facilitate such recreation (e.g., construction of bike paths). Fill placement would adversely affect use of BSWs by airboats. All uses of BSWs that depend upon the wetland community itself are

sensitive to fill placement. Examples include wilderness, study of wetland environments, protection of rare species, and provision of landscape diversity (at least where BSWs are not abundant).

Re-establishment of diverse natural communities on fill surfaces, although likely not compatible with the purposes for which fills are placed, could mitigate some adverse impacts. Bird watching, for example, could occur in shrub thickets on fill surfaces, and revegetated fills would provide open space. Mitigating fill impacts on rare mire species appears infeasible without carefully replicating lost habitats.

The nonconsumptive uses of BSWs also vary with respect to their sensitivity to drainage, but drainage impacts probably are less severe than those associated with fill. Wetland drainage might facilitate most forms of active recreation, particularly summer use of formerly wet trails. In contrast, drainage likely would prevent airboats from using sparsely treed BSWs. Wetland drainage would alter vegetation communities with concomitant effects on passive recreation and use of heritage sites. Although open space uses and nature study could continue, species associations would differ. Impacts of drainage on protection of rare species, particularly hydrophytic plants, likely would be severe, although less than those imposed by fill. Unique geomorphic features resulting from permafrost phenomena might be lost under altered thermal and hydrologic regimes following drainage.

Most adverse impacts of drainage on non-consumptive uses of BSWs would be difficult to mitigate and would require different techniques for different uses. Drainage systems that were sufficiently wide to accommodate airboats might allow continued airboat use but could impair trail use by hikers, snowmobilers, dog sledders, and skiers unless mitigated by placement of culverts or bridges. Habitat manipulation, such as prescribed burning to control woody vegetation, might mitigate the impacts of wetland drainage on some rare species but is unlikely to meet the needs of obligate wetland plants. Mitigating drainage impacts on unique geomorphic features of mires does not appear economically feasible.

DATA GAPS

Few studies directly address socioeconomic uses of BSWs. The existence and magnitude of these uses must be inferred from indirect data. The strength of such inferences often is limited by lack of quantitative harvest records, use of both wetland and nonwetland habitats by target species, and confounding effects of varying market forces on harvests. Perhaps even less information is available for nonconsumptive uses of wetlands. The following discussion identifies data gaps with respect to socioeconomic uses of BSWs.

Consumptive Uses

Indirect data sources for consumptive uses of BSWs sometimes are available in socioeconomic studies of individual communities or regions, records of fish and wildlife harvests, and economic records of commercial activities. Although these sources provide harvest levels for subsistence, personal, and commercial uses of fish and wildlife, they do not partition harvests by habitat or wetland class. A general lack of information relating fish and wildlife habitat use to specific wetland classes exacerbates this problem. In ecological terms, flows of energy and biomass from BSWs to humans and human uses have not been quantified. Synecological studies of BSWs could help fill these data gaps.

Records of resource management and regulatory agencies, if comprehensively examined, might document consumptive uses of BSWs that involve peat mining or mineral extraction. No single repository of such information exists, however, and past and current mining does not address the potential for future mining in or beneath wetlands. Efforts to inventory the peat resources of Alaska by even minimal sampling of peat depths and characteristics have been limited to relatively small areas (e.g., Huck and Rawlinson 1982, Rawlinson 1986). State and federal agencies map Alaska's mineral resources, but correlating these resources with BSWs would require detailed wetland mapping. Further geologic and economic studies of peat and mineral resources in relation to BSWs would help document their existing and potential uses for extraction of economic resources.

Nonconsumptive Uses

Some nonconsumptive uses of BSWs in or near human population centers can be inferred from land management plans, establishment of parks and recreation areas that include such wetlands, and pres-

ence of established trail systems, but quantitative data on use of specific wetland types does not appear to exist. This problem is complicated by the wide variety of nonconsumptive uses, some of which do not require entry into individual wetlands in order to be fulfilled (e.g., aesthetic appreciation) and are poorly amenable to measurement. Virtually no direct data are available for nonconsumptive uses of BSWs away from human population centers. Scientifically designed survey strategies, supplemented by quantitative observations of actual wetland use, might offer a way to elicit information from the populace on their nonconsumptive uses of BSWs.

Use Sensitivity to Impacts

The impacts of filling or draining BSWs on their consumptive and nonconsumptive uses can be inferred but are poorly documented. Reduction in the renewable-resource base through placement of fill concomitantly reduces consumptive uses of plants and animals. Better understanding of the habitat function and consumptive uses of BSWs would help define potential impacts of wetland fill. Research quantifying declining subsistence and personal uses of wild materials in areas of high wetland loss from fill would be helpful, but confounding variables such as shifts in lifestyle from rural to urban might make the research difficult.

The impacts of fill on consumptive uses of nonrenewable resources such as peat or underlying minerals qualitatively appear self-evident. Economic studies of the costs of removing fill to reach underlying resources could provide quantitative documentation of the disincentives to mining imposed by fill placement. Other factors such as property values and land use of filled terrain might provide even stronger disincentives for extraction of peat or mineral resources underlying fill.

Drainage of BSWs without conversion to agriculture or placement of fill is uncommon in Alaska, which limits opportunities for direct studies of drainage impacts on consumptive uses. Nevertheless, studies better documenting the habitat function of BSWs, including their effects on waterbodies and fisheries resources occurring in wetland contexts, would strengthen predictions concerning drainage impacts on wetland-dependent animal species. In a related vein, studies documenting the relationships between distributions of wetland plants and hydroperiods would strengthen predictions concerning changes in plant communities with drainage, which could then be linked to potential changes in consumptive use of renewable wetland resources. Long-term observations of experimentally drained BSWs might provide a similar basis for predicting potential changes in consumptive use. The salutary effects of drainage on extraction of nonrenewable resources appears self-evident and does not require study.

The impacts of filling or draining BSWs on their nonconsumptive uses are undocumented. Some beneficial (e.g., fill for trail construction) and adverse (e.g., loss of wetland study areas) effects are self-evident. The primary gap is lack of data on nonconsumptive uses themselves. Filling this gap would strengthen inferences about the impacts of filling or draining BSWs on their nonconsumptive uses. Experimental verification of predicted changes in wetland communities following drainage is lacking for Alaska, although such changes have been documented elsewhere (e.g., Glaser 1987:67). Previously discussed data gaps concerning habitat and food chain-support functions of BSWs also are relevant to changes in nonconsumptive use following drainage.

SUMMARY AND CONCLUSIONS

Alaska's 70.7 million ha of wetlands include about 14 million ha of ***black spruce wetlands*** (BSWs), which are important boreal ecosystems. For purposes of this report, BSWs are wetlands supporting black spruce of any size or stand density. Regulatory decisions concerning conversion of these wetlands to other uses require knowledge of their ***wetland functions*** and hence their values to society.

The objective of this report is to provide a "functional profile" of Alaska's BSWs for use by scientists, wetland managers, commercial interests, and citizens and to facilitate implementation of the hydrogeomorphic method of wetland classification. This profile cites many studies conducted outside Alaska, usually from boreal forest. Future research should verify extrapolation of cited literature to Alaska's BSWs.

BLACK SPRUCE AND THE TAIGA ENVIRONMENT

Black spruce wetlands occur with the ***taiga***, the northern coniferous forest extending across North America and Eurasia. Taiga occurs under continental climates characterized by extreme temperatures, low precipitation, relatively low rates of evapotranspiration, and large seasonal variation in solar radiation. Vegetation and topography strongly control the amount of solar radiation reaching ground surfaces. Soils of subarctic sites receiving reduced solar radiation or insulated by thick moss cover can remain frozen at depth for periods of ≥2 yr and thus are ***permafrost***. Permafrost distribution in subarctic taiga is discontinuous.

Unique geomorphic features associated with permafrost include ***peat plateaus***, ***patterned ground*** induced by ***ice wedges***, and ice-cored hummocks called ***palsas***. Fire or other disturbance often alters thermal regimes of permafrost sites and increases seasonal depths of thaw. Where ice contents of permafrost soils are high, thaw can create irregular ***thermokarst*** topography and ***thaw lakes*** or ponds. The relative impermeability of permafrost contributes to wetland formation; thus, frost and thaw phenomena in part account for interior Alaska's mosaic of wetlands and nonwetlands.

Pleistocene glaciation, although limited in extent in Alaska, influenced development of present-day taiga ecosystems. In interior Alaska, shrub tundra replaced the Mammoth Steppe of the Pleistocene ~14,000 yr BP, followed after ~10,000 yr BP by forests containing white spruce, paper birch, resin birch, juniper, and American green alder. Black spruce became abundant after 7,000 yr BP, and species composition has remained essentially unchanged since that time.

Within North American taiga, tree size and canopy cover in increase southerly from ***forest-tundra*** to open woodland, main boreal forest, and boreal-mixed forest ecotone. Alaska's taiga primarily comprises open woodland and forest of black and white spruce, tamarack, paper birch, quaking aspen, and balsam poplar. Typical community types of black spruce include *Picea mariana/Vaccinium uliginosum-Ledum groenlandicum/Pleurozium schreberi*, *Picea mariana*/feathermoss-lichen, and *Picea mariana/Sphagnum* spp.-*Cladina* spp.

Fire, at natural return intervals of 100 to 200 yr, and fluvial processes periodically reset taiga succession and create a mosaic of plant communities. The ***semiserotinous cones*** of black spruce increase seed release following fire. Black spruce/feathermoss succession has six generalized stages: newly burned,

moss-herb, tall shrub-sapling, dense tree, hardwood, and spruce. Post-fire succession in black spruce often produces little change in species composition of vascular plants. Wet black spruce sites in lowlands may cycle between treeless wetlands and BSWs.

Erosion in floodplains removes older plant communities, and deposition forms new surfaces for primary succession. These sites succeed to white spruce. Thick moss layers and canopy closure in late successional stages lower soil temperature, cause permafrost aggradation, and increase soil moisture. Black spruce may replace white spruce as soils become waterlogged in old floodplain stands protected from fire.

Black spruce occurs across boreal North America, largely coincident with the taiga, and covers 44% of interior Alaska. This species commonly grows in the Interior on cold, wet sites at elevations of <610 m, where it typically is 4.5- to 9-m tall and 75 to 150 mm in diameter, but also occurs on drier, nutrient-deficient upland sites and as a shrub or as ***krummholz*** at altitudinal treelines ≤832 m. Stem densities of mature trees average 300 ha^{-1} on moist sites.

Black spruce dominates cold, wet sites with low pH, low base element saturation, long turnover times for nutrients and organic matter, high biomass accumulation, and low element concentrations. Mosses compete for and trap nutrients on these sites, account for significant proportions of community production, and cause ***paludification***, which can produce sparsely treed *Sphagnum* ***bogs*** in the absence of fire. Nevertheless, slow growth, low palatability to herbivores, and reproduction by both sexual and vegetative (***layering***) means adapt black spruce to these low-nutrient environments.

BLACK SPRUCE WETLANDS

Vegetation, soils, and hydrologic characteristics are the chief criteria for delineating wetlands in North America. Wetland hydrology drives wetland formation and usually produces ***hydric soils*** and ***hydrophytic*** vegetation. Wetland hydrology can occur where bedrock, marine or lacustrine clays, glacial tills, or permafrost impede drainage. Impeded drainage often exists in lowlands and on slopes underlain by permafrost in the Subarctic.

In North American taiga, black spruce, sometimes growing in mixed stands with tamarack, is the tree species most often associated with treed wetlands. Some BSWs are ***peatlands*** or ***mires***, peat-forming ecosystems having ≥0.4 m peat thickness and generally separated into bogs and ***fens***. Bogs are ***ombrotrophic*** mires, meaning they receive water exclusively as precipitation, which typically has a low nutrient content. Fens are ***minerotrophic*** mires, meaning they receive water that contains moderate to high concentrations of nutrients from contact with mineral soil.

Black spruce occurs in both bogs and fens but does not occupy wet extremes of mire moisture gradients. *Sphagnum* mosses dominate ground cover in bogs and graminoids in fens. Lichens occur on peat surfaces too dry to support mosses.

Black spruce wetlands with ***Histosols***, soils having >0.4 m of organic material, are mires, but peat-forming BSWs with histic epipedons (organic layers ranging from 0.2 to 0.4 m) are not mires by Canadian usage. Black spruce wetlands with histic epipedons occupy a continuum from mire to sites possibly influenced by mineral soils. Sites supporting dwarf trees (<3-m tall) have higher probabilities of being mires than do sites supporting larger trees, but black spruce forests and woodlands also can be mires or have mire inclusions.

Black spruce wetlands primarily fall within the Palustrine Forested Needle-leaved Evergreen and Palustrine Scrub-Shrub Needle-leaved Evergreen classes of the U.S. Fish and Wildlife Service classification system. Sparsely treed (≤30%) graminoid BSWs with few shrubs could fall within the Palustrine Emergent Wetland class. Black spruce is more closely associated with ombrotrophic than minerotrophic conditions but is found in both types of mire. Common plant taxa in BSWs include black spruce, tamarack, willows, ericaceous shrubs, shrub birches, buckbean, sedges, cotton grasses, horsetails, *Sphagnum* and brown mosses, and lichens.

Black spruce community types of interior Alaska have varying probabilities of occurring in wetlands. Based on published descriptions of dominant vegetation, soil moisture conditions, presence or absence of permafrost, slope, and aspect, six common community types array from highest to lowest probability of being wetland as follows: *Picea mariana/Sphagnum* spp.-*Cladina* spp., *Picea mariana/Vaccinium uliginosum-Ledum groenlandicum/Pleurozium schreberi*, *Picea mariana-Betula papyrifera/*

Vaccinium uliginosum-Ledum groenlandicum, *Picea mariana*/feathermoss-lichen, *Picea mariana-Picea glauca/Betula glandulosa*/lichen, and *Populus tremuloides-Picea mariana/Cornus canadensis*. Site-specific investigation of soils and hydrology may be necessary to delineate BSWs within a given community type.

Activities potentially affecting BSWs include filling, draining, flooding (wetland conversion), or clearing; disposing of wastes; or mining peat deposits. Fill provides stable surfaces for transportation, building construction, or resource development but physically buries wetlands, radically changing their functions and values. Draining wetlands facilitates residential and commercial development, transportation, agriculture, and forestry. Stripping vegetation to thaw permafrost can internally drain BSWs. Drainage effects include lower water tables, accelerated peat decomposition, and subsidence of ground surfaces. Flooding wetlands converts them to shallow or deep open-water habitats and generally alters their functions. Effects of flooding BSWs include thermokarst development, altered vegetation, and transition from ombrotrophic to minerotrophic conditions.

Activities such as powerline installation and maintenance, pipeline construction, agricultural development, and logging clear BSWs. Effects include rutting and compaction of peat, reduced aerial biomass and plant species diversity, habitat alteration and fragmentation, nutrient depletion, erosion, and thermokarst development. Disposal of solid wastes in wetlands produces the same impacts as placement of fill but is accompanied by the potential for groundwater contamination by toxic substances. Liquid wastes such as sewage effluent can be treated in wetlands, but effects may include flooding, altered vegetation, and reduced species diversity. Peat mining on a commercial scale alters wetland characteristics. Effects include those of drainage and clearing as well as removal of organic substrates and elevated export of nutrients.

Scientists have not systematically studied the functions and values of BSWs, but silvicultural and ecologic research on black spruce forests and mires, research in individual disciplines related to wetland functions, and directed research on wetland functions conducted in areas outside the distribution of black spruce are applicable. Silvicultural research related to black spruce has focused on methods to improve timber production and promote regeneration following harvest. Studies of ecosystem structure and function that include well-treed BSWs reveal wetland functions. Very little physical science research in Alaska and northern Canada directly examines wetland functions of BSWs, but hydrologic and water quality (including water chemistry) studies that include BSWs can be interpreted to characterize these functions.

Specific studies of mires have largely focused on their hydrology, soil and water chemistry, and vegetation. Eurasian studies of mire classification, vegetation, stratigraphy, uses, and sensitivity to impacts supplement studies conducted in northern Minnesota and Canada. Canadian research documents the stratigraphy, morphology, and vegetation of taiga mires, including the role of permafrost but usually does not directly address wetland functions. Several Alaskan studies document characteristics and development of taiga mires, and others address hydrology and permafrost, but none specifically treat mire functions. Integrated knowledge of BSWs in Alaska is sparse, but many lines of evidence from a variety of locations and disciplines are applicable.

HYDROLOGIC FUNCTIONS

Groundwater discharge, groundwater recharge, flow regulation, and erosion control are hydrologic functions of wetlands. Ombrotrophic BSWs, including bogs, do not perform the groundwater-discharge function. Minerotrophic BSWs perform the groundwater-discharge function if they are supplied by upward groundwater flow. Landscape position and piezometric, water chemistry, or water balance data can document such flow.

The groundwater-discharge function of minerotrophic BSWs is impaired or eliminated by fill placement within the area of discharge. Drains beneath the fill might maintain discharge but usually freeze and fail on permafrost soils. Wetland drainage is unlikely to adversely affect the water-supply aspect of the groundwater-discharge function of minerotrophic BSWs.

Ombrotrophic BSWs perform the groundwater-recharge function, but the magnitude of recharge generally is small and only applies to ***suprapermafrost groundwater*** in regions of widespread discontinuous permafrost. Minerotrophic

BSWs do not perform the groundwater-recharge function unless site-specific piezometric or water-balance studies show otherwise. Trophic status and permafrost extent indicate recharge potential and whether such recharge will affect ***subpermafrost groundwater***.

The groundwater-recharge function of BSWs is sensitive to fill placement and drainage, which convert potential or actual groundwater flows to surface flows. Directing fill runoff to adjacent undisturbed wetlands capable of recharging groundwater could compensate for lost recharge area, if runoff loading of the remaining wetlands did not exceed their infiltration capacity. The detrimental effect of drainage on groundwater recharge is ameliorated by the relatively low hydraulic conductivity of ***sapric peat***, which renders effective drainage difficult and expensive.

Black spruce wetlands perform the flow-regulation function through microtopographic ***detention*** and ***depression storage***, subsurface storage of snowmelt and precipitation, and evapotranspiration, but the magnitude of this function generally is small, often limited by the position of the water table. Minerotrophic BSWs fed by subpermafrost groundwater provide long-term baseflows, but BSWs supplied by suprapermafrost groundwater provide only quantitatively small, short-term baseflows. Black spruce wetlands generally regulate flow less effectively than vegetated, well-drained uplands of low to moderate slope.

Slope may indicate hydraulic response and water balance characteristics for ombrotrophic BSWs. Groundwater discharge indicates the ability of a minerotrophic BSW to provide baseflows but is a negative indictor for subsurface storage.

Fill and drainage diminish the flow-regulation function of ombrotrophic BSWs, and minerotrophic BSWs that do not discharge groundwater, by reducing storage and speeding surface runoff. For minerotrophic BSWs that discharge groundwater, fill reduces potential baseflows to streams. Highly-permeable fill or subdrains on nonpermafrost soils could maintain groundwater discharge for downstream water supplies. Little mitigation for loss of other aspects of flow regulation appears feasible without extensive hydraulic engineering.

Black spruce wetlands perform the erosion-control function by insulating permafrost soils and by mantling erodible mineral soils with a layer of peat. The magnitude of this function may not greatly exceed that of well-drained, mature, upland forest stands. Thickness of the organic mat may indicate potential effectiveness of the erosion-control function. The erosion-control function of BSWs probably is only slightly sensitive to fill placement if the organic mat is intact but somewhat more sensitive to ditching that exposes mineral soil or ice-rich materials.

Black spruce wetlands perform hydrologic functions to varying degrees, primarily determined by trophic status. In general, the magnitudes of hydrologic functions of BSWs are small. Hydrologic functions of BSWs are relatively less important than their water quality and ecologic functions.

Data gaps exist with respect to groundwater discharge and recharge, flow regulation, and sensitivity of hydrologic functions to impacts of fill placement and drainage. These gaps include relationships between groundwater discharge and minerotrophic BSW vegetation and morphology, the distribution and abundance of groundwater-discharge wetlands, effectiveness of BSWs for groundwater recharge, flow regulation by lowland (flat) BSWs, biological importance of baseflows originating in minerotrophic BSWs, effect of drainage on water balances of permafrost BSWs, and effects of fills on hydrologic functions of BSWs.

WATER QUALITY FUNCTIONS

Sediment retention, nutrient uptake, nutrient transformation, and contaminant removal are water quality functions of wetlands. Black spruce wetlands appear to perform the sediment-retention function. Minerotrophic BSWs have a greater opportunity to remove suspended solids from the water column than do ombrotrophic BSWs. Indicators of the sediment-retention function include visible sediment deposits or microtopographic features that slow water movement.

The sediment-retention function of BSWs is sensitive to placement of fill, which often increases sediment loading on remaining wetlands, and to drainage, which may generate solids. Minerotrophic BSWs with surface flow are more sensitive to drainage than are precipitation-driven BSWs. Mitigation might include armoring fill surfaces and drainage ditches and constructing settling ponds.

Black spruce wetlands perform the nutrient-uptake function; this function also occurs in well-drained uplands. Plants characteristic of nutrient-poor ombrotrophic and weakly minerotrophic wetlands can assimilate anthropogenic nutrients, as can plants adapted to the high nutrient levels of minerotrophic BSWs. Because all plant communities take up nutrients from their environments, no specific indicators of the nutrient-uptake function need be applied to vegetated wetlands.

The nutrient-uptake function of BSWs is sensitive to fill, which, unless vegetated, has little capacity for nutrient uptake. Revegetating fill surfaces to achieve dense vegetative cover could ameliorate excessive nutrient loading from fill runoff in the absence of high anthropogenic nutrient inputs (e.g., fertilization), but such surfaces could not remove waterborne nutrients within the wetland. Draining BSWs reduces, but does not eliminate, uptake of waterborne nutrients by wetland plants by channeling flow and reducing nutrient residence time. Maintaining a vegetated surface would partially mitigate drainage impacts on nutrient uptake.

Black spruce wetlands perform the nutrient-transformation function for nitrogen (N) and phosphorus (P), tending to make inorganic forms less available, and are sinks for nutrient elements. Ombrotrophic BSWs may reduce nutrient availability and fix N to a greater extent than do minerotrophic BSWs. Minerotrophic BSWs may mineralize more nutrients, have greater plant uptake of nutrients, and adsorb more P than do ombrotrophic BSWs. Accumulating organic matter indicates nutrient immobilization, and trophic status indicates details of nutrient transformations in a given BSW.

The nutrient-transformation function of BSWs is sensitive to placement of fill, which buries the media responsible for such transformations, but is less sensitive to drainage. Establishing dense vegetation, including N-fixing species, on fill surfaces could mitigate some fill-induced impacts. On-site mitigation of altered patterns of nutrient transformation in drained BSWs does not appear possible without restoring lowered water tables to their original positions.

Black spruce wetlands perform the contaminant-removal function by taking up and storing metals, immobilizing nutrients, and, in some cases, buffering inputs of acids but do not effectively degrade hydrocarbons or, by extension, other toxic organic compounds. Minerotrophy, perhaps supplemented by the presence of acid-buffering vegetation such as tamarack and Labrador-tea, indicates acid buffering capacity, and rapidly accumulating organic matter indicates high nutrient immobilization.

The contaminant-removal function of BSWs is sensitive to placement of fill, which buries chemical and biotic media responsible for the function, but is less sensitive to drainage. Mitigation might include calcareous fill to buffer acid deposition, manipulating warm, aerobic fill surfaces to degrade organic contaminants, and creating constructed wetlands for uptake of metals. Restoring water tables of BSWs to predisturbance elevations would mitigate the effects of drainage on the contaminant-removal function.

Black spruce wetlands perform water quality functions. In general, the magnitudes of these functions are large. Black spruce wetlands are nutrient sinks that offer a range of pH values to facilitate various chemical processes related to water quality. The water quality functions of BSWs appear much more important than their hydrologic functions.

Data gaps exist with respect to the water quality functions of Alaska's BSWs and their sensitivities to fill and drainage. These gaps include studies of sediment retention by individual BSWs as opposed to watersheds containing BSWs, nutrient uptake in the wetter ombrotrophic BSWs and most minerotrophic BSWs, P uptake in minerotrophic BSWs, P precipitation and adsorption in all BSWs, nitrification and denitrification in all BSWs, metal uptake and plaque formation in minerotrophic BSWs, nutrient content of minerotrophic peat, controls on peat accumulation in BSWs, acid-buffering capacities of BSWs, effects of drainage on nutrient transformation and contaminant removal in BSWs, and effects of drainage on net accumulation of organic matter in BSWs.

GLOBAL BIOGEOCHEMICAL FUNCTIONS

Black spruce wetlands function to fix carbon (C) by photosynthesis, store C as organic matter, and release stored C as CH_4 and CO_2 by decomposition and fire. Saturated conditions in BSWs minimize release of C as compared to nonwetlands. Active accumulation of organic matter indicates C storage in BSWs. High water tables and low redox potentials indicate potential CH_4 emission whereas aerobic

surface layers indicate potential CO_2 emission.

The C cycling and storage functions of BSWs is sensitive to placement of fill, which eliminates the vegetation responsible for C fixation. Establishing dense vegetation on a fill surface could mitigate loss of C fixation by wetland plants but would not fully mitigate loss of C storage because most C would return to the atmosphere by rapid decomposition. The effects of drainage on the C cycling and storage function of BSWs are not clear.

Black spruce wetlands are important sinks for atmospheric C. This function is very important with respect to global climate and helping to ameliorate anthropogenic release of CO_2. Documentation of net C balance for a variety of BSWs, as influenced by trophic status, community composition, and hydrologic relationships, is warranted given the importance of CO_2 as a greenhouse gas.

ECOLOGIC FUNCTIONS

Nutrient cycling, nutrient export, food-chain support, and fish and wildlife habitat are ecologic functions of wetlands. Black spruce wetlands perform the nutrient-cycling function. Minerotrophic BSWs likely cycle more nutrients than do ombrotrophic BSWs but are unlikely to approach the nutrient-cycling capabilities of upland deciduous forests. Trophic status may be an indicator of nutrient-cycling rates in BSWs.

The nutrient-cycling function of BSWs is more sensitive to placement of fill than to drainage because fill buries media responsible for the function. Nutrient cycling could be re-established on fill surfaces covered by dense vegetation. Perhaps the only predictions possible with regard to nutrient cycling and drainage of BSWs are that increased decomposition coupled with increased net primary production indicate increased nutrient cycling whereas decreased decomposition coupled with decreased net primary production indicate decreased nutrient cycling. Manipulating the balance of decomposition and production in drained wetlands to simulate predrainage states might mitigate impacts on nutrient cycling.

Black spruce wetlands with outflows perform the nutrient-export function, but the magnitude of such export is small. Minerotrophic BSWs may export more N and P than do ombrotrophic wetlands, but ombrotrophic BSWs may export more C than do minerotrophic wetlands. Discharge of water from a BSW indicates some nutrient export, specifically C if tannic stained, as do highly decomposed wetland surfaces.

The nutrient-export function of BSWs is sensitive to placement of fill, although the effects are ambiguous for N and P, but is enhanced by drainage. Flows emanating from fill surfaces and the concentrations of nutrients in those flows might be adjusted to match natural conditions to mitigate impacts on the nutrient-export function. Mitigating the positive effects of drainage on the nutrient-export function of BSWs appears unlikely.

Black spruce wetlands support grazing and detrital food chains and thus perform the food-chain support function. The magnitude of this function appears to be greater in minerotrophic BSWs than in ombrotrophic BSWs. Although the food-chain support function of BSWs, measured by community production, is lower than that of well-drained taiga uplands, it is essential to organisms limited to wetland environments. Trophic status and direct observation of animal use or presence of forage may indicate the potential magnitude of food chain support by BSWs.

The food chain-support function of BSWs is much more sensitive to placement of fill, which eliminates primary production, than to drainage that leaves vegetated surfaces. Re-establishment of vegetative cover, particularly that emulating the undisturbed wetland, could mitigate the effects of fill placement on food chains but is unlikely to be compatible with fill purposes. Drainage may increase net primary production, particularly that of trees. Habitat manipulation might be used to mitigate shifts in dominance by plant species and potential losses in productivity in drained BSWs.

Alaska's BSWs directly provide habitat to a large number of avian species, especially passerines, a smaller number of mammalian species, and one amphibian species. A large number of waterbirds use waterbodies associated with BSWs, but inclusion of these species in the habitat function of BSWs largely is a matter of the scale at which habitat is addressed. Excluding waterbirds, only about 12 nonraptorial bird species, 7 raptorial bird species, and 13 mammalian species might be judged commonly and consistently present in BSWs. Moose and caribou, although important users of BSWs, do not appear in

these totals because other plant communities are their preferred habitats.

Trophic status might prove a good predictor for presence or absence of selected avian or mammalian species, but such relationships rarely have been tested. Directly sensing avian and mammalian species or their vocalizations, nests, droppings, tracks, preferred forage, browsed or cropped stems, burrows, or dens best evaluates the habitat function of BSWs.

The habitat function of BSWs is much more sensitive to placement of fill, which eliminates food and cover, than to drainage that leaves natural vegetation intact. Revegetating fill surfaces might partially mitigate habitat impacts of fill placement, but re-establishment of cover structure and food density characteristic of the original BSW would be extremely difficult. Habitat manipulation might minimize changes in plant species composition brought about by wetland drainage, and carefully designed artificial ponds could replace lost open-water habitats.

Black spruce wetlands perform ecologic functions. The magnitudes of nutrient-cycling, nutrient-export, and food chain-support functions of ombrotrophic and weakly minerotrophic BSWs are limited in comparison with those of highly minerotrophic wetlands and, in some cases, well-drained uplands. The habitat function of BSWs is important to most taiga birds and mammals. As a group, the ecologic functions of black spruce wetlands are relatively more important than their hydrologic functions, comparing favorably with their water quality functions.

Data gaps exist with respect to the ecologic functions of Alaska's BSWs. Addressing these gaps would require studies of nutrient cycling in sparsely treed BSWs, trophic controls on nutrient cycling in BSWs, nutrient export from all BSWs, the ecologic role of exported C in brownwater systems, primary production in sparsely treed BSWs, partitioning of energy flows between grazing and detrital food chains in all BSWs, effects of trophic status on partitioning of energy flows, secondary production supported by BSWs, synecology of BSWs in relation to trophic status and vegetation structure and composition, effects of drainage on nutrient cycling by BSWs in relation to trophic status, effects of fill and drainage on nutrient export, effects of drainage on partitioning of energy flows and food chain support, mitigation techniques for habitat losses to fill, and effects of drainage on plant species composition.

SOCIOECONOMIC USES

Subsistence, personal, and commercial harvests of wetland-dependent fish, wildlife, and plant resources are the most important consumptive uses of Alaska's BSWs. Consumptive uses of nonrenewable resources such as peat, gravel, and placer and hardrock minerals occurring in or beneath BSWs currently are few in Alaska. The magnitude of consumptive uses of BSWs perhaps is best judged through regional and local socioeconomic studies.

Consumptive use of wetland-dependent renewable resources is more sensitive to placement of fill, which eliminates primary production and animal habitats and buries nonrenewable resources, than to drainage that leaves natural vegetation intact. Re-establishment of productive animal habitats on fill surfaces and minimization of fill depths could mitigate fill impacts. Habitat manipulation designed to maintain populations of fish and wildlife species dependent upon BSWs might mitigate adverse effects of drainage on consumptive use of those populations.

Active recreation in BSWs, particularly in winter, appears to constitute their major nonconsumptive use. Less active uses of these wetlands include open space, biodiversity, nature study, research, rare species, and geomorphic features. Nonconsumptive uses of BSWs are best documented through local and regional surveys, studies, or plans related to outdoor recreation, heritage sites, and land use.

Nonconsumptive uses of BSWs vary in their sensitivity to fill placement and drainage. Fill placement and drainage enhance most means of transportation across mires but diminish passive recreation or heritage site uses. Re-establishment of diverse natural communities on fill surfaces could mitigate some adverse impacts. Most adverse impacts of drainage on nonconsumptive uses of BSWs would be difficult to mitigate and would require different techniques for different uses. Habitat manipulation might mitigate the impacts of wetland drainage on some rare species but is unlikely to meet the needs of obligate wetland plants.

Black spruce wetlands provide for socioeconomic uses. The magnitude of consumptive uses

probably exceeds that of nonconsumptive uses, based on the importance of harvests of fish, wildlife, and plant materials in Alaska's socioeconomic fabric. Comparison of socioeconomic uses of BSWs with their wetland functions may not be fully appropriate, but the importance of such uses appears to compare favorably with the importance of ecologic and water quality functions.

Few studies directly address socioeconomic uses of BSWs. Filling data gaps would require studies of the relationships between wild harvests and various types of BSWs, synecology of BSWs, distribution and abundance of peat and mineral resources in relation to BSWs, nonconsumptive uses of BSWs through scientific surveys and direct observations, impacts of wetland loss on wild harvests, effects of BSWs on adjacent waterbodies and fisheries resources, effects of drainage on plant communities,

CONCLUSIONS

Black spruce wetlands are prominent features in taiga landscapes. These features have been cast as having little biological or socioeconomic importance. Examination of the characteristics of Alaska's BSWs reveals that they perform low-magnitude hydrologic functions, perform several substantial water quality and ecologic functions, and provide for important socioeconomic uses.

Characteristics which limit the hydrologic functions of BSWs, particularly ombrotrophic wetlands, include permafrost and the low hydraulic conductivities of decomposed peat. These characteristics impede exchange of deep and near-surface groundwater, speed surface and near-surface runoff, and reduce baseflows.

Characteristics which enhance the water quality functions of BSWs include peat and peat-forming vegetation. Peat-forming vegetation such as *Sphagnum* mosses compete for nutrients and form a sediment-trapping microtopography in bogs. Some vegetation responds to nutrient input with increased uptake. Peat accumulation sequesters nutrients and contaminants.

Characteristics which influence the ecologic functions of BSWs include their extensive distribution and their trophic status. Most of Alaska's birds and mammals appear adapted to use BSW habitats to greater or lesser degrees. Ombrotrophy limits nutrient cycling and food chain support, but minerotrophy enhances these functions.

Socioeconomic uses of Alaska's BSWs appear strongly influenced by the strength of their ecologic functions, particularly the habitat function.

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APPENDIX A
WETLAND CLASSIFICATION

Circumboreal mire vegetation is similar, especially in bogs (Sjörs 1963 *in* Moore and Bellamy 1974:181, Sorenson 1948 *in* Moore and Bellamy 1974:181), as is mire morphology. For example, *Sphagnum magellanicum* and *S. papillosum* characterize nutrient-poor mires in the Amur River valley (Botch and Masing 1983); both species also occur in North American wetlands (Vitt et al. 1988:53). Aapa mires (patterned mires) and palsa mires (wetlands containing ice-cored mounds) occur in Fennoscandia (Moore and Bellamy 1974:12-30, Sjörs 1983, Eurola et al. 1984), Siberia (Botch and Masing 1983), and North America (Moore and Bellamy 1974:44,182). Pleistocene glaciation influenced formation of many taiga wetlands, as well (Strahler 1963:532-533, Zoltai and Pollett 1983, Masing 1984, Hollis and Jones 1991).

Despite widespread similarities of peatland vegetation and morphology, many methods of classification have been described, often on a country-by-country basis (e.g., Cowardin et al. 1979, Ruuhijärvi 1983, Sjörs 1983, Zoltai and Pollett 1983, Moore 1984). Two broad-based wetland classification systems apply to boreal regions of North America: the U.S. Fish and Wildlife Service system (Cowardin et al. 1979) and the Canadian system (Natl. Wetlands Working Group 1988).

U.S. FISH AND WILDLIFE SERVICE SYSTEM

The National Wetlands Inventory of the U.S. Fish and Wildlife Service classifies and maps wetlands in the United States using the hierarchical system of Cowardin et al. (1979). The classification is divided into five systems at its broadest level: Marine, Estuarine, Riverine, Lacustrine, and Palustrine. Subsystems, classes, subclasses, and dominance types are successively narrower classification divisions. This report addresses selected wetlands in the Palustrine System.

Vegetated (≥30% cover of trees, shrubs, persistent emergents, emergent mosses, or lichens), freshwater (<0.5‰ ocean-derived salts) wetlands generally form the Palustrine System. Small (<8 ha), shallow (<2 m), sparsely-vegetated freshwater wetlands lacking wave-formed or bedrock shorelines also are palustrine. No subsystems are used to classify palustrine habitats. Eight classes based on dominant life form occur within the Palustrine System, three of which are relevant to BSWs: Emergent Wetland, Scrub-Shrub Wetland, and Forested Wetland.

Forested Wetland must have ≥30% areal cover of tall ≥6 m) woody vegetation. Areas with <30% cover by woody vegetation ≥6 m in height, but with ≥30% total cover by woody vegetation are Scrub-Shrub Wetland. Needle-leaved Evergreen, Broad-leaved Evergreen and Broad-leaved Deciduous are subclasses of Forested Wetland and Scrub-Shrub Wetland.

Rooted herbaceous vegetation standing above the surface of periodically wet soil or water forms the Emergent Wetland Class. Mosses and lichens form a separate stratum and are not included in this class. Subclasses of Emergent Wetland are Persistent and Nonpersistent based on whether or not the plants remain standing between growing seasons.

CANADIAN SYSTEM

The Canadian system of wetland classification uses three hierarchical levels: class, form, and type (Natl. Wetlands Working Group 1988:416). Bog,

fen, swamp, marsh, and shallow open water are the five wetland classes used in the Canadian system. This system subdivides bogs into 18 wetland forms, fens into 17 forms, swamps into 7 forms, marshes into 15 forms, and shallow water into 13 forms (Zoltai 1988). The third hierarchical level of the system uses eight general physiognomic types of vegetation (treed, shrub, forb, graminoid, moss, lichen, aquatic, and nonvegetated) as descriptors of wetland forms. Specific types (e.g., "coniferous treed," "tall shrub," or "sedge") occur within several of the general types (Natl. Wetlands Working Group 1988:426).

Wetland scientists divide Canada into wetland regions and subregions (Natl. Wetlands Working Group 1986). Two of these regions, the Subarctic and Boreal, encompass the taiga and thus much of the distribution of black spruce. Within the Subarctic and Boreal wetland regions of Canada, bogs and fens are the wetland classes supporting black spruce or closely associated with BSWs.

APPENDIX B
SUBARCTIC AND BOREAL BOGS AND FENS IN THE CANADIAN CLASSIFICATION SYSTEM

The following text quotes physical descriptions of subarctic and boreal bog and fen characteristics from the National Wetlands Working Group (1988:417-420) and summarizes descriptions of vegetation from Zoltai, Tarnocai et al. (1988) and Zoltai, Taylor et al. (1988). Black spruce wetlands of Alaska presumably share some of the characteristics of comparable wetlands described for Canada.

BOGS

Basin Bog - A bog situated in a basin that has an essentially closed drainage, receiving water from precipitation and from runoff from the immediate surroundings. The surface of the bog is flat, but the peat is generally deepest at the centre. Basin bogs occur in the Boreal Wetland Region. Vegetation may include black spruce, Labrador-tea, leatherleaf, bog kalmia, cotton grass, *Smilacina trifolia*, cloudberry, *Sphagnum fuscum*, *S. magellanicum*, and *S. fallax*.

Collapse Scar Bog - A circular or oval-shaped wet depression in a perennially frozen peatland. The collapse scar bog was once part of the perennially frozen peatland, but the permafrost thawed, causing the surface to subside. The depression is poor in nutrients, as it is not connected to the minerotrophic fens in which the palsa or peat plateau occurs.

Domed Bog - A large (usually more than 500 m in diameter) bog with a convex surface, rising several metres above the surrounding terrain. The centre is usually draining in all directions. Small crescentic pools often form around the highest point. If the highest point is in the centre, the pools form a concentric pattern, or eccentric if the pattern is off-centre. Peat development is usually in excess of 3 m. Vegetation of domed bogs, which occur in the southeastern portion of the Boreal Wetland Region, include black spruce and tamarack, at least on portions of the dome, with leatherleaf, Labrador-tea, and bog kalmia in the shrub layer. *Sphagnum nemoreum*, *S. fuscum*, and *Pleurozium schreberi* may be present as ground cover.

Flat Bog - A bog having a flat, featureless surface. It occurs in broad, poorly defined depressions. The depth of peat is generally uniform. Flat bogs occur in the northern (High) portion of the Boreal Wetland Region. Vegetation may include black spruce, leatherleaf, bog kalmia, Labrador-tea, cloudberry, *Smilacina trifolia*, *Sphagnum fuscum*, *S. fallax*, *S. angustifolium*, and occasionally lichens (*Cladina* spp.) on elevated peat surfaces.

Northern Plateau Bog - A raised bog elevated 0.5-1 m above the surrounding fen. The surface is generally even, characterized only by small wet depressions. The plateau bog is usually teardrop-shaped, with the pointed end oriented in the down-slope direction. Northern plateau bogs form in the Continental High Boreal Wetland Region. Vegetation may include black spruce, Labrador-tea, leatherleaf, *Kalmia angustifolia*, cloudberry, mountain-cranberry, bog cranberry, *Sphagnum fuscum*, and lichens.

Palsa Bog - A bog composed of individual or coalesced palsas, occurring in an unfrozen peatland. Palsas are mounds of perennially frozen peat and mineral soil, up to 5 m high, with a maximum diameter of 100 m. The surface is highly uneven, often containing collapse scar bogs. Palsa bogs occur in the Subarctic and Boreal

wetland regions. Vegetation may include sparse black spruce, narrow-leaf Labrador-tea (*Ledum decumbens*), and cloudberry, but lichens such as *Cetraria* spp. and *Cladina* spp. dominate the ground surface.

Peat Plateau Bog - A bog composed of perennially frozen peat, rising abruptly about 1 m from the surrounding unfrozen fen. The surface is relatively flat and even, and often covers very large areas. The peat was originally deposited in a nonpermafrost environment and is often associated with collapse scar bogs or fens. Peat plateau bogs occur in the Subarctic and Boreal wetland regions. Vegetation may include black spruce, narrow-leaf Labrador-tea, Labrador-tea, bog-rosemary, resin birch, mountain-cranberry, cloudberry, and lichen ground cover (*Cladina* spp., *Cladonia amaurocraea*). *Sphagnum* spp. sometimes are present in newly forming mats adjacent to existing peat plateaus or in collapse scars on bog surfaces. Additional species such as willow, paper birch, leatherleaf, cotton grass, sedge, feathermosses, and *Sphagnum* spp. occur on peat plateaus in the Boreal Wetland Region.

Polygonal Peat Plateau Bog - A perennially frozen bog, rising about 1 m above the surrounding fen. The surface is relatively flat, scored by a polygonal pattern of trenches that developed over ice wedges. The permafrost and ice wedges developed in peat originally deposited in a nonpermafrost environment. Polygonal peat plateau bogs, similar to peat plateau bogs, are found in the Subarctic Wetland Region. As in the latter wetlands, lichens (*Cladina* spp., *Cetraria* spp., and *Alectoria* sp.) dominate the ground cover of these elevated surfaces. Vegetation may also include resin birch, Labrador-tea, and krummholz forms of black spruce; wet polygon trenches may support *Sphagnum fuscum*.

Veneer Bog - A bog occurring on gently sloping terrain underlain by generally discontinuous permafrost. Although drainage is predominantly below the surface, overland flow occurs in poorly defined drainage-ways during peak runoff. Peat thickness is usually less than 1.5 m. Veneer bogs develop in the Low Subarctic and High Boreal wetland regions. Larger, more diverse vegetation in runnels on the veneer bog surface may include black spruce, tamarack, paper birch, resin birch, *Alnus rugosa*, American green alder, sedges, and mosses. In contrast, black spruce, Labrador-tea, narrow-leaf Labrador-tea, cloudberry, leatherleaf, feathermosses (*Pleurozium schreberi*, *Hylocomium splendens*), and *Sphagnum fuscum* hummocks characterize vegetation in interrunnel areas. Lichens (*Cladina* spp.) occur in the ground cover.

FENS

Basin Fen - A fen occupying a topographically defined basin. However, the basins do not receive drainage from upstream and the fens are thus influenced mainly by local hydrologic conditions. The depth of peat increases towards the centre. Basin fens occur in the Boreal Wetland Region of Canada. Vegetation on the surface of these fens may include tamarack, *Betula pumila*, *Carex aquatilis*, *Sphagnum angustifolium*, *C. lasiocarpa*, *Drepanocladus exannulatus*, *D. revolvens*, *Campylium stellatum*, *Calliergon giganteum*, and *C. richardsonii*; but bulrush, cattail, willow, and bluejoint (*Calamagrostis canadensis*) occur at fen margins.

Channel Fen - A fen occurring in a topographically well-defined channel which at present does not contain a continuously flowing stream. The depth of peat is usually uniform. Channel fens are found in the Subarctic Wetland Region. Vegetation may include tamarack, resin birch, willow, *Scirpus hudsonianus*, *Scheuchzeria palustris*, *Rhynchospora alba*, *Carex limosa*, *Sphagnum fuscum*, *Tomenthypnum nitens*, and *Pleurozium schreberi*.

Collapse Scar Fen - A fen with circular or oval depressions, up to 100 m in diameter, occurring in larger fens, marking the subsidence of thawed permafrost peatlands. Dead trees, remnants of the subsided vegetation of permafrost peatlands, are often evident.Collapse scar fens occur in the Subarctic and Boreal wetland regions. Vegetation may include stunted black spruce, willow, leatherleaf, resin birch, *Vaccinium myrtilloides*, sedges, *Sphagnum* spp., feathermosses, and *Drepanocladus* spp. at the periphery with sedges, wild calla (*Calla palustris*), and mosses (*Drepanocladus* spp., *Calliergon cordifolium*) in the wetter center.

Feather Fen - A fen situated on a long, narrow ridge

of mineral soil. The centre of the ridge is occupied by a bog, but many narrow, subparallel drainage-ways originate from the ridge and are occupied by a feather fen. Water from the fen drainage-ways is usually collected by a stream running parallel to the ridge. The average depth of peat is 1.5 m. Feather fens are found in the Boreal Wetland Region. Although black spruce, leatherleaf, and *Sphagnum* spp. may be present in the closely associated ridgetop bogs, vegetation of the feather fens may include tamarack, a number of sedge species, and *Sphagnum warnstorfii*. Black spruce swamps may occur along streams between feather fen ridges.

Horizontal Fen - A fen with a very gently sloping featureless surface. This fen occupies broad, often ill-defined depressions, and may be interconnected with other fens. Peat accumulation is generally uniform. Horizontal fens occur in the Boreal Wetland Region. Bog formations can be present as black spruce "islands" within the fen. Fen vegetation may include tamarack, *Betula pumila*, buckthorn, bulrushes, swamp horsetail, sweetgale, sedges, cotton grass, *Habenaria dilatata*, buckbean, and mosses (*Sphagnum teres*, *S. warnstorfii*, *S. fallax*, *Campylium stellatum*, *Drepanocladus revolvens*, and *Scorpidium scorpiodes*).

Northern Ribbed Fen - A fen with parallel, low peat ridges ("strings") alternating with wet hollows or shallow pools, oriented across the major slope at right angles to water movement. The depth of peat exceeds 1 m. Northern ribbed fens are found in the Subarctic and Boreal wetland regions. Vegetation of flarks may include sedges, buckbean, *Utricularia* spp., arrow grass, cotton grass and mosses (*Scorpidium scorpioides*, *Drepanocladus revolvens*, *Meesia triquetra*, *Pohlia* sp. and *Cinclidium stygium*); *Sphagnum balticum* and *S. compactum* form "lawns" around flarks. Vegetation on low, wet strings may include resin birch, *Betula pumila*, willows, bog-rosemary, sedges, and mosses (*Tomenthypnum nitens*, *Campylium stellatum*, and *Sphagnum warnstorfii*). Tamarack, *Betula pumila*, Labrador-tea, narrow-leaf Labrador-tea, bog kalmia, leatherleaf, bog-rosemary, *Sphagnum warnstorfii*, *S. fuscum*, and *Tomenthypnum nitens* may occur on strings of intermediate height. The highest ridges support black spruce, tamarack, *Betula pumila*, Labrador-tea, leatherleaf, *Carex disperma*, *Sphagnum fuscum*, *S. magellanicum*, *Pleurozium schreberi*, *Dicranum undulatum*, and lichens (*Cladina* spp.). Strings may form peat plateau bogs if sufficiently elevated by permafrost to become ombrotrophic.

Spring Fen - A fen nourished by a continuous discharge of groundwater. The surface is marked by pools, drainage tracks, and, occasionally, somewhat elevated "islands." The nutrient level of water is highly variable between locations. Spring fens develop in the Boreal Wetland Region. Vegetation may include *Carex lasiocarpa*, *C. interior*, *C. limosa*, *Scirpus caespitosus*, *Eleocharis quinqueflora*, *Scorpidium scorpioides*, *Drepanocladus revolvens*, and *Campylium stellatum*. Treed "islands," potentially supporting black spruce, occur in less minerotrophic areas of spring fens.

Palsa Fen - A fen with mounds of perennially frozen peat (sedge and brown moss peat) and mineral soil, up to 5 m high and 100 m in diameter although they can be much smaller. Palsa fens generally occur in unfrozen peatlands and are frequently associated with collapse scar fens.

APPENDIX C
PHYSICAL DESCRIPTIONS OF REPRESENTATIVE BLACK SPRUCE COMMUNITY TYPES OF ALASKA

The following physical descriptions of black spruce community types are quoted from Foote (1983:29-48).

PICEA MARIANA/SPHAGNUM SPP.-*CLADINA* SPP. COMMUNITY TYPE

Stands typifying this community type occur on valley bottoms or on north-facing slopes where ice-rich permafrost is present and a perched water table is common. A surface horizon of organic material 0.3 m to over 1 m thick overlies loess or valley alluvium. Soils on these sites are cool and moist. Surface soils melt to a depth of 30 cm by late June and 60 cm by August. Excess water from melting frozen soil and precipitation collects in low depressions and thaw ponds or is absorbed by the mounds of *Sphagnum* spp. which have very high water-holding capacities. The permafrost layer prevents the downward movement of water.

PICEA MARIANA/VACCINIUM ULIGINOSUM-LEDUM GROENLANDICUM/PLEUROZIUM SCHREBERI COMMUNITY TYPE

Stands typifying this community type may be found on all mesic black spruce sites; i.e., on both slopes and valley bottoms whenever the soil is not too wet. Usually a 5- to 25-cm-thick surface horizon of organic material overlies a layer of loess, stony residual soil, or valley alluvium. Ice-rich permafrost is generally present. The surface soil is kept cool and moist by the permafrost below and the moss insulation above. Surface soil temperatures increase throughout the summer; the soil thaws to a depth of 30 cm by late June and to 50 cm by August.

PICEA MARIANA-BETULA PAPYRIFERA/VACCINIUM ULIGINOSUM-LEDUM GROENLANDICUM COMMUNITY TYPE

Stands typifying this community type can be found wherever mesic black spruce sites occur; i.e., on slopes of all aspects or on valley bottoms where a modest amount of drainage occurs. Permafrost may or may not be present. By July the ground thaws to a maximum depth of 50 cm. These sites, therefore, may have slightly cooler soil temperatures than sites where the *Populus tremuloides-Picea mariana/Cornus canadensis* community type occurs.

PICEA MARIANA/FEATHERMOSS-LICHEN COMMUNITY TYPE

Stands typifying this community type occur wherever black spruce sites are found; i.e., on slopes of all aspects and gradients and on valley bottoms. A surface horizon of organic material overlies loess, weathered bedrock, or valley alluvium. The depth of the organic layer varies from 5 cm in the lichen-dominated openings to 20 cm in the moss and tree-dominated areas. Permafrost may or may not be present.

PICEA MARIANA-PICEA GLAUCA/BETULA GLANDULOSA/LICHEN COMMUNITY TYPE

Stands typifying this community type occur on east- or west-facing slopes above 700 m or near timberline. These slopes are cool and dry to mesic. A thin surface layer of organic material 0-3 cm thick overlies stony soils and shallow bedrock.

POPULUS TREMULOIDES-PICEA MARIANA/CORNUS CANADENSIS COMMUNITY TYPE

Stands typifying this community type occur on warm, well-drained black spruce sites; i.e., on slopes with southerly exposures or on slightly raised, better drained areas on upland valley floors. The organic layer is shallow, about 12 cm, and overlies loess, bedrock, or river alluvium. By late June the seasonal soil frost melts to a depth of 50-60 cm, and by August, when the seasonal frost is gone, pockets of permafrost may occur 65 cm or more below the surface.

APPENDIX D
INTERPRETATION OF AVIAN SURVEYS WITH RESPECT TO BLACK SPRUCE WETLAND HABITATS

Studies of bird distribution and abundance are not always keyed to specific habitats or may be keyed to habitat classification systems that do not include BSWs. The following discussion and tables present evidence for interpreting specific studies as applying to BSWs. I also include studies of low/medium shrub thicket habitats (tall shrub excluded) because BSWs often include significant shrub components in their understories, particularly when sparsely treed. For conservatism, I interpret "muskeg" as sparse "black spruce" without reference to wetland status. Common usage of this term in the Interior usually connotes wetland, however.

ALASKA

Avian surveys that provide sufficient information to draw inferences about bird use of BSWs in Alaska include Spindler and Kessel (1980) in the eastern Interior (Table D-1), Cooper et al. (1991:279-280) near Tok and Gulkana (Table D-2), Martin et al. (1995) near Fairbanks (Table D-3), Spindler (1976) near Fairbanks (Table D-4), and Kessel et al. (1982) near the Susitna River at the boundary between the Southern and Interior regions (Table D-5.).

Less specifically, Hogan and Tande (1983) surveyed Anchorage mires, but data are not specific to vegetation communities within mire complexes. I interpret bird use of these areas as occurring in "mires." West and DeWolfe (1974) and Kron (1975), recorded bird observations on several trails through a variety of taiga habitats near Fairbanks, and Cooper et al. (1991:284-290) observed birds (not associated with specific habitats) during spring and fall migrations. I interpret bird observations on the trails near Fairbanks and during migration in the eastern Interior as occurring in a "mixed taiga landscape." Heglund (1988, 1992) studied bird use of waterbodies in the Yukon Flats. I interpret bird use of waterbodies surrounded, or influenced, by BSWs as showing a habitat relationship to those wetlands.

CANADA

Avian surveys in the taiga of northern Canada that provide habitat-specific information include Carbyn (1971) in the Northwest Territories (Table D-6), Gillespie and Kendeigh (1982) in Manitoba (Table D-7), and Erskine (1977) for all Canadian boreal habitats (Table D-8). Larsen (1982:271) provides a table of breeding bird species for northern bogs, defined as in this profile, which I interpret as black spruce mires.

LOWER 48 STATES

An avian survey of Michigan "bogs," Ewert (1982), applies to BSWs (Table D-9). Gibbs et al. (1991) also provide habitat preferences of birds using Maine "bogs."

Table D-1. Interpretation of avian surveys by Spindler and Kessel (1980) in eastern interior Alaska with respect to black spruce wetlands.

Plot or Transect Identifier	Community Description	Wetland Indicators	Comments	Name in Black Spruce Profile
Black Spruce "Bog" (two plots)	Black spruce with *Sphagnum* mat or cotton grass tussocks for ground cover	Apparently on permafrost, tamarack (FACW) on one plot	Trees <5 m in height, cotton grass site probably minerotrophic	Black Spruce Wetland
Coniferous Forest (several plots)	Black spruce, tamarack with Labrador-tea, bog blueberry, *Sphagnum* in lowland plots	Black spruce (FACW) and tamarack (FACW)	Both upland (probably nonwetland) and lowland (probably wetland) plots	Black Spruce Forest
Low and Medium Shrub Thicket (≤2.4 m in height, three plots)	Willows, shrub birches, bog blueberry, leatherleaf, Labrador-tea, cotton grass tussocks	Wetland vegetation, one plot was sedge meadow	Apparently minerotrophic wetlands	Shrub Thicket

Table D-2. Interpretation of breeding bird surveys by Cooper et al. (1991:279-280) near Tok and Gulkana, Alaska, with respect to black spruce wetlands.

Plot or Transect Identifier	Community Description	Wetland Indicators	Comments	Name in Black Spruce Profile
Black Spruce (several plots)	Black spruce with ericaceous shrubs, mosses, lichens, and cotton grass tussocks	Boggy, poorly drained soils, wetland vegetation, numerous pools of standing water in one plot	High probability of being wetland	Black Spruce Wetland
Medium-Low Shrub Thicket (all <4 m, presumably most ≤2.4 m)	Willows, shrub birch, cotton grass	Moist to wet meadow	At least partially wetland	Shrub Thicket

Table D-3. Interpretation of breeding bird surveys by Martin et al. (1995) in the Badger Slough watershed near Fairbanks, Alaska, with respect to black spruce wetlands.

Plot or Transect Identifier	Community Description	Wetland Indicators	Comments	Name in Black Spruce Profile
Coniferous Forest (multiple sample points)	Tamarack, black spruce, white spruce	Tamarack (FACW), black spruce (FACW), discontinuous permafrost	Probably most black spruce-tamarack plots are wetland and plots with white spruce are nonwetland	Black Spruce Forest
Intermediate/ Low Shrub Thicket (≤2.4 m in height, multiple sample points)	Not described, presumably willows and shrub birch	Study area mainly wetland	Same vegetation classification as Spindler and Kessel (1980)	Shrub Thicket

Table D-4. Interpretation of avian habitat studies by Spindler (1976) on the Fairbanks Wildlife Management Area with respect to black spruce wetlands.

Plot or Transect Identifier	Community Description	Wetland Indicators	Comments	Name in Black Spruce Profile
Black Spruce	Black spruce, tamarack, white spruce, resin birch, willows, thinleaf alder (*Alnus tenuifolia*), bog cranberry, mountain cranberry, bog blueberry, Labrador-tea, cloudberry, bluejoint, *Sphagnum*, lichens	Mean depth to permafrost <0.5 m, saturated above permafrost table, fibric peat soil to ≥1 m, marshy areas present	Sample plot predominantly wetland	Black Spruce Mire
Tussock-Low Shrub "Bog" (actual heights not given)	Paper birch (sparse), thinleaf alder (sparse), black spruce (sparse), willows, dwarf arctic birch, mountain cranberry, bog blueberry, Labrador-tea, bluejoint, cotton grass, cloudberry, *Sphagnum*, lichens	Mean depth to permafrost <0.5 m, ice-wedge polygons, peaty soil ≥1 m, one pit entirely sapric peat	Gradient from cotton grass to *Sphagnum* and ericaceous shrubs, sparse black spruce in some communities; predominantly wetland	Shrub Mire

Table D-5. Interpretation of avian surveys by Kessel et al. (1982) near the Susitna River, Alaska, with respect to black spruce wetlands.

Plot or Transect Identifier	Community Description	Wetland Indicators	Comments	Name in Black Spruce Profile
Black Spruce Dwarf Forest	Black spruce, bog blueberry, mountain cranberry, crowberry (*Empetrum nigrum*), Labrador-tea, shrub birches, moss	Water seepage through plot, some hummocky ground, stunted trees (2.9 m high at 80 yr)	Highly probable wetland	Black Spruce Wetland

Table D-6. Interpretation of avian survey plots used by Carbyn (1971) in Northwest Territories, Canada, with respect to black spruce wetlands.

Plot or Transect Identifier	Community Description	Wetland Indicators	Comments	Name in Black Spruce Profile
Plot 2	Black spruce/ feathermoss surrounding a "sedge marsh"	Tamarack (FACW), black spruce (FACW), several shrub species (FAC)	Moisture gradient between marsh and white spruce on high ground within plot	Black Spruce Forest
Plot 3	Black spruce/ lichen, buffaloberry, *Potentilla fruticosa*, resin birch, Labrador-tea	Mossy depressions	Nonwetland	Black Spruce Forest
Plot 4	Similar to Plot 2	Similar to Plot 2	Wetland status uncertain	Black Spruce Forest
Plot 5	Open black spruce/*Sphagnum* bog with hummocks	Predominantly FACW and FAC shrub layer	Clearly a wetland	Black Spruce Mire

Table D-7. Interpretation of avian surveys by Gillespie and Kendeigh (1982) in Manitoba, Canada, with respect to black spruce wetlands.

Plot or Transect Identifier	Community Description	Wetland Indicators	Comments	Name in Black Spruce Profile
Herriot Creek Forest Plot	Black spruce, white spruce, tamarack, resin birch, willow, alder	"Bog" meadows, open water, *Sphagnum* hummocks	Site appears predominantly wetland with drier areas	Black Spruce Wetland
Herriot Creek Forest-Edge Plot	Alder, willow, shrub birch	Riparian strip with sedges and sweetgale	Dense shrubs ≤2.3 m in height, adjacent to spruce-tamarack stand	Shrub Thicket
Gillam Forest-Edge Plot	Black spruce scrub with scattered tamarack, willow, alder, Labrador-tea, cloudberry, sedges	Peat mounds, water-filled depressions, no upland species	Clearly wetland	Black Spruce Wetland

Table D-8. Interpretation of descriptions by Erskine (1977) of avian habitat use in boreal Canada.

Plot or Transect Identifier	Community Description	Wetland Indicators	Comments	Name in Black Spruce Profile
Spruces	Predominantly black spruce with white spruce and balsam fir (eastern boreal forest)	None	Nonwetland	Black Spruce Forest
Bog Forest	Predominantly tamarack with black spruce and alder	Dominants (FACW) occurring on wet ground, often around depressions and in swales	Probably wetland	Black Spruce Wetland
Fen	None given	Water table at surface	Minerotrophic wetland structurally similar to open bog	Fen (Mire)
Bogs	Black spruce, tamarack, ericaceous shrubs, shrub birches, willows, sedges, sweet gale, peatmosses	Wet sites, may include open water	Ombrotrophic to weakly minerotrophic wetland	Black Spruce Mire or Shrub Mire (depending on vegetation)

Table D-9. Interpretation of avian surveys by Ewert (1982) in Michigan "bogs" with respect to black spruce wetlands.

Plot or Transect Identifier	Community Description	Wetland Indicators	Comments	Name in Black Spruce Profile
Black Spruce-Tamarack "Bog"	Black spruce, tamarack, *Andromeda glaucophylla*, leatherleaf, bog kalmia, *Vaccinium* sp., Labrador-tea, *Sphagnum*, cotton grass	Hummocks, small pools (<1 m diameter) of standing water, surrounded by open peat mat	Wetland, trees <8 m in height	Black Spruce Mire
Open "Bog" (two sites)	Leatherleaf, *Andromeda glaucophylla*, bog kalmia, *Vaccinium* sp., *Sphagnum*, cotton grass	Hummocks, small pools (<1 m diameter) of standing water	Wetland, high coverage by low ericaceous shrubs	Shrub Mire

GLOSSARY

Acrotelm: The highly permeable, aerobic, partly living upper organic layer of mires (Ingram 1983).

Active Layer: "The layer of ground above the permafrost which thaws and freezes annually" (Gabriel and Talbot 1984:7).

Api: Taiga snow characterized by little within-year variability in thickness in a given region but great between-year variability in thickness (Pruitt 1978:12-14). Taiga snow usually has low density and hardness except in exposed areas like frozen lakes (Pruitt 1984).

Aufeis: "Sheets of ice formed by the freezing of overflow water"; see ***naled*** (Gabriel and Talbot 1984:12).

Black Spruce Wetland (BSW): For purposes of this report, a wetland containing black spruce of any size or stand density.

Bog: A mire exclusively supplied by precipitation, which typically has a low nutrient content (i.e., water that is oligotrophic), also known as an ***ombrotrophic*** mire (Gore 1983, Gabriel and Talbot 1984:77, Damman 1987).

Catotelm: Highly decomposed, anaerobic peat of low hydraulic conductivity that underlies the *acrotelm* (Ingram 1983).

Depression Storage: Water storage provided by topographic depressions up to the depth at which overflow occurs (i.e., depression storage must be satisfied before runoff is initiated) (Woo 1986).

Detention Storage: Short-term water storage provided by topographic depressions filled to a depth greater than the elevation of the surface outlet (i.e., that portion of the stored water that subsequently leaves the depression by surface flow) (Woo 1986).

Ectothermic: Refers to organisms whose internal temperatures largely are controlled by their environments.

Fen: A mire at least partly supplied by water that contains moderate to high concentrations of nutrients (i.e., water that is mesotrophic or eutrophic) from contact with mineral soil, also known as a ***minerotrophic*** mire (Boelter and Verry 1977, Gore 1983, Gabriel and Talbot 1984:71).

Fibric Peat: Undecomposed peat consisting of easily-identified plant parts.

Flark: Wet depression oriented transverse to the direction of flow and located between peat ridges in a patterned peatland such as a northern ribbed fen (Natl. Wetlands Working Group 1988:435).

Forest-Tundra: The transition zone between taiga and tundra (Pruitt 1978:33) "characterized by a mosaic of forest communities, **krummholz**, tree islands, or trees growing along river and lake shores or in sheltered positions, and a tundra vegetation on exposed ridges between the rivers and in xeric habitats" (Gabriel and Talbot 1984:47).

Histosol: "Soil that has organic materials in more than half of the upper 32 in (80 cm) or of any thickness if overlying bedrock" (Natl. Res. Counc. 1995:286).

Hydric Soil: "A soil that is saturated, flooded, or ponded long enough during the growing season to develop anaerobic conditions in the upper part" (Natl. Tech. Comm. Hydric Soils 1991:1).

Hydrophytes: "Macrophytic plant life growing in water, soil, or on a substrate that is a[t] least periodically deficient in oxygen as a result of excessive water content" (Tiner 1989:17).

Ice Wedge: Massive structure ranging from 0.01 to

3 m in width and 1 to 10 m in height when viewed in transverse section (i.e., end-on view) and up to 15 m in length when viewed in longitudinal section (i.e., face-on view) (Péwé 1975:49).

Krummholz: Stunted, scrubby, twisted growth forms of species genetically capable of tree growth (Gabriel and Talbot 1984:63).

Layering: Vegetative reproduction by rooting of lower branches and growth of new individuals to form a clone (Zasada 1986).

Microbivores: Organisms that feed on microbial algae, bacteria, or fungi (MacLean 1980).

Minerotrophic: See ***fen***.

Mire: A peat-forming ecosystem having ≥0.4 m peat thickness, generally separated into ***bog*** and ***fen*** based on vegetation, water source, and water chemistry, all of which are related variables (Boelter and Verry 1977, Gore 1983, Gabriel and Talbot 1984:71-72, Zoltai 1988, Swanson and Grigal 1989).

Muck: In common Alaska usage, a mixture of well-decomposed organic material and mineral soil (Gabriel and Talbot 1984:73).

Naled: "stream icing"; see ***aufeis*** (Gabriel and Talbot 1984:75).

Ombrotrophic: See ***bog***.

Palsa: Peat-covered mound or hummock from ~0.1 to 10 m in height and from ~3 to 100 m in diameter that contains a core of segregated ice and is found in peatlands (Brown and Péwé 1973, Péwé 1975:66, Kershaw and Gill 1979, Seppälä 1982, Natl. Wetlands Working Group 1988:417-420).

Paludification: The process of bog expansion over forest, grassland, or bare rock that occurs as peat accumulation impedes drainage (Gore 1983, Natl. Wetlands Working Group 1988:438).

Patterned Ground: The expression of an underlying polygonal pattern of ice wedges on the surface of the ground (Brown and Péwé 1973). Patterned ground may also occur through intense seasonal frost processes in nonpermafrost areas with severely maritime climates and low mean annual temperatures (Henderson 1968).

Peat Plateau: A raised permafrost feature with an internal structure similar to a palsa but having a flat surface that may cover several square kilometers (Kershaw and Gill 1979).

Peatland: See ***mire***.

Permafrost: Soil, rock, or other substrates that continuously remain at temperatures below 0°C for ≥2 yr (Brown and Péwé 1973).

Pingo: Large mound or hill ranging from 30 to 1,000 m in diameter and from 3 to 70 m in height and containing massive ice heaved above the surrounding landscape by artesian or hydrostatic pressure (Holmes et al. 1963, Brown and Péwé 1973, Péwé 1975:56, Ferrians 1988).

Primary Mires: Those mires that occur with the growth of peat-forming vegetation directly on wet mineral soils (Sjörs 1983).

Pukak: Depth hoar crystals that grow in a columnar structure at the base of the snowpack and form a subnivean space that provides a favorable microclimate for overwintering plants and animals (Pruitt 1984).

Redoximorphic Features: Patterns of color related to chemical reduction or oxidation of iron or manganese (J. Bouma, Rep. of Int. Comm. on Aquic Soil Moisture Regimes, Circular 10).

Redox Potential: Potentiometric measure of the oxidizing or reducing intensity of a solution (Wetzel 1983:298).

Sapric Peat: Highly-decomposed peat (muck) in which individual plant fibers are not visible.

Saprovores: Organisms that directly consume decaying organic matter.

Semiserotinous Cones: Cones that disseminate seed over several years or longer after seed maturation (Gabriel and Talbot 1984, Zasada 1986).

String: Peat ridge oriented transverse to the direction of flow in a patterned wetland such as a northern ribbed fen (Natl. Wetlands Working Group 1988:441).

Subpermafrost Groundwater: Water that is confined beneath a layer of ***permafrost***.

Suprapermafrost Groundwater: Water that occupies the saturated portion of the ***active layer*** above the ***permafrost*** table.

Taiga: "The wooded vegetation of boreal-subarctic latitudes that occupies the subarctic climatic zone adjacent to the treeless tundra" (Gabriel and Talbot 1984:112).

Talik: Thawed zone within, or extending through, ***permafrost***, often beneath a waterbody, that can connect ***suprapermafrost groundwater*** and ***subpermafrost groundwater*** (Gabriel and Tal-

bot 1984:112, Woo 1986).

Terrestrialization: The process whereby aquatic environments infill with peat (Sjörs 1983).

Thaw Lake: Cave-in lake on flat or gently sloping terrain underlain by fine-grained sediments that forms when water ponds in a thermokarst depression and promotes radial thaw and bank caving, which may continue for long periods of time with eventual coalescence of thaw ponds into larger lakes (Wallace 1948, Hopkins et al. 1955:140, Hopkins and Kidd 1988).

Thermokarst: The landscape features that result when permafrost thaws and "creates an uneven topography which consists of mounds, sinkholes, tunnels, caverns, short ravines, lake basins, and circular lowlands caused by melting of ground ice" (Péwé 1975:65).

Wetland Function: A physical, chemical, or biological process occurring in a wetland. Examples include storage of water, denitrification, and photosynthesis.

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