ECOLOGY OF THE VEGETATION OF THE SASKATCHEWAN RIVER DELTA

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Herman John Dirschl

ABSTRACT

The vegetation of the Cumberland Marshes, a 2,760 km^2 portion of the Saskatchewan River Delta in east-central Saskatchewan, was examined with respect to vegetation types, site characteristics, environmental control of vegetational variation, and soil and peat forming processes.

As a means of obtaining an overview of the landscape and its major components, a physiognomic-floristic reconnaissance map of the vegetation was initially prepared through interpretation of aerial photographs and 190 ground checks. Field study was subsequently confined to a representative block of 660 km^2.

Vegetational and environmental measurements were obtained from 98 stand-samples that included all common vegetation types. These data were classified by the association analysis technique into 10 groups, distinct on the basis of species presence and absence, which fell into five environmental categories: aquatic, fen, wooded fen, bog, and alluvial stream levee. Lists of major species and average environmental attributes were prepared for all groups and typical community structures described. To examine vegetational and environmental relationships, the stand-samples of bog, fen, and wooded stream levee vegetation were further subjected to ordination by principal component analysis.

Moisture regime and nutrient status were found to be major environmental gradients that interact in controlling overall vegetational composition. Relative site maturity and man-made disturbance are additional important gradients causing diversity of forest communities on alluvial levees. The floristic composition of bog communities is primarily determined by a complex gradient of relative ombrotrophy

which incorporates decreasing pH values and nutrient content, and increasing organic matter content and water-holding capacity through the accumulation of _Sphagnum_ moss.

Periodic measurements of water-table depth and soil temperature along representative field-transects during three consecutive growing seasons showed that frost within the peat layer holds melt water at the surface of fens during the early part of the growing season. In sites with immobile ground water-tables, ice lenses persist until early July and in _Sphagnum_ peat until at least early September. The presence of a continuous frost layer within the _Sphagnum_ substrate of the black spruce bogs, during most of the growing season, isolates these communities from the surrounding minerotrophic fens and thus is instrumental in maintaining their ombrotrophic character. Wide floating mats which surround the shallow lakes of the study area, move up and down with fluctuating lake water levels, and thus possess a fairly stable moisture regime.

Macroscopic examination of peat cores from representative field-transects showed peat deposits of open basins with moving sub-surface waters to be less than 1.5 m thick and derived from fen and aquatic plants. Floating mats consist of buoyant, fibric fen peat. The growth of _Phragmites communis_ is now restricted to the outer edge of the floating mats, but the presence of old culms and rhizomes at lower levels of the peat, further landward, suggests that the species initiated the encroachment of the organic mat into the lake basins but was later replaced by sedges as the main peat-forming plants. Closed basins with impeded drainage, typically have peat deposits more than 3 m thick. Basin-filling through seral replacement of aquatic communities by fens and, eventually, by _Sphagnum_ bogs is evident from the stratigraphy of the examined cores.

The spatial and dynamic relationships of vegetation and environment in the Cumberland Marshes are visualized as primarily dependent on the original landform and drainage pattern and, secondarily, on the modifying influence of peat accumulation on moisture and nutrient regime. Man-made disturbance has also initiated some adjustments in the vegetation. Compared to the rapid, cyclic changes evident in the wetland vegetation of the neighbouring aspen grove and grassland regions, the vegetation changes in the study area are slower, less fluctuating, and essentially unidirectional.

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This study was carried out while the author was employed by the Canadian Wildlife Service, Department of Indian Affairs and Northern

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1. INTRODUCTION

The Saskatchewan River Delta is the most southerly of three large deltas formed by major rivers in the boreal forest region of western Canada: the Mackenzie, the Athabasca, and the Saskatchewan. Although situated close to agricultural districts, the region has remained fairly inaccessible until recently and its appearance has not been greatly altered by man's efforts. The Saskatchewan River Delta thus is a relatively natural, unique ecosystem of interest to environmental biologists and naturalists. Because of its location within a few hundred miles of large population centres, the Delta has an obvious potential for satisfying ever-increasing demands for such forms of outdoor recreation as hunting, fishing, bird watching, and wildlife photography (Richards 1967, Dirschl *et al*. 1967).

At least since 1921, the Saskatchewan River Delta has also been viewed as a land reserve for agricultural expansion. In that year the Dominion Water Power and Reclamation Service began a three-year study of engineering problems in gaining flood control and an investigation of soils and vegetation. The study concluded that, although agricultural development would be possible, such an undertaking should await not only the development of hydro-electric power on the Saskatchewan River, but also realization of maximum development of better agricultural lands elsewhere in Saskatchewan (Clayton and Ellis 1952).

Since that time a number of surveys have been carried out in a continual effort to delineate areas of favourable agricultural potential (e.g., Kuiper 1956). It is only within the last few years, with growing acceptance of the multiple-use concept, that development of other resources has become a factor in determining the feasibility of development of the delta lands.

In 1964, concern regarding the unsatisfactory socio-economic condition of the approximately 1,000 Indians and Metis residing at Cumberland House in the western part of the Delta resulted in the formation, by the Government of Saskatchewan, of the Saskatchewan River Delta Development Committee. That committee subsequently encouraged studies of the Delta by various disciplines, in order to determine present and potential use of the area's renewable resources. From these studies, a master land-use plan has now been prepared (Anon. 1969) which allocates portions of the area to those uses for which they are considered most suited through their inherent biological capability in conjunction with the pertinent social and economic considerations.

The Canadian Wildlife Service, Department of Indian Affairs and Northern Development, cooperated in this effort through studies aimed at determining (1) present use of the Delta by waterfowl and (2) potential waterfowl productivity under a system of intensive water level manipulation. The work reported here forms part of this investigation.

Disregard of physical and biological laws, and the intricate interrelationships of biotic and abiotic features of the landscape in many previous land-use projects has resulted in needless disappointment and wasteful destruction of natural ecosystems.

The natural vegetation of a site is the result of the sum-total of all environmental factors affecting that site. The existing vegetation pattern in the Saskatchewan River Delta may, therefore, be regarded as a comprehensive expression and inventory of the environmental processes that have been operating in the area.

An understanding of the relationship of plant communities to major environmental gradients such as macroclimate, moisture, and soil, and effects of fire, logging, and grazing makes it possible to conclude from the presence and distribution of these communities in the landscape what the macroclimatic, microclimatic, and edaphic conditions must be. This information in turn becomes a tool in planning optimum use of the land.

Detailed vegetation research and inventory has not previously been undertaken in the Delta. This study, therefore, attempts an initial ordering of the present landscape pattern and seeks to identify past and ongoing developmental processes. Specifically, the study aims to (1) classify the more extensive vegetation types of the study area, (2) characterize the sites in which they occur, (3) examine relationships between vegetation and site in order to identify the environmental gradients that control the distribution of major species, and (4) investigate evolutionary processes through macroscopic analysis of peat cores.

Field work for the study was carried out between May 1964 and September 1968.

2. LITERATURE REVIEW

Literature dealing with the ecology of North American and European peatlands is voluminous but comprehensive reviews of earlier North American studies have been previously compiled by Rigg (1940, 1951) and for much of the European work by Gorham (1953, 1957). The present review is, therefore, restricted to selected publications pertinent to this study and, specifically, to ecological studies of lowlands in which it is attempted to relate vegetation to major environmental gradients, or to investigate developmental processes of peatlands.

The differing viewpoints held by peatland ecologists have, over the years, resulted in a large array of terms which have been compiled and discussed by Tansley (1939), Sjörs (1948), Pearsall (1950), Dansereau and Segadas-Vianna (1952), Gorham (1953), Drury (1956), Heinselman (1963), and Burnett (1964). In the present study, broad landscape units are distinguished according to the nature of the source of mineral nutrients (Sjörs 1948, 1950a, 1950b, 1959, 1961, 1963; DuRietz 1949). Sites in which the rooting zone is subject to inwashing of silt and mineral soil water are termed "minerotrophic", peat surfaces which no longer receive an inflow of mineral soil water, and thus receive nutrients only from precipitation or wind-blown particles, are termed "ombrotrophic". Minerotrophic sites are referred to as "fen" whereas ombrotrophic sites are termed "bog". Bellamy (1966, 1969), stressing water circulation, employed the roughly corresponding terms "rheophilous mire" and "ombrophilous mire".

Little quantitative information exists for lowland vegetation in the southern part of the boreal forest in western Canada. In Saskatchewan, the only previous study is that of Jeglum (1968), who classified the peatland and moist forest vegetation of the Candle Lake area - approximately 200 km (125 miles) west of Cumberland House - and related types to moisture regime and mineral status.

Ecological studies of upland forests of the region (Ritchie 1956, Rowe 1956b, van Groenewoud 1965, Swan 1966, Swan and Dix 1966) have included moist forest community types, similar to those encountered in the Cumberland Marshes. Various descriptive studies of peatlands and moist forests in the boreal forest zone of Alberta have been reviewed by Moss (1953b, 1955).

The importance of moisture regime and nutrient status in controlling vegetational composition has been stressed in many studies dealing with peatlands. The publications of Sjörs (1948, 1950), Persson (1961, 1962) and Malmer (1962a, 1962b) describe lines of vegetational variation in Swedish bogs and fens according to differences in water-table and ionic composition of peat and water. Rutter (1955), working in wet heathland in southeastern England computed significant multiple regressions of the abundance of _Molinia caerulea_ and _Erica tetralix_ on mean summer water-table depth and tussock height, as well as simple regressions of the species on water-table fluctuation. Water-table depth and fluctuation were found to be mainly determined by geological and physiographic features, independent of the vegetation, and thus were considered as important causes of the variation in botanical composition. Studies dealing with pronounced changes of water regime in natural and man-made water bodies (Kadlec 1960, 1962, Harris and Marshall 1963, Walker 1965) showed subsequent rapid vegetative changes. Several authors have further found that it is not only the actual depth of water that is important in determining vegetation pattern, but also the degree to which the water level fluctuates both within and between seasons (Millar 1964, Walker 1965, Smeins 1967, Walker and Coupland 1968).

Water circulation and peat accumulation, as two interacting factors affecting both moisture and nutrient regime, have been emphasized by Kulczynski (1949), Dansereau and Segadas-Vianna (1952), Heinselman (1963), Gorham (1966), and Bellamy (1966, 1969). Most wetlands are characterized by the accumulation, under waterlogged and anaerobic conditions, of partially decomposed organic plant matter. Initially, the organic deposits are mixed with silt, but as the peat increases in depth and area, the proportion of silt decreases with reduced inwashing of mineral soil waters (Gorham 1966). With time, drainage tends to be increasingly blocked by peat accumulation (Kulczynski 1949, Dansereau and Segadas-Vianna 1952, Bellamy 1966). This development ultimately may lead to ombrotrophic bog, in which the peat surface is isolated from mineral soil water and receives its nutrients only from precipitation and dust. Such conditions are usually caused by the growth of Sphagnum spp. above the highest level of mineral soil water (Rigg 1940, 1951, Osvald 1949).

In his comprehensive treatise on the peat bogs of Polesie, a region in eastern Poland (since World War 2 part of the U.S.S.R.), Kulczynski (1949) stressed water circulation as the major governing factor in peatland development. He pointed out that water circulation includes vertical as well as horizontal components, and distinguished three main drainage systems: (1) mobile surface water, (2) mobile ground water, and (3) immobile ground water. Numerous examples are provided of processes such as river capture and drainage channel blockage which lead to the development of raised bogs within an expanse of fen (valley bog).

The classes of hydrotopography of Swedish scientists, as defined by Sjörs (1948), are designed to relate water movements to their influence on nutrient status: "Limnogenous" sites directly receive waters from rivers or lakes; "soligenous" sites are those where the soil water surface is distinctly sloping and, therefore, mineral-laden water percolates through them; "topogenous" sites are undrained depressions with horizontal soil water surfaces; and "ombrogenous" sites possess nutrient-poor ground waters; derived entirely from precipitation.

In his monograph on the extensive peatlands in the former bed of Glacial Lake Agassiz in north-central Minnesota, Heinselman (1963) emphasized that water movements and degree of isolation from mineral-influenced ground water are key factors controlling distribution of vegetation types, but that the hydrologic system has itself been modified by peat accumulation.

Bellamy (1969) has produced a classification of peatlands which, according to water circulation, distinguishes seven "hydrological types" that fall into the following three categories:

(1) Group A. Rheophilous - mires under the influence of flowing ground waters derived from outside the immediate catchment of the mire.

(2) Group B. Transition - mires under the influence of flowing ground water derived solely from the immediate catchment of the mire.

(3) Group C. Ombrophilous - mires which are never subject to the influence of flowing ground water.

The developmental processes that have led to the present organic terrain, have been investigated in a few major studies through macroscopic examination of peat cores. Kulczynski (1949) analysed peat borings to obtain additional information on the physiographic and vegetational processes that culminated in the present pattern of bogs and fens in the region of Polesie. Chapman (1964a, 1964b) carried out an intensive stratigraphic study of a bog in Northumberland, England, which included macroscopic examination, pollen analysis, and chemical analysis of the various profiles of peat cores taken at predetermined intervals along representative transects across the bog. Both studies indicated successional changes in plant composition as the peat deposits increased in thickness. Based on knowledge of the ecology of the main peat-forming plants, it was then possible to relate past vegetational development to changes in water circulation and nutrient availability.

Some studies dealing primarily with boreal forest vegetation have included discussions of forest types, similar to those found in the Saskatchewan River Delta. Linteau (1955) classified forests in eastern Quebec on combinations of two sub-canopy species of shrub, herb, moss, or lichen. Moisture and fertility regimes were considered as important factors controlling the vegetation. Clausen (1957), in a study of conifer swamps in Wisconsin, found an inverse relationship between water-holding capacity of the surface soil and mineral content. These changes were related to increases in the depth of Sphagnum. A description of the vegetation of 14 forest types, including six lowland types, in southeastern Manitoba by Mueller-Dombois (1964), was based on "silviculturally significant differences of soil moisture and nutrient regime", as interpreted through vegetation, soil, and landform.

It is probably presumptive to attempt to draw general conclusions from this brief survey of literature on wetland ecology, but a common thread runs through the publications mentioned - and many others - that may be stated as follows: The processes that have led to the development of present-day peatland communities are initiated by the nature of the original landform; the main operating forces are physiographic, causing differences in the pattern of water circulation and thus in the moisture and nutrient regimes. The resultant gradual increase in organic material, however, itself exerts a modifying influence on the moisture and nutrient regimes and, therefore, contributes to the ultimate pattern of landscape development.

3. THE AREA

3.1 Location and access

The area under consideration is that part of the Saskatchewan River Delta which lies between the Carrot River on the south, the Old Channel of the Saskatchewan River on the north, the Manitoba-Saskatchewan boundary on the east, and Kennedy Creek on the west (Fig. 1). Commonly referred to as the Cumberland Marshes, it extends from 53°30'N to 54°00'N and from 101°40'W to 103°10'W and encompasses approximately 2,760 square kilometers (1,070 square miles).

Following preliminary field investigations and vegetation mapping in 1964, a 660-km^2 (255-square mile) representative block was selected (see Section 5.1) for detailed field study.

This reduction of the area of investigation was primarily necessary because of the severe transportation problems encountered. An all-weather road to Cumberland House did not exist until the summer of 1967; therefore, during the first three years of the study, all supplies and personnel had to be transported by chartered aircraft from Carrot River, Saskatchewan. A further eight-mile trip by boat was then required to reach the Canadian Wildlife Service cabin on the banks of the Saskatchewan River which had been built to serve as headquarters for the study (Figs. 1 and 2).

Travel within the Delta was difficult because of (1) shallow water which ruled out the use of conventional boats, (2) the wide floating shorelines around most lakes which made travel on foot a tedious and sometimes hazardous undertaking, and (3) the level terrain with few landmarks for navigation.

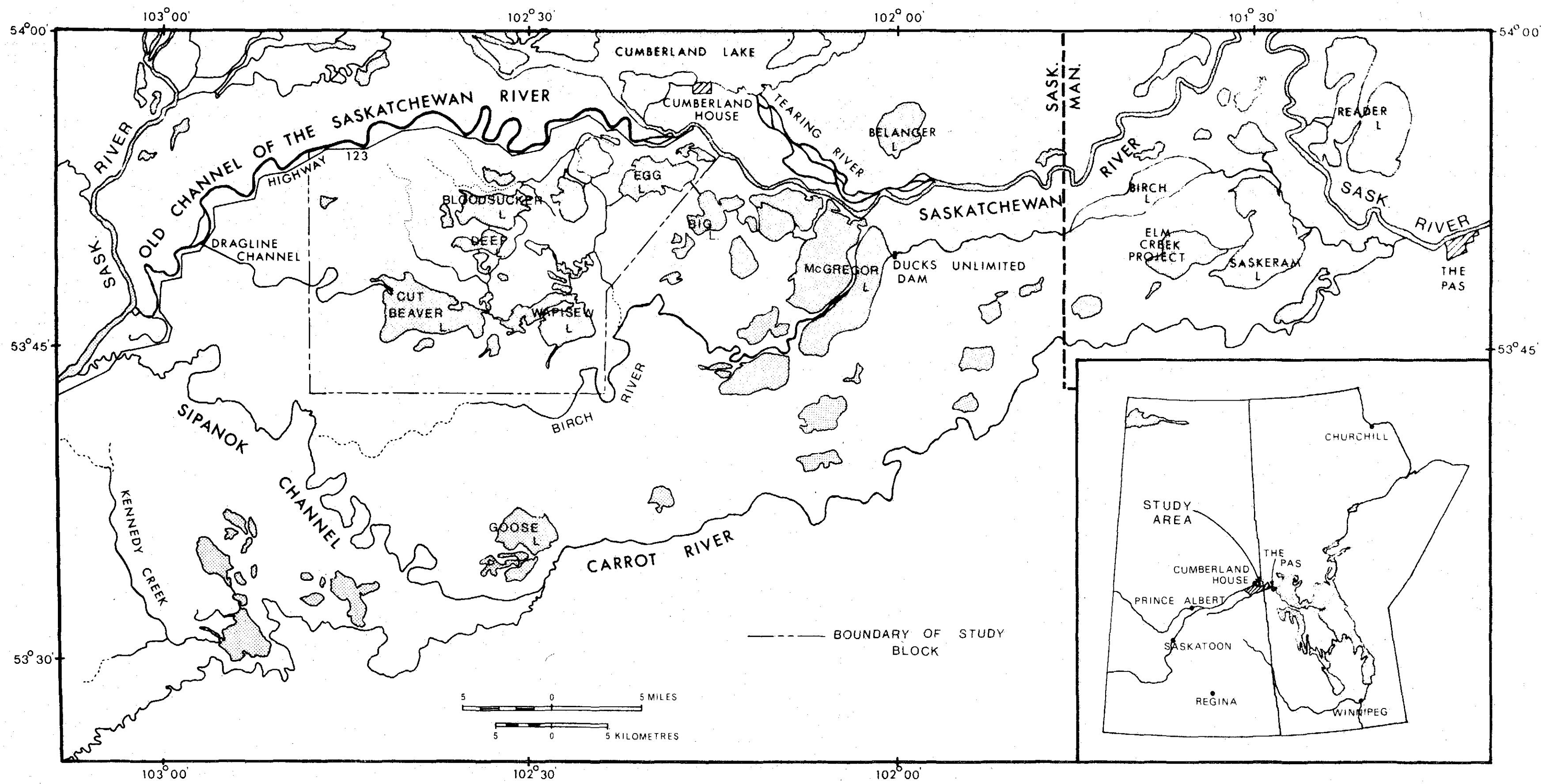


Fig. 1. Geographic location of the study in the Saskatchewan River Delta. Vegetation mapping covered the area between the Saskatchewan and Carrot rivers, and between Kennedy Creek and the Manitoba border. The block used for intensive study is also outlined.

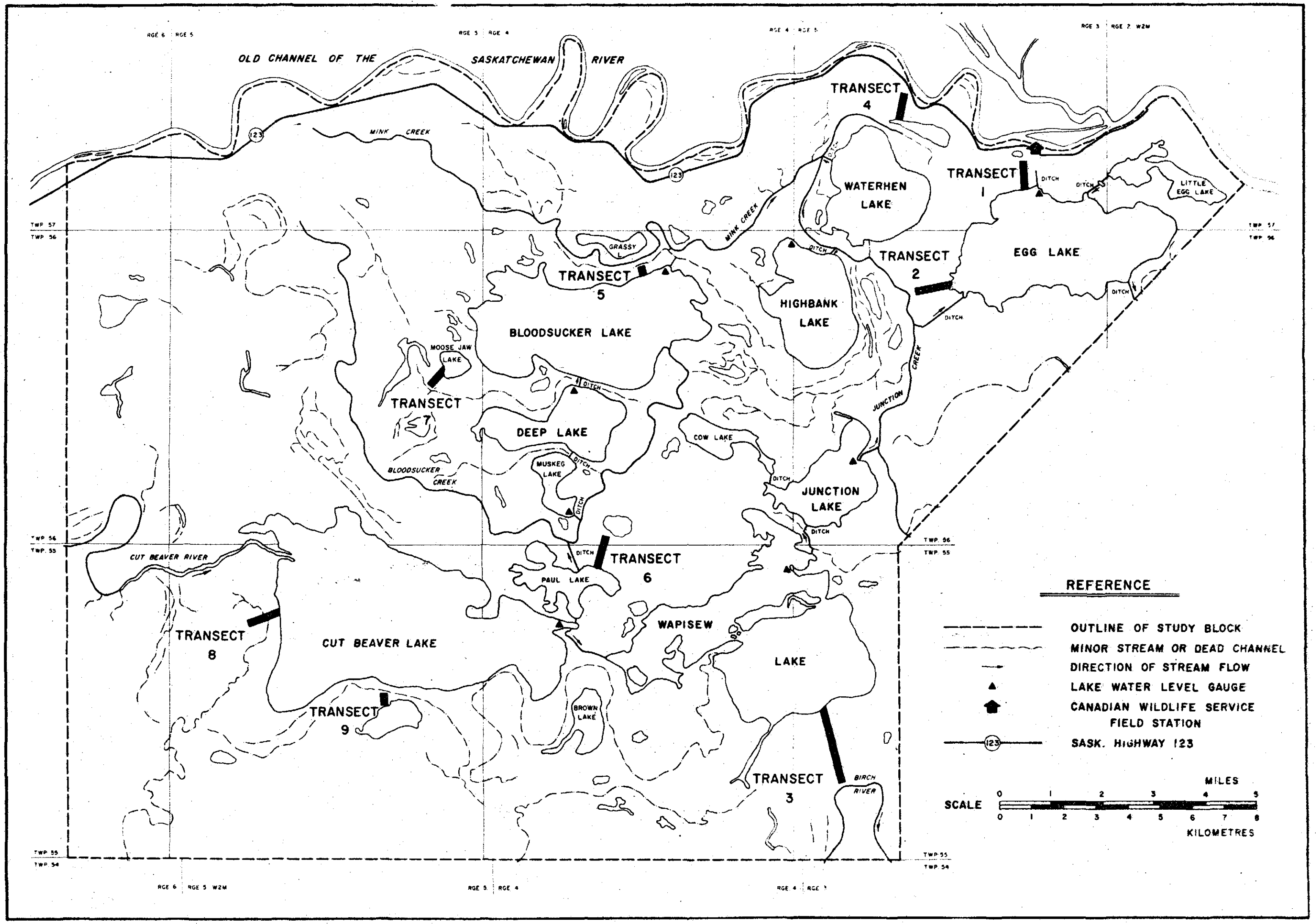


Fig. 2. Outline map of the study block, showing the location of field-transects and lake water level gauges.

3.2 Physiography and soils

The lower portion of the 64 km (40 mile)-wide valley of the Saskatchewan River and its main tributaries, the Carrot and Torch rivers, forms the Cumberland Lake Lowland Division of the Manitoba Lowland Physiographic Region (Acton et al. 1960).

The valley descends in a broad plain from an elevation of approximately 335 m (1,100 feet) above sea level at Nipawin to 260 m (852 feet) in the flood plain at The Pas, where the river has cut a gap through higher morainic deposits to reach Cedar Lake and, eventually, Lake Winnipeg (Ellis and Graveland 1967).

Geologically, the area is a lacustrine plain, representing the western extension of a series of glacial lakes contemporaneous with Glacial Lake Agassiz in present-day Manitoba and Minnesota. This lake plain has been modified greatly by the subsequent activity of the rivers which have cut valleys through the higher portions of the plain and laid down a pattern of alluvial and flood plain deposits in the lower area. This process of alluvial deposition is still active (Clayton and Ellis 1952) but is expected to slow, owing to changes in river flows resulting from the upstream Gardiner and Squaw Rapids hydro-electric dams.

The alluvial-lacustrine plain is flat and lies below the flood levels of the rivers that meander through it. The rivers are bordered by natural levees of alluvium which show little soil profile development, probably because of fluctuating water tables and periodic gleysolic conditions. The dominant soil profile on the levees is a weakly developed wooded calcareous type. In the best drained sites, limited podzolization has led to Dark Gray Wooded and Gray Wooded profiles

(Ellis and Graveland 1967).

Shallow, eutrophic lakes and marshes are surrounded mostly by wide bands of floating sedge mats. Peat, varying in thickness from 0.3 to 4 m (1-13 feet) covers the remainder of the flood plain.

Until the early 1870's, the flow of the Saskatchewan River through the western portion of the Delta was contained in what is now called the "Old Channel" (Fig. 1, p. 11). At that time, a large ice jam formed during spring ice breakup and diverted the river northwestward through a series of inter-connected lakes that drained into Cumberland Lake (P. Carriere, pers. comm.). The resulting "New Channel" soon became the main river course, and now carries about 80 percent of the river's discharge (J. Crook, pers. comm.). This change in the river system is considered to have decreased the frequency of inundating floods in the study area and thus has contributed to greater stability of vegetation and soil development during the past hundred years.

3.3 Climate

The area lies within the Humid Continental Cool Summer (Dfb) climatic region of the Köppen classification (Geographical Branch 1957). According to the Thornthwaite system, the Cumberland Marshes fall into the Dry Subhumid (C) moisture region (Sanderson 1948). Mean annual precipitation at Cumberland House is 433 mm (17.02 inches) - of which 254-280 mm (10-11 inches) fall during the growing season (Ellis and Graveland 1967) - and 430 mm (16.98 inches) at The Pas. On the average, there is an annual water deficiency of 100 to 150 mm in the area (Sanderson 1948).

The thermal climatic type at Cumberland House is Microthermal

(C_2^1) (Sanderson 1948). The daily mean temperature for July is 18°C (65°F), whereas that for January is 23°C (5°F). Currie (1953) has characterized the seasons of central Canada by the progression of daily mean temperatures through the year (Table 1). Summers are warm and winters cold, and the autumn and spring seasons are relatively short. The growing season, defined as the average annual period with mean temperatures of 5.5°C (42°F) or higher, at Cumberland House is 153 days, and the mean duration of the frost-free period is about 102 days (Kendrew and Currie 1955). The ground remains frozen for five to six months in well-drained sites, while bogs and fens may remain frozen until July or August.

3.4 Vegetation

Rowe (1959) includes the Saskatchewan River Delta within the Manitoba Lowland Section of the Boreal Forest Region. The plant communities, that have developed in response to the broad range of physical habitats present, form an intricate mosaic:

On the natural stream levees, extensive and well-developed moist forest, dominated by white spruce (*Picea glauca*) and balsam poplar (*Populus balsamifera*) exists. Floristically, this is probably the richest forest vegetation in Saskatchewan and marks the northwestern limit of distribution of white elm (*Ulmus americana*) and mountain maple (*Acer spicatum*). Tall shrub communities, in which willows (*Salix* spp.) and speckled alder (*Alnus rugosa*) predominate, also occur on the stream levees.

In moister locations, on peat substrate of variable depth, fens, dominated by sedges (*Carex* spp.), reedgrass (*Calamagrostis* spp.), and low willows (*Salix* spp.), are extensive.

Table 1. Selected climatic parameters for Cumberland House and The Pas.

MOISTURE		
Mean annual precipitation (mm) at Cumberland House	433	E*
Mean annual precipitation (mm) at The Pas	430	
Percentage of annual precipitation falling as snow	30	K
Percentage of annual precipitation falling during growing season (period with mean daily temperature ≥ 5.5°C)	62	E
Mean annual potential evapotranspiration (mm).	430-570	S
Mean annual water deficiency (mm)	0-140	S
TEMPERATURE		
Daily mean temperature for July at The Pas (°C)	18.3	E
Daily mean temperature for January at The Pas (°C)	-22.8	
DURATION OF SEASONS AT CUMBERLAND HOUSE		C
Summer (days with mean temperature ≥ 5.5°C)	153	
Warm summer (days with daily maxima ≥ 21°C)	63	
Autumn (days with mean temperatures between 0° and 5.5°C).	19	
Winter (days with mean temperatures ≤ 0°C)	176	
Cold winter (days with mean temperatures below -18°C) . .	46	
Spring (days with mean temperatures between 0° and 5.5°C).	17	

*Data compiled from the following sources:

E - Ellis and Graveland 1967
K - Kendrew and Currie 1955
S - Sanderson 1948
C - Currie 1953

A characteristic feature of the study region is the wide floating shorelines of most of the shallow lakes. These floating mats consist of a buoyant layer of poorly decomposed fen peat, forming a moist habitat for marsh plants that is relatively unaffected by water level changes. Predominant plants are various Carex spp., cattail (Typha latifolia), Salix candida, and Salix pedicellaris. Reed (Phragmites communis var. berlandieri), growing to a height of three meters (10 feet), forms a dense narrow band along the outer edge of most floating mats.

In the open water of the shallow, eutrophic lakes of the Delta, and near the shores of the deeper lakes, stands of bulrushes (Scirpus acutus and Scirpus validus) are extensive. Yellow pond-lily (Nuphar variegatum) is abundant in most water bodies where the floating leaves of the plant often appear to completely cover the water surface. Various submerged aquatics, including Myriophyllum exalbescens and Ceratophyllum demersum, occur in dense masses in shallow water.

Deep peat has developed in locations of impeded drainage. Present vegetation consists of extensive areas covered by bog birch (Betula glandulifera) shrub, and of small islands of black spruce (Picea mariana) and tamarack (Larix laricina) on a Sphagnum moss substrate. Ericaceous species such as Ledum groenlandicum, Kalmia polifolia, Oxycoccus quadripetalus and other typical bog plants, e.g., Sarracenia purpurea are commonly associated with those trees.

3.5 Birds and mammals

The Delta's mosaic of marshes, fens, bogs, and shrub and forest communities supports an abundance of wildlife*. Numerous species of

*Nomenclature for birds is according to the American Ornithologists' Union (1957) check-list, and according to Beck (1958) for mammals.

birds and mammals occupy the broad array of ecological niches present.

Waterfowl populations are predominated by diving ducks, particularly Lesser Scaup (*Aythya affinis*) and Ring-necked Duck (*Aythya collaris*). Redhead (*Aythya americana*) and Canvasback (*Aythya valisineria*) are less common. The most abundant dabbling duck is the Blue-winged Teal (*Anas discors*). Mallard (*Anas platyrhynchos*), Gadwall (*Anas acuta*), American Widgeon (*Mareca americana*) and several other dabbler species are also found in the Delta (Dirschl *et al*. 1967).

Other characteristic breeding avian species are the Bald Eagle (*Haliaeetus leucocephalus*), Golden Eagle (*Aquila chrysaetos*), Harrier (*Circus cyaneus*), Common Crow (*Corvus brachyrhynchos*), American Coot (*Fulica americana*), Virginia Rail (*Rallus limicola*), American Bittern (*Botanaurus lentiginosus*), Ruffed Grouse (*Bonasa umbellus*), Red-winged Blackbird (*Agelaius phoeniceus*), Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*), Black Tern (*Chlidonias niger*), Franklin's Gull (*Larus pipixcan*), and many songbirds (Houston and Street 1959, Dirschl *et al*. 1967).

Muskrat (*Ondatra zibethicus*), mink (*Mustela vison*), beaver (*Castor canadensis*), and weasels (*Mustela* spp.) comprise the major furbearers of the study region. Other common mammals are black bear (*Euarctos americanus*), timber wolf (*Canis lupus*), coyote (*Canis latrans*), snowshoe hare (*Lepus americanus*), striped skunk (*Mephitis mephitis*), red squirrel *Tamiasciurus hudsonicus*), and various species of mice, shrews, and ground squirrels.

A population of approximately 2,000 moose (*Alces alces*), the major big game species, is largely restricted to the stream levees and the extensive wooded area along the Sipanok Channel during most of the year. The marshes themselves are used only during a brief period in the summer (Dirschl _et al_. 1967). White-tailed deer (_Odocoileus virginianus_) and wapiti (_Cervus canadensis_) are found in smaller numbers in the forested areas.

3.6 Land use

Approximately 1,000 people, mostly Metis and Cree Indians, reside at Cumberland House at the northern edge of the study region. Another 300 Crees inhabit several reserves along the Carrot River at the southern limit of the area.

Cumberland House is the oldest permanent settlement in Saskatchewan; it originated in 1774 when Samuel Hearne of the Hudson's Bay Company chose the site for the company's first inland post. As a consequence, trapping of furbearers, particularly muskrats, has been the major source of income for the Delta's inhabitants for the past two centuries. In the late 1930's and early 1940's, the Hudson's Bay Company attempted to improve muskrat production in the Cumberland Marshes by ditching through the levee of the Saskatchewan River to permit river water to flow into the lakes and marshes of the interior plain. Additional works included a log dam on the Birch River in the eastern part of the area, and smaller ditches connecting individual marshes and lakes. This water management system was improved and expanded by Ducks Unlimited (Canada) in 1962 and continues to be operated to maintain desirable water levels for muskrat and waterfowl production (Townsend 1966, Dirschl 1969). Thus, during the past 25 to 30 years, water levels have been artificially held high, and it is evident that this has had a significant effect on the vegetation pattern of the Cumberland

Marshes. For instance, comparison of air photos taken in 1946 and 1964 shows a substantial decrease in emergent aquatic vegetation in the shallower water bodies during that interval (Townsend 1965).

Logging practices have had a significant effect on the composition and structure of the forest vegetation on the levees of the Saskatchewan, Birch, and Carrot rivers. Commercial logging was first undertaken in the early years of the current century by The Pas Lumber Company which selectively cut out white spruce along the levee of the Saskatchewan and floated the logs to The Pas. This "high-grading" practice without regard to ensuring regeneration has been continued ever since by private operators licensed by the Saskatchewan Department of Natural Resources. For instance, in the 10-year period between 1954 and 1964, a total of 55 million board feet of white spruce saw timber were removed from this area (Kabzems and Senyk 1966). Since regeneration of *Picea glauca* on rich alluvial soils, in competition with herbaceous and deciduous species, is extremely poor (Rowe 1955), forest stands are now mainly dominated by various hardwoods and possess dense strata of tall and low shrubs, and herbs.

Repeated fires, caused by lightning and by careless trappers have also had significant effects on forest and shrub vegetation throughout the area.

Hunting of moose for food by local residents or for recreation by sportsmen, and limited commercial fishing on the two deepest lakes, Cut Beaver and Wapisew, are other uses of the resources of the area.

4. FIELD AND LABORATORY METHODS

4.1 General approach and phasing

Because of the large area and the wide range of vegetation types involved, it was decided at the outset that an understanding of vegetation/environment interrelations and developmental processes could only be gained by a combination of extensive and intensive methods.

Review of pertinent literature (see Section 2) had indicated that the distribution of marsh, fen, and bog communities likely relates mainly to fine differences in the water regime, particularly to the nature of the moisture supply and the position and stability of the water-table throughout the growing season.

In order to obtain meaningful comparative data on seasonal water supply with which various plant community-types are in equilibrium, it was considered inadequate to rely on single measurements. Therefore, it was decided to establish a number of permanent field-transects, each containing at least several examples of abundant vegetation types, and to measure the position of the water-table at several locations along each transect at two-week intervals over several growing seasons.

To obtain quantitative information on the total variation of the vegetation and the associated environmental attributes would have necessitated the analysis of hundreds of stands - an effort clearly beyond the scope and capability of this study. It was, therefore, necessary to carefully and subjectively select samples of all major vegetation types and prevailing habitat conditions for detailed analysis. It was arbitrarily decided to initially sample approximately 80 stands and to carry out a preliminary analysis of this complement in order to determine whether or not the vegetation/environmental relationships could be satisfactorily explained at this point. In the event that the data were inadequate, additional stand-samples could be added in the final year of field work to complete the analysis.

The approach proved to be a profitable one and resulted in a total sample of 98 stands. In addition, a complementary part of the study aimed at explaining developmental processes that led to the present pattern of the landscape of the Cumberland Marshes.

The study was conducted in the following sequence:

1964 - reconnaissance field work on 190 stands
- familiarization with flora
- vegetation mapping from aerial photographs

1965 - selection of 660 square-km study block for intensive field research
- selection and marking of eight permanent field-transects, installation of water-table gauges, and lake water level markers
- vegetation sampling in 66 stands
- periodic environmental measurements begun

1966 - environmental measurements continued
- soil samples collected from all stands
- profiles of transects and elevation of water gauges surveyed

1967 - vegetation sampling of 79 stands completed
- 9th field-transect selected and marked
- preliminary association analysis of vegetation data carried out to determine adequacy of sample

1968 - additional 19 stands sampled

- peat cores obtained from three field-transects at known intervals and stratigraphically examined
- final analysis of data begun

1969 - data analysis continued

1970 - study completed.

4.2 Transportation

Owing to the trackless terrain in which the study was undertaken, motor cars and conventional boats could not be employed for field work. Instead the following vehicles were used:

(1) Two- and three-place helicopters served to reach remote sections of the study area, and particularly those forest and shrub stands that were separated from lakes and water courses by wide bands of floating sedge mats. Helicopters were also used to obtain oblique aerial photographs of stands and field-transects.

(2) An airboat, i.e., a flat-bottomed fiberglass boat powered by a rear-mounted 150 h.p. aircraft engine, was used as the principal means of transportation on the lakes and water courses of the Delta (Plate 1). This craft is capable of manoeuvering in less than 5 cm of water.

Without the use of airboat and helicopter many of the plant communities included in this analysis could not have been reached.

(3) A power toboggan was used in winter to survey profiles of field transects and the elevations of lake-level and water-table gauges (see Section 4.6).

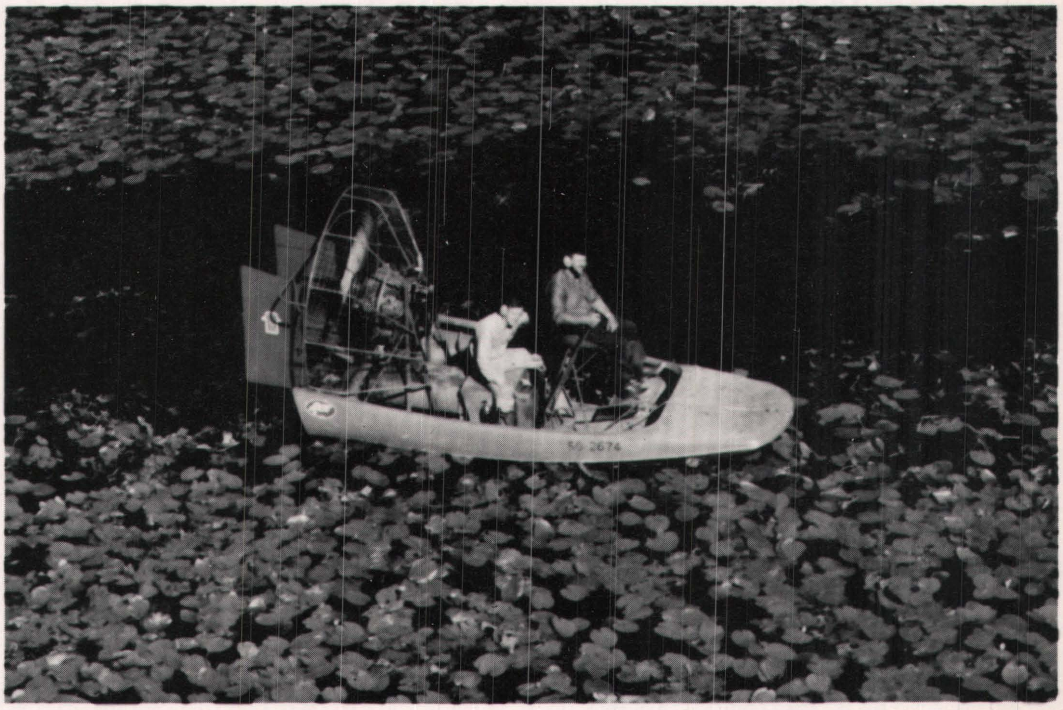


Plate 1. Airboat used for travel over shallow water bodies.

4.3 Reconnaissance vegetation classification and mapping

To achieve an overview of the landscape of the Delta, and the distribution of its major elements, which could be used in planning approaches and techniques for further detailed study, it was decided to prepare a reconnaissance map of the vegetation of the Delta. Interpretation of available aerial photographs was the only suitable method by which such a map could be prepared relatively quickly. Of the various types of vegetation maps, e.g., floristic, ecological, and physiognomic (Küchler 1967), a combination physiognomic-floristic map was considered most desirable for a reconnaissance of the vegetation since that approach lends itself readily to photo-interpretation techniques.

4.3.1 Classification

To derive a suitable scheme for classifying the vegetation of the area, a rapid ground survey of 190 subjectively selected locations was carried out. Physiognomy and composition of the vegetation, nature of the site, and position in the landscape in relation to other cover types was recorded. Oblique aerial photographs of many of these locations were taken from a helicopter. In the course of this reconnaissance survey it became apparent that the whole vegetation complex could be classified into 12 broad vegetation types, according to the physiognomy of the upper vegetation strata (Table 2).

4.3.2 Interpretation of aerial photographs

The spatial distribution of the 12 mapping categories was obtained by interpretation of stereo-pairs of recent black-and-white aerial photographs of the Delta by means of a Wild ST-4 mirror stereoscope at

Table 2. Criteria employed in the preparation of the reconnaissance vegetation map for the Saskatchewan River Delta study area.

Mapping category	Characteristic structure and predominant taxa	Appearance on aerial photographs (scale 1:15,840)*	Illustrations
White spruce - hardwoods forest	Forest stands, 20-30 m tall, variably dominated by white spruce, balsam poplar, trembling aspen (<u>Populus</u> tremuloides), various other deciduous trees present in lesser amounts; understory of tall shrubs, low shrubs, and dense herbaceous cover usually present.	Tonal range: 0.20-0.70. Texture: coarse-stippled, variable, according to species composition. Stereoscopic form: variable appearance depending on dominant species, height and density of the canopy. Species identifiable according to crown characteristics, e.g., (i) white spruce - large conical crowns of dark tone, (ii) balsam poplar - narrow conical crowns, tufted appearance, dark tone, canopy appears honey-combed, (iii) trembling aspen - rounded open crown, fuzzy appearance, light tone.	Plates 2-3

*Definitions:

<u>Tone</u> - a distinguishable shade variation from white to black according to the standard Gray Scale (Eastman Kodak Co. 1968):

0.00 white	0.70 light charcoal
0.10 grayish white	1.00 charcoal
0.20 light gray	1.30 dark charcoal
0.30 gray	1.60 dull black
0.50 dark gray	1.80 black

<u>Texture</u> - frequency of change and arrangement of tones:
(1) stippled - mixture of light and dark tones as a pattern of dots of uniform size (fine, medium, and coarse).
(2) mottled - mixture of light and dark tones as a pattern of irregular shaped blotches (fine, medium, and coarse).
(3) uniform.

<u>Stereoscopic structure</u> - three-dimensional appearance of individual plants or groups of plants under the stereoscope

. . . cont'd

Table 2 continued.

Mapping category	Characteristic structure and predominant taxa	Appearance on aerial photographs (scale 1:15,840)*	Illustrations
Black spruce - tamarack forest	Dense stands of black spruce, 5-15 m tall; tamarack commonly associated around the edges, occasionally as a dominant. Field layer consists of ericaceous shrubs and other bog plants on *Sphagnum* moss.	Tonal range: 0.50-1.30 (black spruce) 0.30-1.00 (tamarack) Texture: medium-stippled to fine-mottled. Stereoscopic form: regular canopy, frequently with a gradient in height from centre to edge of stand; black spruce with slender, pointed tops; tamarack with cone-shaped crowns, lighter than black spruce.	Plate 4
Tall willow - alder shrub	Canopy of deciduous shrubs, 3-8 m tall with a large layer of low shrubs, herbs, grasses and sedges. *Salix bebbiana* *Salix discolor* *Alnus rugosa*	Tonal range: 0.20-1.00 Texture: coarse-stippled. Stereoscopic form: canopy "fluffy"; irregular height and crown diameters, occasional gaps; individual crowns rounded, average diameter approximately 1/2 of deciduous tree crowns.	Plate 5
Medium willow shrub	Canopy of deciduous shrubs, 2-3 m tall, with a field layer of sedges and grasses. *Salix* spp.	Tonal range: 0.30-1.30 Texture: medium-stippled. Stereoscopic form: canopy height fairly uniform, individual crowns just recognizable, round, average crown diameter about 1/4 of deciduous tree crowns.	Plate 5

. . . cont'd

Table 2 continued.

Mapping category	Characteristic structure and predominant taxa	Appearance on aerial photographs (scale 1:15,840)*	Illustrations
Low willow shrub	Dense canopy of shrubs, < 2 m tall, with a field layer, dominated by *Carex* spp.	Tonal range: 0.20-1.00 Texture: fine-stippled. Stereoscopic form: canopy nearly regular, grainy, individual crowns not quite recognizable.	Plate 6
Bog birch shrub	Shrub thickets, 1-2 m tall, with a field layer of *Carex* spp. *Betula glandulifera* *Salix candida* *Myrica gale*	Tonal range: 0.50-1.00 Texture: fine- to medium-mottled. Stereoscopic form: canopy flat, individual plants not recognizable.	Plate 6
Broadleaved sedge - reedgrass meadow	Level fen, < 1 m tall, dominated by *Carex atherodes*, *Calamagrostis* spp., *Carex rostrata*, occasional presence of low *Salix* shrubs.	Tonal range: 0.00-0.20 Texture: uniform. Stereoscopic form: no perceivable relief.	Plate 7
Narrowleaved sedge - cattail meadow	Level fen, < 1 m tall, dominated by *Carex lanuginosa*, *Typha latifolia*, *Equisetum fluviatile*	Tonal range: 0.20-0.50 Texture: uniform with occasional reticulate patterns. Stereoscopic form: usually no perceivable relief.	Plate 7

. . . cont'd

Table 2 concluded.

Mapping category	Characteristic structure and predominant taxa	Appearance on aerial photographs (scale 1:15,840)*	Illustrations
Phragmites swamp	Dense thickets of *Phragmites communis*, 2.5-3 m tall.	Tonal range: 0.00-0.10 Texture: uniform. Stereoscopic form: slight fuzzy appearance, abrupt boundary with meadow communities or adjacent water surface.	Plate 8
Bulrush swamp	Circular clones of *Scirpus acutus* or *S. validus* in shallow, open water.	Tonal range: 1.00-1.60 Texture: uniform for individual clones. Stereoscopic form: individual clones show a slight suggestion of relief.	Plate 8
Water-lily pad	Leaves of *Nuphar variegatum* floating in shallow water of lakes and streams	Tonal range: 0.20-0.30 Texture: fine-stippled. Stereoscopic form: none.	Plate 8
Water-lily - bulrush mixture	Water surface between clones of *Scirpus* spp. covered by floating leaves of *Nuphar variegatum*. A combination of preceding two types.	Tonal range: 0.50-1.60 Texture: uniform, dark, rounded patches in a lighter, fine-stippled matrix. Stereoscopic form: no perceivable relief.	Plate 8

Plate 2. Mapping category: White Spruce-Hardwoods Forest.

Stereogram of white spruce (Picea glauca)-dominated forest outlined in white on the left member of the pair of photographs.

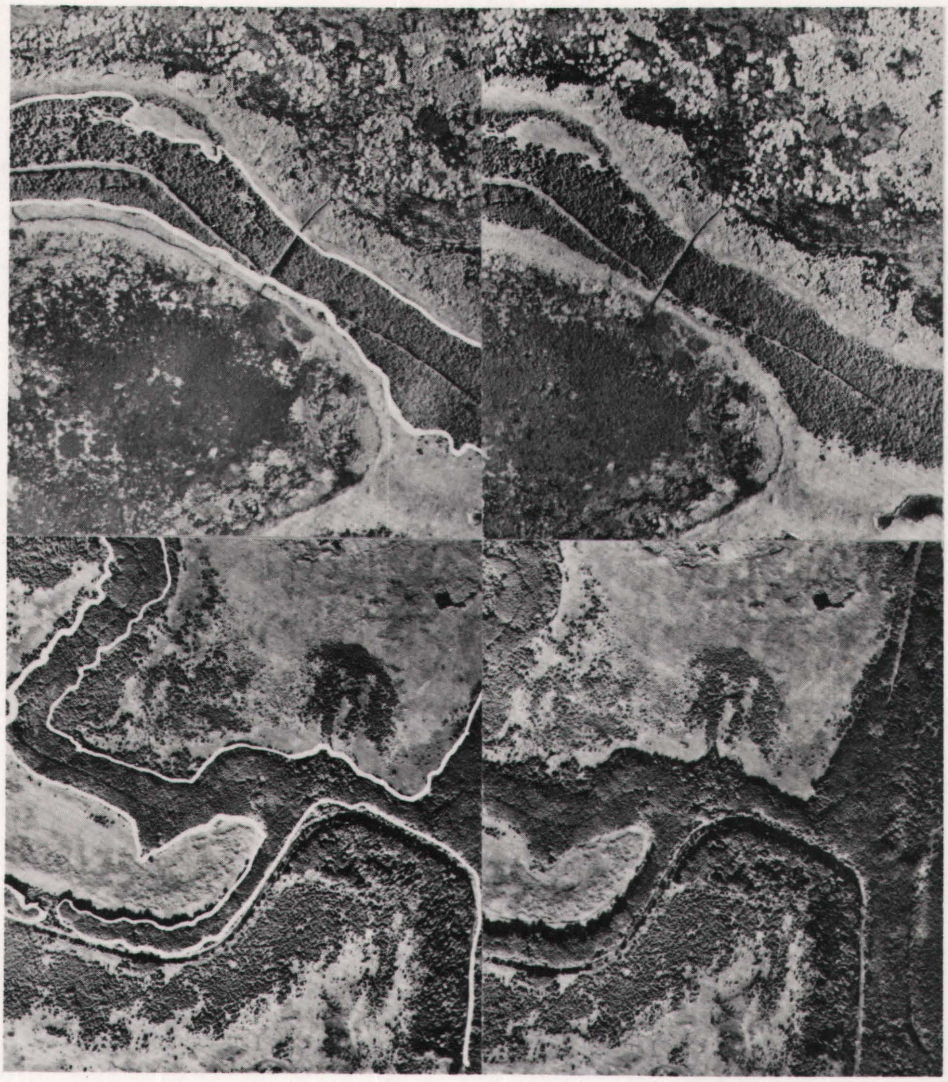


Plate 3. Mapping category: White Spruce-Hardwoods Forest.

Above. Stereogram of balsam poplar (Populus balsamifera)-dominated forest.

Below. Stereogram of trembling aspen (P. tremuloides)-dominated forest.

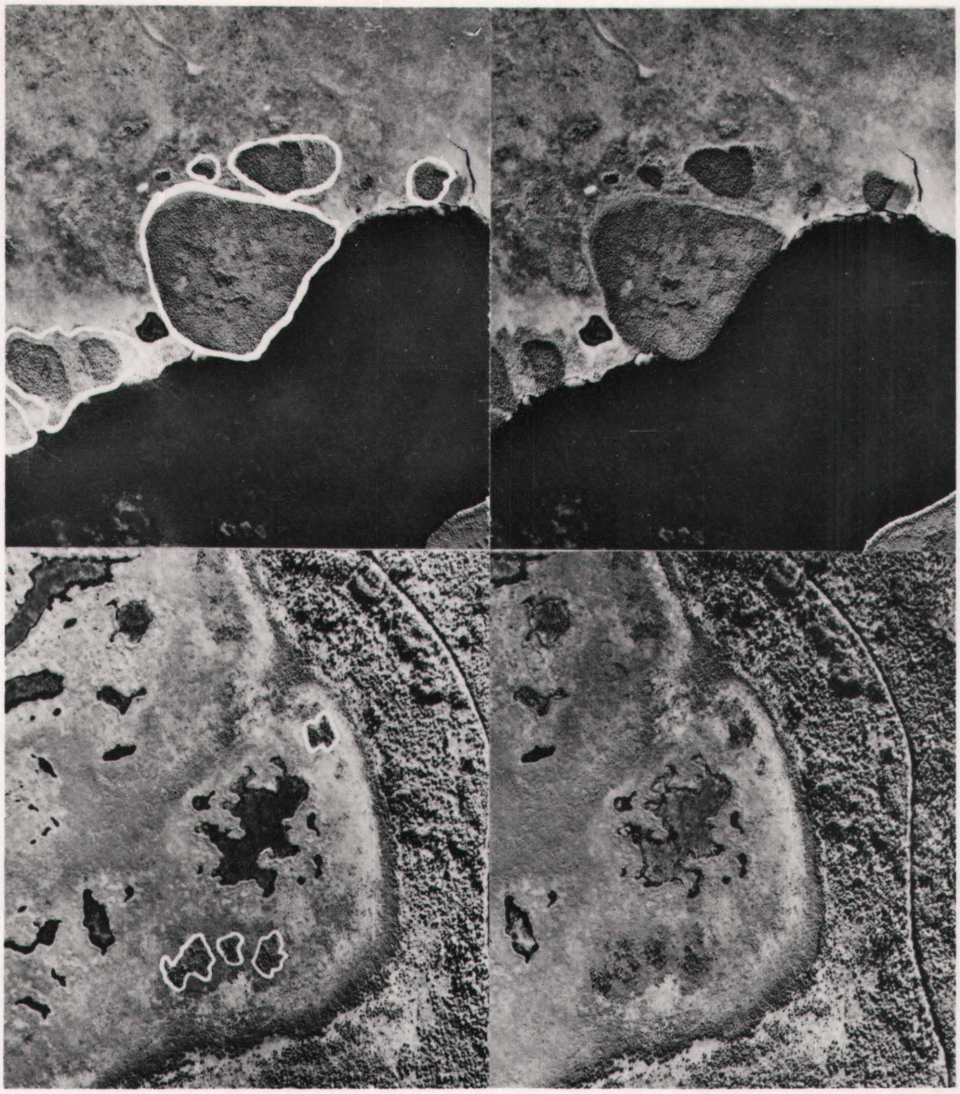


Plate 4. Mapping category: Black Spruce-Tamarack Forest.

Above. Stereogram of black spruce (*Picea mariana*)-dominated forest.

Below. Stereogram of tamarack (*Larix laricina*)-dominated forest.

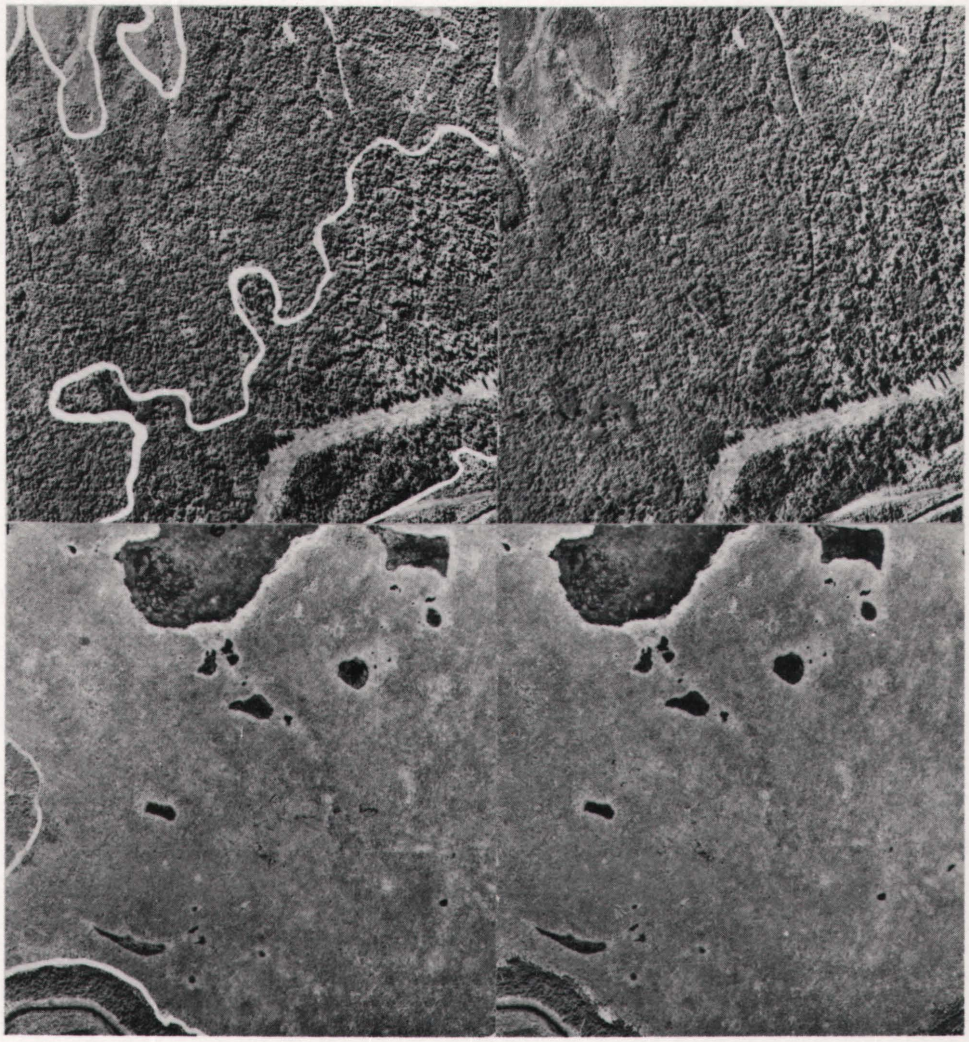


Plate 5. Above. Stereogram of Tall Willow-Alder Shrub.

Below. Stereogram of Medium Willow Shrub.

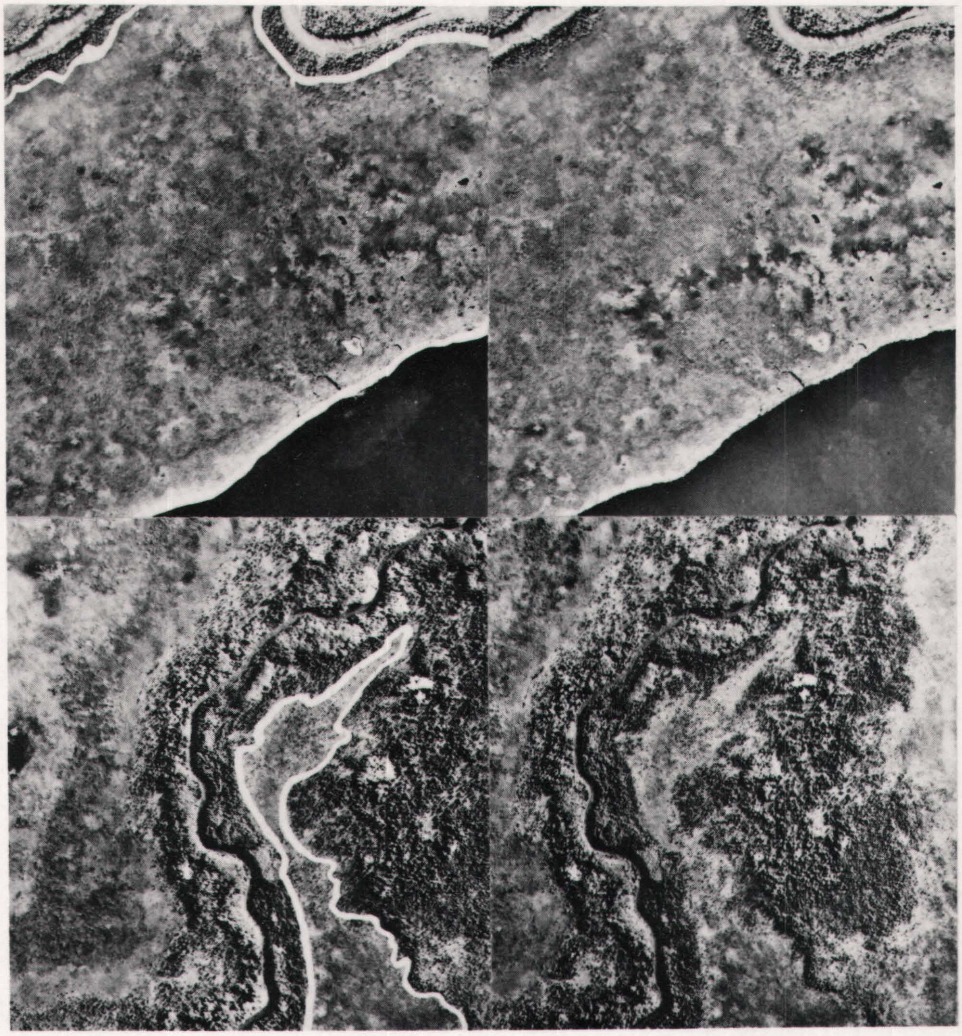


Plate 6. Above. Stereogram of Low Willow Shrub.

Below. Stereogram of Bog Birch Shrub.

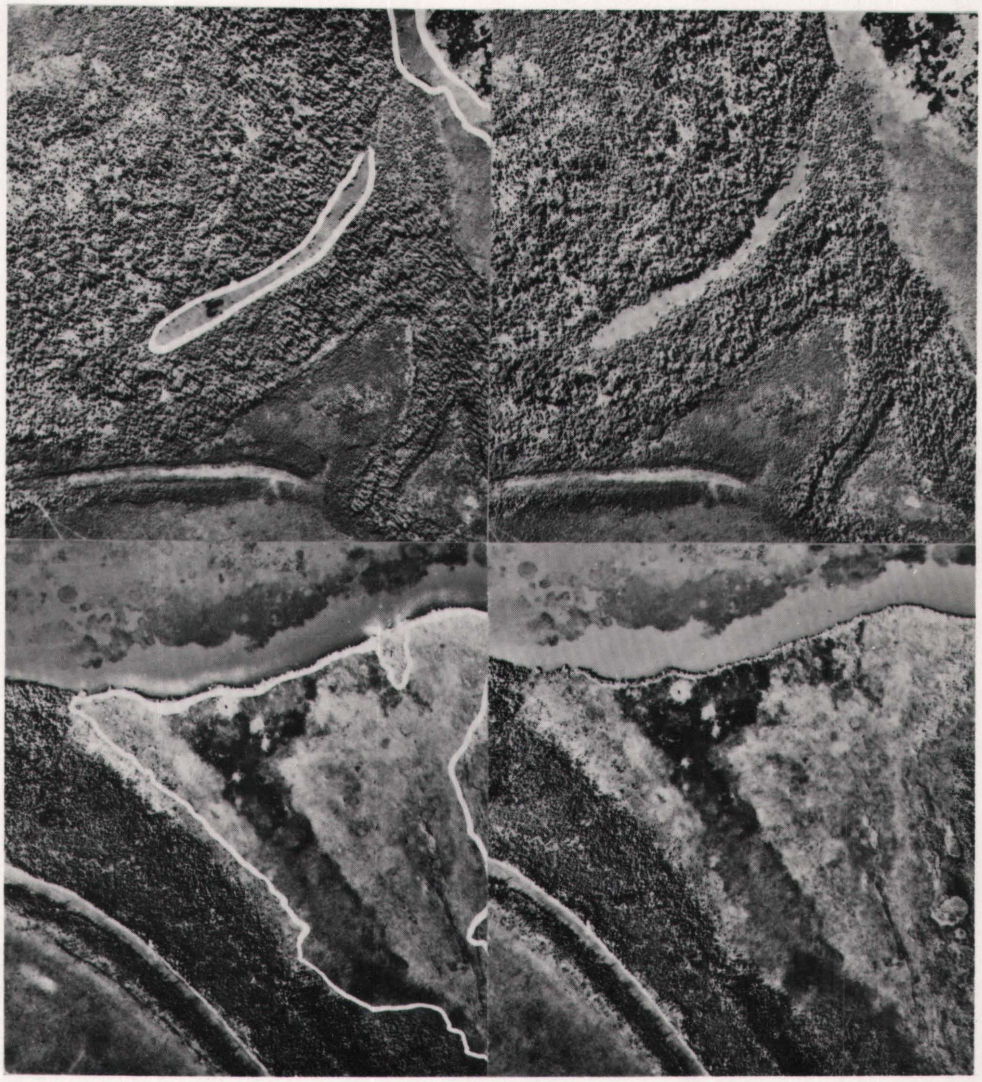


Plate 7. Above. Stereogram of Broadleaved Sedge-Reedgrass Meadow.

Below. Stereogram of Narrowleaved Sedge-Cattail Meadow.

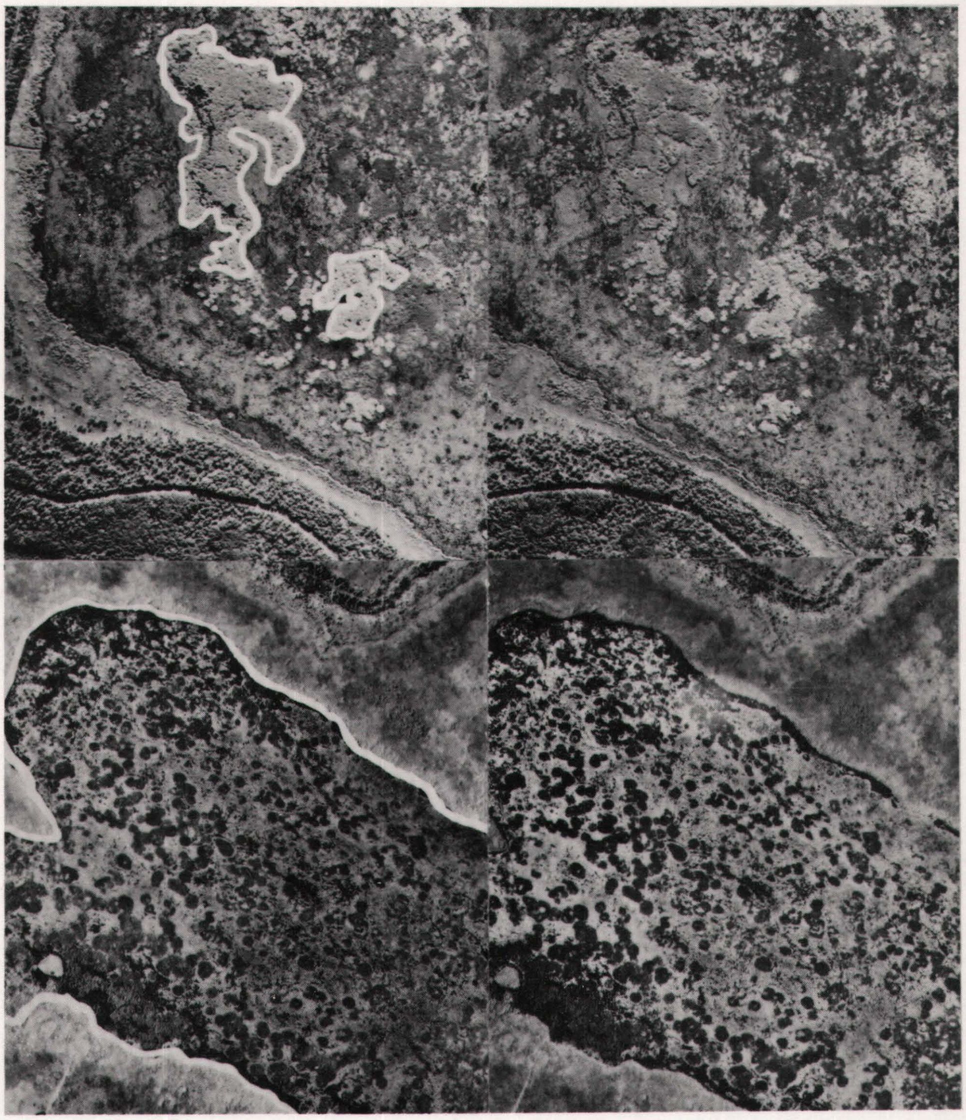


Plate 8. Above. Stereogram of Phragmites Swamp.

Below. Stereogram of Bulrush-Water-lily Mixture.

3X magnification, and outlined directly on the photographs (Plates 2-8). The appearance under the stereoscope of the 190 ground controls (tone, texture, and stereoscopic form) and the interpreters' familiarity with the area ensured reasonable accuracy in this work (Table 2). Interpretation of forest vegetation (White Spruce-Hardwoods type and Black Spruce-Tamarack type) was mainly based on crown characteristics (Sayn-Wittgenstein 1960, Zsilinsky 1963) and checked against forest inventory maintenance maps, prepared by the Saskatchewan Department of Natural Resources in 1965. The publications by Radforth (1955, 1958) on organic terrain recognition through airphoto interpretation provided additional background information.

The aerial photographs used were flight lines 4-14, 16-18, 21-22 of the 1964-65 coverage (Interdepartmental Committee for Air Surveys, Ottawa, Job No. 64-26), at an approximate scale of 1:15,800 (1 inch = 1,320 feet). Wherever gaps in the photography existed, 1954 airphoto coverage at an approximate scale of 1:31,600 (1 inch = 2,640 feet) was employed. This proved necessary for a strip, 6.5 km (4 miles) wide, through Kennedy, Meadow, and Goose lakes near the southern edge of the study region.

4.3.3 Map preparation

Base maps of the major topographic features of the area were obtained from the Forestry Branch of the Saskatchewan Department of Natural Resources. These base maps were prepared from the 1964 airphoto coverage and were thus of the same scale as the majority of the prints used for interpretation. Therefore, vegetation boundaries could be directly transferred onto acetate tracings of the base map information.

Subsequently, the manuscript maps were photographically reduced to half size, corrected for errors and omissions, and again reduced to the final scale of 1:63,360 or 1 inch = 1 mile. A colour code was then added and the vegetation map was printed in four basic colours (in back pocket of thesis).

4.4 Selection of field-transects and stands

Through examination of the reconnaissance vegetation map and oblique and vertical airphotos, eight field-transects, oriented transverse to the contours of the land, and extending from lake shore to high point on the levee, were selected within the study block in the spring of 1965. A ninth transect was added in 1967. These field-transects were chosen to represent typical landscape zonations or gradients (see Fig. 2, p. 12); they varied in length from 0.8 to 3.2 km (0.5 to 2 miles).

Each transect was permanently marked by a central cut-line, about 1.5 m wide and, at intervals, by angle iron stakes topped by orange-coloured squares of flat iron.

Subsequently, a total of 37 stands, representing common plant communities, were marked out adjacent to the transect lines. In addition to those located on transects, 61 stand-samples were subjectively chosen throughout the study block in order to obtain further detail on the total vegetation pattern. Randomized selection of stands, which would have been statistically more satisfactory, could not be done owing to the rarity of definite landmarks in this large area, and the need to rely on transport by helicopter. Precise locating in the field of randomly preselected sampling sites was impossible under these circumstances.

Care was taken to include in the sample a number of stands from each of the mapping categories (Table 3) to be able to assess, at a later date, to what extent physiognomic differences reflect ecological differences. The actual number of stand-samples depended on the apparent variability of the communities included in each mapping category.

To be acceptable for sampling, a stand had to satisfy the following criteria:

(1) It had to display visual homogeneity of vegetation and land-form. Vegetational complexes and mosaics of microstands (Hanson and Churchill 1961) which were regularly or randomly distributed, such as hummocks and hollows, were accepted within the scope of homogeneous sites.

(2) It had to be sufficiently large to allow vegetational sampling with the methods employed, i.e., from 0.2 ha (0.5 acres) for herbaceous vegetation to 0.8 ha (2 acres) for forest stands.

(3) It had to have a minimum of disturbance. This criterion was difficult to apply since most of the area appears to have experienced fire at some period in the past, and since most of the forest has been selectively logged for white spruce in the course of the last 60 years. Consequently, stands in which the degree of disturbance was judged relatively slight were included in the sampling program.

4.5 Vegetational measurements

Preliminary work in the first year of the study indicated a wide range of physiognomic types present in the study area, and a relatively complex structure of the forest and tall shrub communities. Because

Table 3. Number of stands sampled in the physiognomic mapping categories of the reconnaissance vegetation map.

Mapping category	No. of stands
White Spruce-Hardwoods Forest	20
Black Spruce-Tamarack Forest	13
Tall Willow-Alder Shrub	7
Medium Willow Shrub	6
Low Willow Shrub	12
Bog Birch Shrub	8
Broadleaved Sedge-Reedgrass Meadow	5
Narrowleaved Sedge-Cattail Meadow	13
Phragmites Swamp	6
Aquatic communities (bulrush swamp, water-lily pad, submerged aquatics)	8
Total	98

of this, structure and composition of the vegetation was examined by separate sampling of each of the following, arbitrarily designated, strata:

(1) Ground stratum; including all herbaceous species, dwarf shrubs, and small seedlings to a height of 85 cm.

(2) Low shrub stratum; consisting of shrubs 86 to 200 cm tall, and tree seedlings with a diameter at breast height (dbh) < 2.5 cm.

(3) Tall shrub stratum; containing shrubs above 200 cm in height and tree saplings with 2.5-7.5 cm dbh.

(4) Tree stratum; consisting of trees, with a dbh > 7.5 cm.

In each stand, the ground stratum was sampled, as were those woody strata sufficiently represented to permit quantitative vegetational measurement.

The abundance of bryophytes was not measured but an estimate was made of the percentage of the ground covered by mosses.

4.5.1 Ground stratum

The vegetation data for the ground stratum in each stand consisted of the frequency distribution of the species in 0.5 m x 0.5 m quadrats that were placed at regular intervals along two parallel lines across the stand.

This particular quadrat size was chosen because (1) preliminary trials with nested quadrats had shown it to be the best compromise for the widely diverse plant communities encountered, and (2) it has been used in a number of other studies of wetland and forest vegetation in Saskatchewan (e.g., Swan 1966, Swan and Dix 1966, Walker 1968, Walker and Coupland 1968, Jeglum 1968) and elsewhere (e.g., in Sweden by

Sjörs 1948, and the Red River Valley by Smeins 1967, and Dix and Smeins 1967) and thus its use facilitates comparison. Earlier trials had also shown that, in most stands, 10 to 20 quadrats provided an adequate sample, i.e., a 10 percent increase in area sampled yielded additional species $\leq$ 5 percent of the total present (Cain 1938). In a few of the more complex stands, however, up to 27 quadrats had been needed. To ensure adequate sampling, 30 to 40 quadrats were, therefore, sampled in each stand, except in seven simple communities of submerged aquatics where 15 quadrats were sufficient.

Occurrences in quadrats of the three principal species from the first 65 stands sampled were used to test homogeneity of the ground stratum by means of a Chi-square (2 x 2 contingency) test. All but two of the stands were found homogeneous by this criterion. Upon resampling of the latter, previously unnoticed, abrupt vegetation and site boundaries became apparent.

4.5.2 Shrub and tree strata

The abundance of species in each of the three woody strata was sampled with the point-centre quarter (P.C.Q.) method (Cottam and Curtis 1956). Measurements taken for shrubs were as follows:

(1) Distance in cm from point to centre of nearest clump (of any species) in each quarter;

(2) Mean diameter in cm of clump at breast height, or at crown for shrubs of smaller stature;

(3) Number of rooted stems per measured shrub; and

(4) Average height in m of predominant species.

The following determinations were made of trees, saplings, and seedlings:

(1) Distance in cm from point to centre of nearest individual in each quarter;

(2) Mean dbh of stem in cm; and

(3) Average height of predominant species.

Sampling points were systematically distributed along two to four parallel lines extending through the stands. Distances between points depended on the density of the vegetation, and their number was set to result in at least 30 individual measurements for the dominant species in each stratum. In practice, a 30 m steel tape was stretched out along compass lines and sampling points were set at equal intervals (e.g., 5 m). All three woody strata, if present, were sampled in turn from the same points.

Subsequently, the following figures were computed for each stratum:

(1) Absolute density, i.e., number of individuals and rooted shoots per hectare, derived from distance measurements and mean number of stems for each shrub species;

(2) Relative density of individuals and rooted shoots of the species present;

(3) Absolute dominance (total basal area in cm^2 per ha) for tree boles and the corresponding figures for clumps of shrub species; and

(4) Relative dominance, i.e., the percentage of the total basal area comprised by individuals of the species present.

4.5.3 Species-presence list

Following completion of the field sampling procedure, a complete presence list was prepared for each stand which included, in addition to the enumerated plants of all strata, any species casually observed to be present.

4.5.4 Taxonomic matters

Voucher specimens were collected of the 182 species of vascular plants and 14 bryophytes encountered in the stands; these are lodged in the herbarium of the Prairie Migratory Bird Research Centre at the University of Saskatchewan, Saskatoon. Nomenclature is according to Scoggan (1957) with the following exceptions and additions: (1) The lowland birch has been referred to as *Betula glandulifera* following Dugle (1966); (2) *Salix lutea* Nutt. was included with *Salix rigida* on the advice of Dr. G. W. Argus; and (3) *Salix lasiandra* Benth., not listed by Scoggan, was found to occur sparsely in the area. The author's identification of vascular plants has been verified by Dr. G. W. Argus or Mr. J. H. Hudson, of the W. P. Fraser Herbarium, University of Saskatchewan. The bryophytes were identified by Dr. C. D. Bird, University of Calgary.

An annotated list of all collections made in the Saskatchewan River Delta in the course of this and related studies has been published (Dirschl and Dabbs 1969).

Owing to difficulties in the field of distinguishing between some species by vegetative characters alone, the following taxonomic complexes were established: *Calamagrostis canadensis-inexpansa-neglecta*, *Galium labradoricum-trifidum*, *Ribes americanum-hudsonianum*, *Ribes hirtellum-lacustre-oxyacanthoides*, and *Sonchus arvensis-asper*. Since specific ecological amplitudes may pertain to each complex and since all were frequently recorded in the vegetation data, they were retained in the analysis.

During the first three years of the study, the white birch in the study block was considered to be *Betula papyrifera* Marsh. Following publication of the taxonomic work by Dugle (1966), it became evident that *Betula resinifera* Britton or, more correctly, *Betula neoalaskana* Sargent (see Dugle 1969) was present as well. Since quantitative rectification of this fact would have required time-consuming re-sampling of a number of forest stands, it was decided to continue to treat all white birch as *Betula papyrifera*.

4.6 Environmental measurements

4.6.1 Lake water levels

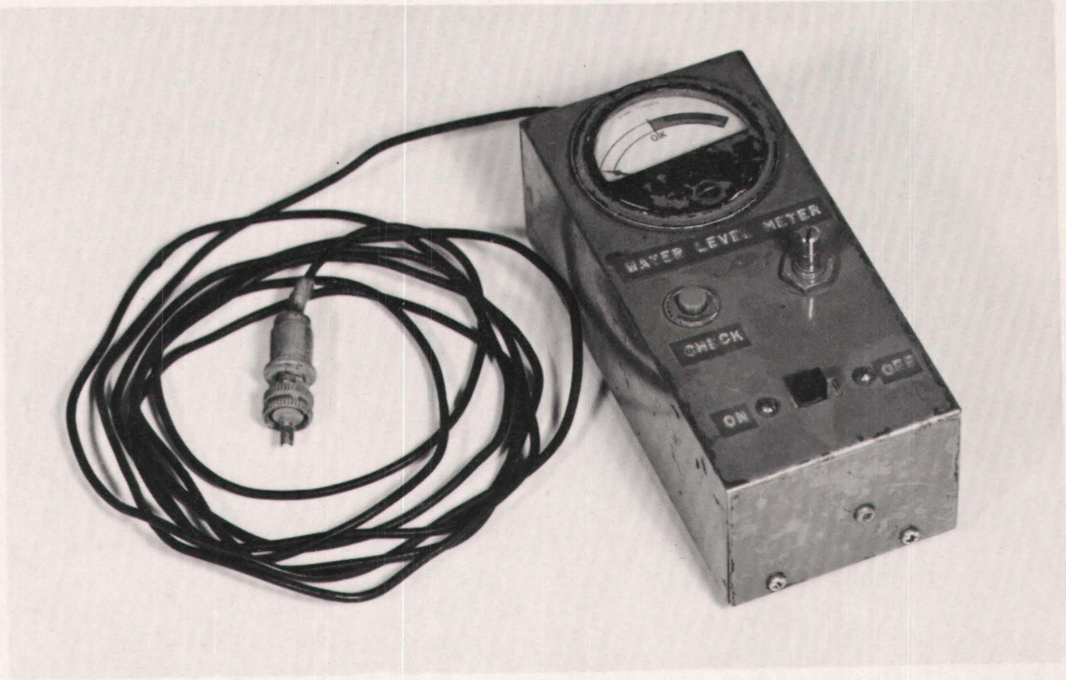
Available moisture is an important environmental gradient that has influenced the development of the vegetational pattern in the Delta. Within the study block, the natural, seasonal fluctuations of the levels of the major water bodies, and possibly the water-tables of adjacent peat and alluvial deposits, have been modified by artificial means. Thus in order to achieve a quantitative measure of the seasonal pattern of water level changes in the lakes and, possibly, to relate those fluctuations to available moisture in major vegetation types, lake water levels were monitored during the open water periods of 1965 through 1968.

Staff gauges were established near the shores of seven lakes in the study block: Egg, Junction, Cut Beaver, Muskeg, Deep, Bloodsucker, and Highbank. Lengths of angle iron stakes were driven into the lake bottom until firmly established, with the top of each stake about 1.5 m above the water. The distance between water surface and the top of the stake was then read at intervals of approximately two weeks on relatively calm days. The exact elevations of the stakes were checked, during the winter following each field season, by reference to bench marks previously established by the Canada Department of Agriculture along the banks of the Saskatchewan River.

4.6.2 Position of the water-table

At several locations along each of the nine field-transects, a perforated steel pipe, 3.8 cm (1.5 inches) in diameter and sealed at the bottom, was placed vertically into the ground by means of a screw-type auger. Because of the level terrain, hydrostatic pressure was assumed to be negligible; thus the level to which ground water rose in the pipe was taken as the level of the water-table in the vicinity. This assumption was found valid when ground water surfaces in several large pits were compared with those recorded from nearby perforated pipes.

Reading of ground water levels was facilitated by a simple instrument, built for the author by Mr. K. R. Bindle of the Department of Biology, University of Saskatchewan. It consisted of an ohm-meter, powered by a B-cell, with positive and negative poles attached to an electric cord, which was marked in cm (Plate 9). The cord was lowered into the pipe and a reading taken when a deflection of the needle indicated that the electric circuit had been closed by contact with the water surface. Readings were obtained at two-week intervals during the field seasons of 1965, 1966, and 1967.



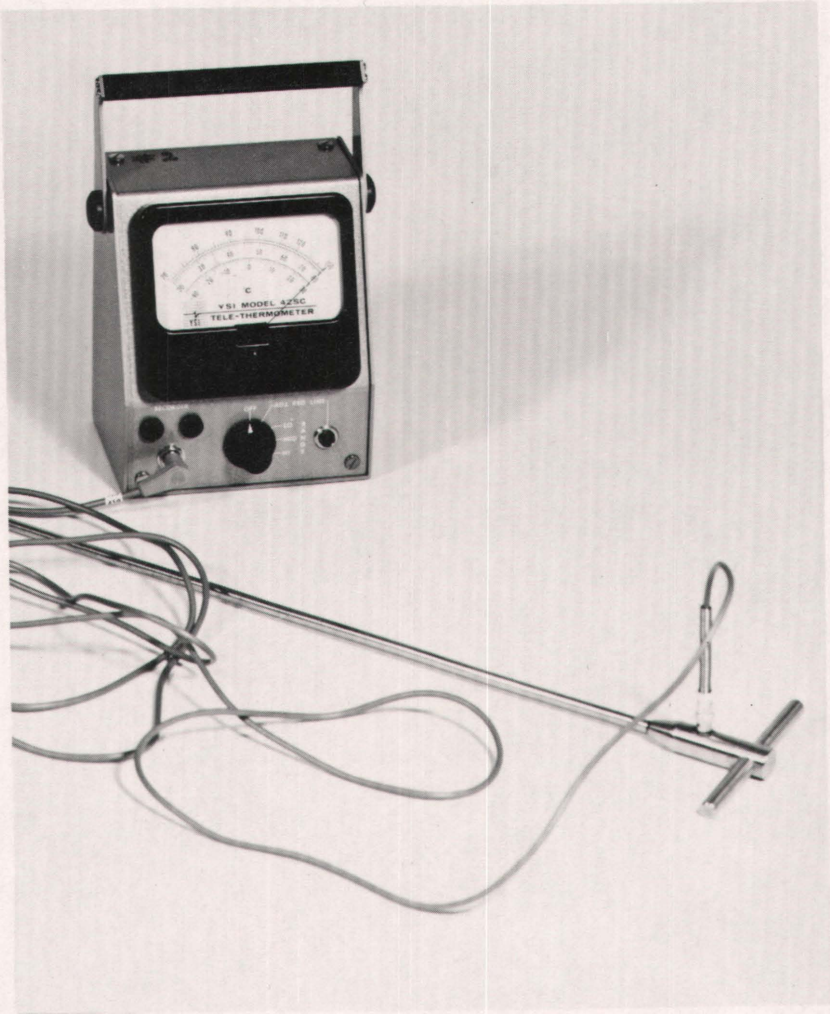


Plate 9.

Above. Instrument used to record position of water-table.

Below. Telethermometer and probe used for soil temperature measurements.

4.6.3 Soil temperature

The temperature of the substrate in the vicinity of the water-table gauges was measured at two-week intervals during the field seasons of 1965, 1966, and 1967 by means of a battery-powered tele-thermometer (Yellow Springs Instrument Co., Model 42) and a stainless steel insertion probe (Plate 9).

Temperatures were recorded at mid-day at 15 and 60 cm below the surface; each record was the average of three measurements.

4.6.4 Soil and water samples

Compound soil samples were obtained from each stand at three depth intervals: 0-30 cm, 31-90 cm, and 91-180 cm by means of an 8 cm (3-inch)-diameter bucket auger. For the aquatic stands, samples of the bottom muck and the clay base were obtained with scuba diving gear.

The samples were immediately put into plastic bags and transported by helicopter or airboat to the field headquarters where, within four hours of sampling, pH and electrical conductivity (= specific conductance) were measured from a thick paste. Records were also made at that time of the apparent botanical origin of peat samples.

The remainder of the soil samples were then air-dried, placed into cardboard containers, and stored for later transfer to the Saskatchewan Soil Testing Laboratory at the University of Saskatchewan, Saskatoon Campus, where the following additional analyses were performed: ash content, soluble Na^+, Ca^{++}, Mg^{++}, and K^+ (by spectrophotometry), available N, available P, available K, sodium adsorption ratio, and moisture saturation percentage.

In addition, the texture of mineral soil samples (with ash contents

> 85%) was determined. All peat samples were further grouped, according to ash content, into the following four classes: fibric peat (0-10% ash), mesic peat (11-25% ash), humic peat (26-70% ash), and mineral peat (71-85% ash).

One-litre water samples were collected from each of the major water bodies in the study area, and from surface water or from auger holes in 69 of the 98 stands during the summer of 1968. Samples were not obtained from the remaining stands, either because the water-table was deeper than 180 cm (the length of the auger used), or because helicopter transportation was not available at the time.

The water samples were put into opaque, brown polyethylene bottles by means of a pipette and transported to field headquarters by helicopter, within two to three hours, where specific conductance and pH were determined. A few drops of formalin were then added to stop bacterial activity, and the bottles were stored in the dark. Following the end of the field season, the water samples were shipped to the Water Quality Division of the Department of Energy, Mines and Resources, Ottawa, where the following analyses were performed: CO_2, $CaCO_3$, Ca^{++}, Mg^{++}, Na^{+}, HCO_3^{-}, $SO_4^{=}$, Cl^{-}, F^{-}, $PO_4^{\equiv}$, NO_3^{-}, $SiO_2^{=}$, and sodium adsorption ratio. The analytical methods used are described in Thomas (1953).

4.6.5 Profiles of field-transects

In order to place the vegetational and environmental data from the field-transects into proper relationship to each other along an elevational gradient, and to study possible interactions between lake water levels and sub-surface water depths, the elevation of the ground surface in each transect was surveyed at 20 to 200 ft. (6.1-61 m) intervals in winter. The elevation of each water-table pipe and the mean elevation of each stand-sample on the transects was also determined. Elevations, initially based on arbitrary datum, were later related to existing bench marks, and scaled profile diagrams were drawn for all transects.

4.7 Stratigraphy of field-transects

As an aid in understanding the successional processes that led to the present pattern of fen and bog vegetation, a macroscopic analysis of peat cores was carried out as an adjunct to the main study. Peat stratigraphy was restricted to five of the nine field-transects; Transects 4 to 6 and 8 were omitted owing to access problems. Core samples were taken in early May 1968, while peat deposits remained largely frozen. The tool used to extract the peat cores was obtained through the courtesy of Mr. R. J. E. Brown of the National Research Council's Division of Building Research, Ottawa, and consisted of a steel tube, 2.5 cm in diameter and 15 cm long, open along one side and tipped with a serrated edge. It was attached to a sectional steel pipe and T-handle.

This tool was screwed into the peat at sampling points more or less systematically distributed along the selected transects. A composite of three cores was obtained at each point within a radius of 3 m. The 15 cm long core samples were individually put into plastic bags, labelled, immediately placed into styrofoam chests containing dry ice. They were then transferred to a deepfreeze until they could be transported, still frozen, to Saskatoon for analysis.

Although analysis of vertical zonation of plant macrofossils has been used in various studies of peatlands (e.g., Kulczynski 1949, Chapman 1964a, 1964b), little detail is available in the literature regarding the exact laboratory techniques used. An exception is the work of Watts and Winter (1966) who compared analysis of plant macrofossils (mainly seeds) with pollen diagrams obtained from the same cores.

The techniques for the stratigraphic analysis of peat cores and the peat classification used in this study (Table 4), were adapted from Day (1968). Reference works for the identification of bryophyte fossils were Conard (1956) and Bird (1968), and for seed identification Martin and Barkley (1961). The procedure was as follows:

Frozen core segments from equal depths at each sampling location were placed together in an enameled tray and allowed to thaw. Each segment was then split lengthwise and its colour compared with a Munsell chart (= unrubbed colour, see Day 1968). The mean value of the three readings was recorded. Half of the material in the tray was then placed in a graduated cylinder and its volume determined by water displacement. The contents of the graduate cylinder were then poured on a 100-mesh sieve (0.15 mm diameter) and thoroughly washed. The volume of fibers remaining on the screen was again measured by displacement (= unrubbed fiber content).

The remaining portion of the peat sample in the tray was formed into a ball and squeezed 10 times by hand. The ball was broken into half, and the colour of the broken face was compared with a Munsell chart (= rubbed colour). The percentage of fiber remaining after squeezing was then determined by washing on a screen as described above (= rubbed fiber content).

Table 4. Criteria and classification used in the stratigraphic analysis of peat cores. (Adapted from Day 1968).

A. Degree of decomposition

Fibric peat	Mesic peat	Humic peat
Unrubbed fiber content $\geq$ 6/10 of organic volume	Unrubbed fiber content 3/10-6/10 of organic volume	Unrubbed fiber content $<$ 6/10 of organic volume
Rubbed fiber content $\geq$ 4/10	Rubbed fiber content $>$ 1/10	Rubbed fiber content $<$ 1/10
	or	
	Unrubbed fiber content $>$ 6/10 Rubbed fiber content 1/10-4/10	

B. Categories according to predominant constituents

Compositional category	Typical constituents
1. Forest litter	Duff of forest floor, generally fibrous: twigs, leaves, coniferous needles, forbs, mosses, e.g., *Hylocomium*
2. Fen	*Carex*, *Phragmites*, *Typha*, *Equisetum*
3. *Sphagnum* moss	*Sphagnum* spp. with admixtures of Ericaceae and litter derived from *Picea mariana* and *Larix laricina*
4. *Hypnum*-type moss	*Hypnum*, *Calliergonella*, *Campylium*, and *Drepanocladus*
5. Sedimentary matter (aquatics)	*Potamogeton*, *Nuphar*, *Myriophyllum*, and other submerged aquatics
6. Typic (unidentifiable) organic matter	Bottom muck or highly decomposed peat
7. Mineral soil	Soil containing $\leq$ 30% organic matter
8. Included layer	Sand, silt or charcoal seams within a peat matrix

. . . cont'd

Table 4 concluded.

C. Classification of peat core segments

1. Sylvo	- fibric peat - mesic - humic	5. Sedimentary	- mesic peat - humic
2. Fenno	- fibric peat - mesic - humic	6. Typic	- mesic peat - humic
3. Sphagno	- fibric peat - mesic - humic	7. Mineral soil textural class	
4. Hypno	- fibric peat - mesic - humic	8. Included layers	

5. VEGETATION ANALYSIS

5.1 Reconnaissance vegetation map

The absolute and relative extent of the recognized physiognomic-floristic mapping categories (Section 4.3) was determined by means of a randomized dot grid for the entire area mapped and, separately, for the 660 km^2-study block (Table 5).

Examination of the map (in back pocket of thesis) shows that the 660 km^2-study block contains examples of all the major components of the vegetation and landform features and in reasonably similar proportions. It may thus be considered a representative segment of the entire area.

Interesting patterns of distribution of the various physiognomic types in relation to each other and to physiographic features are apparent from the vegetation map. Water covers 14.3 percent of the area of the Delta, of which 2.4 percent is occupied by emergent *Scirpus* spp. and floating *Nuphar variegatum*, either separately or in mixture. Of the remaining vegetation, White Spruce-Hardwoods Forest and Tall Willow-Alder Shrub were the most extensive types, 24.7 percent and 15.9 percent, respectively. The White Spruce-Hardwoods Forest type is mainly distributed in east-west trending bands that parallel the course of the Saskatchewan, Birch, and Carrot rivers, and Petabec Creek. It also forms a broader expanse along the Sipanok Channel in the south-western part of the area. The type thus occupies the raised levees of alluvium which those streams have built up during flood stages. White Spruce-Hardwoods Forest is also found throughout the Delta in narrow, meandering bands paralleling smaller interior water courses or former

Table 5. Extent of the physiognomic vegetation types used in reconnaissance mapping.

	I. Total area mapped			II. Study block		
	Area			Area		
Vegetation type	sq km	sq mi	Percentage	sq km	sq mi	Percentage
White Spruce-Hardwoods Forest	681.2	263.0	24.7	84.7	32.7	12.8
Black Spruce-Tamarack Forest	61.6	23.8	2.2	9.8	3.8	1.5
Tall Willow-Alder Shrub	440.3	170.0	15.9	114.5	44.2	17.4
Medium Willow Shrub	258.7	99.9	9.4	52.1	20.1	7.9
Low Willow Shrub	219.9	84.9	8.1	87.5	33.8	13.2
Bog Birch Shrub	404.0	156.0	14.6	89.9	34.7	13.7
Broadleaved Sedge-Reedgrass Meadow	49.7	19.2	1.8	13.0	5.0	1.9
Narrowleaved Sedge-Cattail Meadow	215.0	83.1	7.8	68.6	26.5	10.4
Phragmites Swamp	34.4	13.3	1.2	24.1	9.3	3.6
Bulrush Swamp	12.4	4.8	0.4	6.2	2.4	0.9
Water-lily Pad	44.5	17.2	1.6	18.9	7.3	2.8
Water-lily-Bulrush Mixture	12.2	4.7	0.4	11.1	4.3	1.7
Open Water	328.7	126.9	11.9	80.3	31.0	12.2
Total	2,762.6	1,066.8	100.0	660.7	255.1	100.0

drainage channels which have become blocked through river capture, silt deposition, or other delta-building processes. The Tall Willow-Alder Shrub type is spatially associated with the above type of vegetation, apparently occupying slightly lower positions on the levees.

Medium Willow Shrub and Low Willow Shrub are extensive physiognomic types, jointly covering 17.5 percent of the area. Medium and low willow shrub vegetation is mainly distributed between the raised levees and the open fen vegetation of the lake shores.

Broadleaved Sedge-Reedgrass Meadows and Narrowleaved Sedge-Cattail Meadows together cover nearly 10 percent of the area. This open fen vegetation is extensive adjacent to shallow lakes in the northern and southwestern portions of the area. Phragmites communis-dominated vegetation amounts to 1.2 percent of the area and is distributed on shorelines and islands in the shallowest lakes and marshes. Emergent and floating aquatic vegetation also appears confined to the shallower bodies of water.

The two remaining physiognomic types, Bog Birch Shrub and Black Spruce-Tamarack Forest, consist of 14.6 percent and 2.2 percent of the area, respectively. The Betula glandulifera-dominated vegetation occurs in large contiguous areas in interior basins, that are more or less completely enclosed by raised levees. Black Spruce-Tamarack Forest mainly is located as small islands within expanses of Big Birch Shrub.

As well as being a static portrayal of present vegetation cover, the reconnaissance vegetation map is useful in focusing attention on aspects of the dynamic interrelations between vegetation and environment. In suggesting to the investigator various mechanisms that may have been instrumental in producing the present landscape, the map becomes a valuable tool for further, detailed field research:

(1) For example, does the lack of clear-cut positioning in the landscape of Low Willow Shrub and open fen meadows suggest very fine differences in water and nutrient regime, or is it a reflection of past environmental conditions rather than present ones? Have the floating lake shores, where those two vegetation types frequently occur as mosaics, been caused by artificially increased water level fluctuations?

(2) The location of black spruce stands as small islands within larger acreages of big birch, and the presence of dead coniferous trees in their vicinity, suggests that those stands were once more extensive but have since regressed, possibly also because of a higher water-table.

The following sections describe the results of field research that was conducted to reach a better understanding of the ecology of the Delta's vegetation.

5.2 Preliminary association analysis

It was assumed in this study that the total species complement of a stand reflects present ecological conditions more faithfully than the dominants of the canopy alone. This is particularly so in a landscape where water regime changes and other man-made disruptions have taken place in recent years and disturbed the steady state that previously existed between the plant community and the complex of site factors.

5.2.1 Treatment of the data

Following completion of sampling in 79 stands (in August 1967) a preliminary analysis of the data was carried out through the method of association analysis, as developed by Williams and Lambert (1959, 1960, 1961), Lambert and Williams (1962, 1966), Williams et al. (1966), and

Lance and Williams (1965, 1968). Those authors and others (Ivimey-Cook and Proctor 1966, Crawford and Wishart 1966, Greig-Smith et al. 1967, Walker 1968) have shown the method to be useful in explaining major lines of variation and in producing reasonably homogeneous groups of stands for subsequent comparison.

The specific technique selected from the various forms of association analysis, was a monothetic-divisive one based on an information model as the parameter determining division (Lance and Williams 1968). Of the three aspects of association analysis (normal, inverse, and nodal) only normal analysis was performed. Inverse analysis gave poor results in the analysis of other wetland vegetation in Saskatchewan (Walker 1968) and nodal analysis has severe limitations in its present form (Ivimey-Cook and Proctor 1966, W. T. Williams as quoted in Walker 1968; G. N. Lance, personal communication). The analysis was carried out by the Division of Computing Research of the Commonwealth Scientific and Industrial Research Organization at Canberra, Australia, using the DIVINF program written for the CDC 3600 digital computer (Lance and Williams 1968).

Depending on the presence or absence of the species involved, the computer program divides the data in an hierarchical manner into a number of groups of individuals (stands), so that each division of a group into two component sub-groups removes a greater proportion of the total variance than any other division that could have been made. Each division, therefore, is based on that species (attribute) which is causing the highest amount of disorder in the parent group. The resulting hierarchy, as plotted by the computer, may be examined in two ways: (1) the classification of homogeneous groups, and (2) the nature and sequence of the divisions themselves.

A serious fault of a method based on presence-absence data is the positioning of a stand in a group to which it does not belong, owing to the chance presence or absence of a dividing species (Lambert and Williams 1966, Orloci 1967a). It is, therefore, necessary to examine the position of all stands in the final groups to which they belong on the basis of their total species complement. If the investigator would have immediate access to the computer, the simplest and soundest procedure would be to add the missing species to the data card for the stand and to rerun the analysis. Since in this study that approach would have been too costly, assignment of misplaced stands to the correct groups was done by inspection.

5.2.2 Results

In the application of the association analysis technique it is necessary to decide on the number of terminal groups to be produced. Some programs include a stopping rule based on set reduction in variance (Lance and Williams 1965), but the applicability of probabilistic stopping rules to classificatory problems is somewhat controversial (Webb _et al_. 1967). The ultimate test of a division, in any case, has to be its meaningfulness to the user, in this case its ecological significance. The intent of the preliminary association analysis was to reveal the utility of the technique in classifying the total vegetation spectrum into broad categories with affinities for particular positions in the landscape of the study area. Analysis was, therefore, carried no further than the arbitrary level of 10 terminal groups.

Following re-allocation of several misplaced stands, tables were constructed for the 10 groups, listing, for each stand (1) the physiognomy of the vegetation, (2) nature and degree of recent disturbance, (3) physiography of site, (4) type of substrate, and (5) specific conductance and pH of the soil (e.g., Appendix A). Average conditions were subsequently determined for each attribute. Two of the groups did not show any clear differences and were, therefore, recombined.

The hierarchy of divisions, as plotted by the computer, is presented in Fig. 3. The prevailing habitat characteristic of the parent and end-groups were added after the analysis had been completed. Vertical distances between divisions reflect relative progressive reduction in information content - a measure of heterogeneity of floristic composition. A brief resume of the major points of the analysis will indicate its value as an initial sorting tool, and the action taken from its results.

The initial division was on the presence or absence of Rosa acicularis, resulting in a clear-cut separation of stands on alluvium of stream and river levees from peat and aquatic stands. The second divison, on Carex rostrata, separated meadow and shrub communities on fen peat from the remainder. Subsequent divisions on the left side of the analysis (Fig. 3), were on Andromeda polifolia, separating submerged aquatic stands from ericaceous shrub and Picea mariana communities on deep Sphagnum peat, and on Betula glandulifera and Sparganium eurycarpum, resulting in three final groups of fen vegetation: (1) bog birch (B. glandulifera) thickets on deep peat of closed basins, (2) meadow and low shrub vegetation of floating mats, and (3) meadow and shrub vegetation on shallow, anchored fen peat.

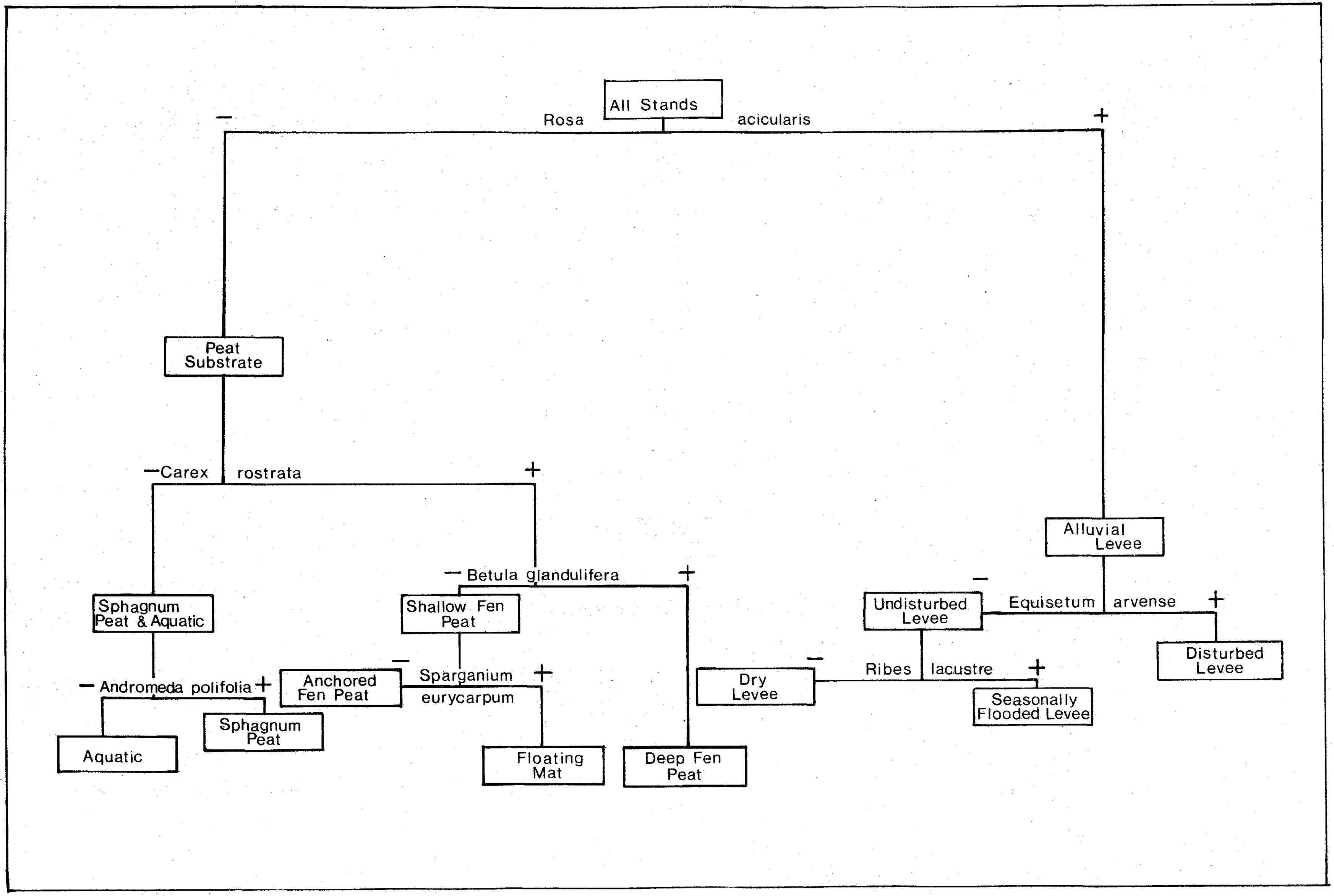


Fig. 3. Hierarchy of divisions from the preliminary association analysis of 66 stands. Apparent spatial associations of the parent and end-groups with main landscape components have been added.

The 25 stands of levee vegetation were further split into three groups with fairly distinct ecological characteristics. Disturbance by fire or logging appeared to distinguish a group of stands that were separated from the remainder on the presence of Equisetum arvense. Finally, division on the presence or absence of the taxonomic complex Ribes hirtellum-lacustre-oxyacanthoides (see Section 4.5.4) accomplished a separation of hardwoods and tall shrub stands on seasonally flooded, low levees from those on higher levees.

Considered as a whole, the analysis was successful in separating out and characterizing groups of stands that occupied distinct sites. The analysis was most efficient in splitting off groups of stands at the extremes of the water regime and fertility gradients, e.g., ombrotrophic bog and aquatic stands, it was less efficient in producing significant groups from the stands of tall shrub and forest vegetation on the alluvial levees.

It was, therefore, decided to increase the number of stand samples of stream levee vegetation and, in addition, to include stands of vegetation types which were poorly represented in the preliminary analysis (e.g., Larix laricina-dominated communities on peat) in order to permit better characterization of these vegetation/site complexes.

5.3 Final association analysis

Based on the results of the preliminary association analysis, an additional 19 stands of selected vegetation and site types were sampled in order to fill gaps which the results of the preliminary analysis had brought out. Sampling procedures were necessarily identical.

5.3.1 Purpose and analytical treatment

The purpose of the final association analysis again was to classify the total vegetational variation into a small number of categories which, although floristically and structurally still relatively heterogeneous, occupy definite positions in the landscape, or which are associated with distinct segments of the principal environmental gradients. It was intended to subsequently apply ordination techniques to these groups in order to clarify details of vegetation/environment relationships of stands and major species (Section 6). Recent evidence has suggested that classification is likely to be more satisfactory at higher levels and ordination at lower levels of vegetational variation. Thus some combination of the two approaches likely will be more informative than either alone (Gittins 1965a, 1965b, 1965c, Ivimey-Cook and Proctor 1966, Greig-Smith *et al*. 1967, Swan 1970, W. T. Williams, personal communication). Jeglum *et al*. (1969), in analyzing data from lowlands in central Saskatchewan by means of subjective classification and principal component ordination, reached similar conclusions.

The vegetation data from all 98 stands were subjected to association analysis, employing the DIVINF program of the CSIRO. Two runs were performed:

(1) Using complete species presence lists without regard to abundance;

(2) Using a modified matrix that excluded 44 species which failed to reach a minimum frequency of 20 percent in the ground stratum of any stand.

The latter modification was undertaken because there is some evidence that the inclusion of a large number of minor species in the analysis may induce ecologically meaningless divisions at lower levels of heterogeneity (G. N. Lance, personal communication; Greig-Smith *et al*. 1967).

The two runs of the DIVINF computer program were carried to the level of 12 final groups and the resulting hierarchies compared with each other in respect to the sequence of divisions and the nature of the final groups.

It became immediately apparent that the two runs gave very similar results. The sequence of upper-level divisions was identical, and the dividing species also were the same. At lower levels of information content, the two hierarchies differed slightly in terms of sequence of divisions, dividing species, and the composition of some of the final groups. It appeared, however, that fewer misplaced stands existed in the final groups of the modified matrix than in the full one, therefore the former was selected for further analysis (Fig. 4).

As in the preliminary association analysis, it was found that a number of stands were misplaced owing to chance presence or absence of dividing species. For the reasons outlined in Section 5.2.1, misplaced stands were relocated to groups into which they best fitted according to the sum-total of available information. The following anomalies in stand positioning were corrected:

(1) Group 14 on the left side of the hierarchy consisted of three misplaced stands: Stands 31 and 84, being tall shrub and balsam poplar communities, had been misplaced because of the chance absence of *Rosa acicularis*. They were, therefore, added to Groups 10 and 23, respectively. Stand 91 (black spruce on fen peat) was relocated to Group 6.

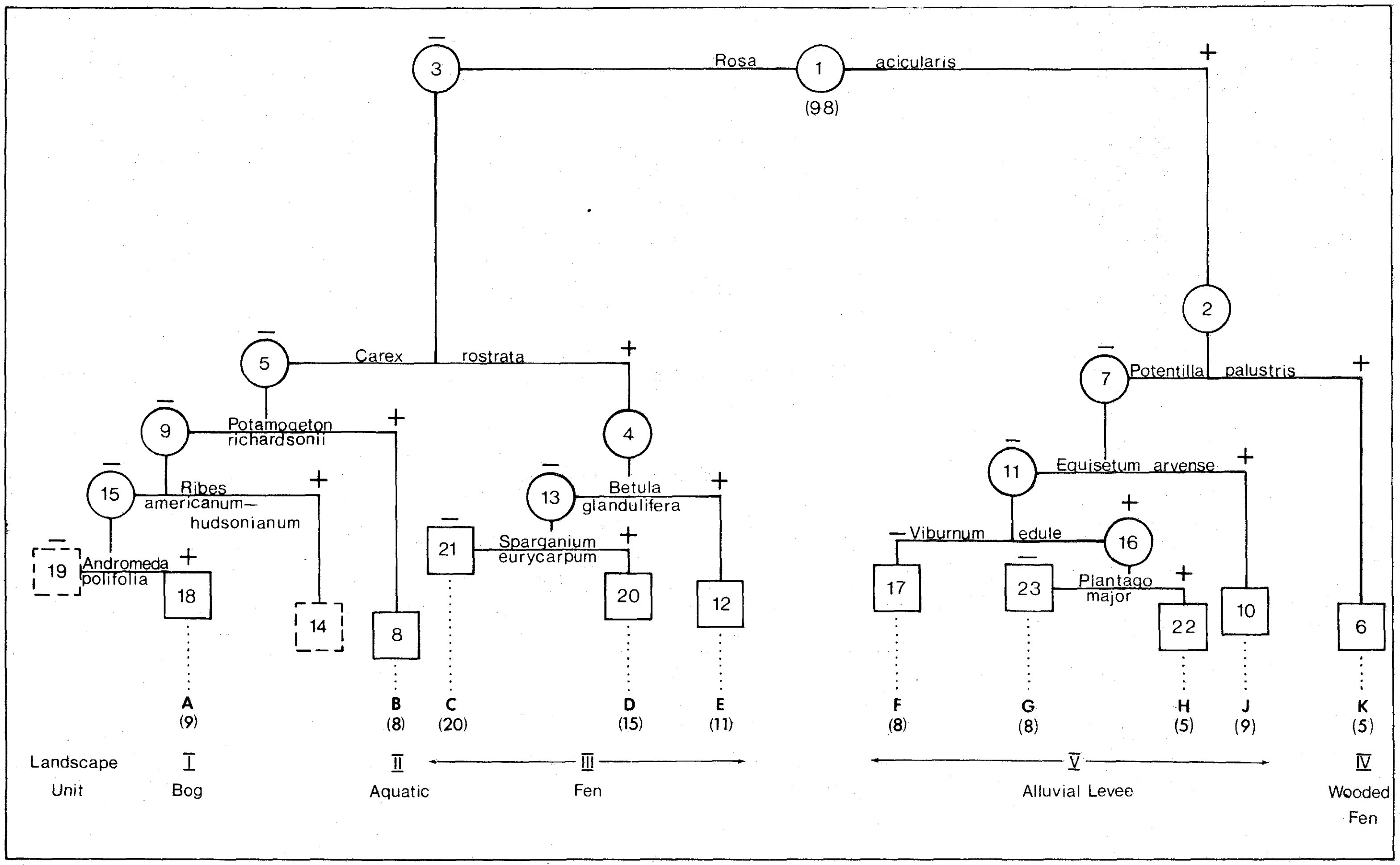


Fig. 4. Hierarchy of divisions from the final association analysis of 98 stands. Enclosed figures are group numbers of parent (○) and terminal (□) groups. ⌜⌟ refers to small groups of misplaced stands that are relocated by inspection. A-K refers to the 10 terminal groups (number of stands is given in parentheses) whose affinities with main landscape components are also indicated.

(2) Group 19, consisted of a residuum of nine floristically impoverished stands which because of this feature had been positioned at the extreme left of the hierarchy. On the basis of their total species complement, those stands were relocated as follows:

Stand 8 to Group 21

Stands 22, 24, 93, 96 and 97 to Group 20

Stand 88 and 89 to Group 12

Stand 90 to Group 6

Thus the number of final groups was reduced from 12 to 10 by assigning misplaced stands to those groups into which they best fitted. These adjusted terminal groups were labelled A to K to simplify reference to them (Fig. 4).

5.3.2 Summarization of attributes for adjusted terminal groups

In order to characterize and compare the adjusted terminal groups, tables were constructed for each group, listing species and environmental data for all stands. To take into account all available information, quantitative abundance measurements for the species were used in addition to the presence data.

Species were placed into the following five classes according to presence in the stands (cf. Braun-Blanquet 1951, Knapp 1958):

Presence Class I	.....	occurring in 1-20 percent of the stands
II	.....	21-40
III	.....	41-60
IV	.....	61-80
V	.....	81-100

Quantitative abundance data used were percent frequency for the ground stratum and percent relative dominance for the woody strata. Mean abundance percentages in stands present were computed for all species and transformed into five classes of abundance as follows:

Abundance Class 1 ..... 1-20 percent mean abundance

2 21-40

3 41-60

4 61-80

5 81-100

Table 6 lists the prevalent and locally abundant ground stratum species, and the associated shrubs and trees for each of the 10 adjusted terminal groups. "Prevalent" species were considered to be all ground stratum plants which occurred in more than 60 percent of the stands (Presence Class IV and V), regardless of abundance. "Locally abundant" species were those which occurred in 60 percent or fewer of the stands (Presence Class I-III) but were frequent in individual stands.

An example of the procedure by which the species were compiled is given in Appendix B.

Selected environmental attributes for each stand were categorized and group-averages were determined (Table 7) to permit subsequent evaluation of the environmental relationships of the groups.

In the description of the results, the hierarchy of divisions will be briefly discussed before the relationships between the groups themselves are examined.

5.3.3 Hierarchy of divisions

To carry the analysis to the desired 12-group level, a total of 11

Table 6. Lists of major ground stratum species and of associated upper strata species for the 10 terminal groups of the final association analysis.

Major species of ground stratum		Associated upper strata species: Low shrub stratum		Tall shrub stratum		Tree stratum	
Group A (9 stands, 53 species)							
PREVALENT							
*Andromeda polifolia	V-4**	Picea mariana	III-5	Picea mariana	III-5	Larix laricina	II-5
*Chamaedaphne calyculata	IV-4	Betula glandulifera	III-2	Betula glandulifera	II-3	Picea mariana	I-5
Ledum groenlandicum	IV-4	Salix pedicellaris	II-3	Larix laricina	II-3		
*Kalmia polifolia	IV-3	Larix laricina	I-1	Alnus rugosa	I-5		
Betula glandulifera	IV-1			Betula papyrifera	I-1		
LOCALLY ABUNDANT							
Equisetum fluviatile	III-5						
Oxycoccus quadripetalus	III-4						
Rubus chamaemorus	III-4						
Carex lanuginosa	III-3						
Potentilla palustris	III-3						
Salix petiolaris	II-4						
Carex deweyana	I-4						
Group B (8 stands, 15 species)							
PREVALENT							
*Potamogeton richardsonii	V-2						
*Potamogeton zosteriformis	V-2						
*Ceratophyllum demersum	IV-4						
*Nuphar variegatum	IV-4						
*Anacharis canadensis	IV-3						

*Signifies "differential species", i.e., those which are prevalent in that group only.

**Roman numerals refer to presence class, whereas Arabic numerals refer to abundance class (see text for explanation of classes).

. . . cont'd

Table 6 continued.

Major species of ground stratum		Associated upper strata species: Low shrub stratum		Tall shrub stratum		Tree stratum
Group B continued						
LOCALLY ABUNDANT						
Potamogeton pectinatus	II-3					
Scirpus acutus	I-2					
Group C (20 stands, 53 species)						
PREVALENT						
Carex atherodes	V-4	Salix discolor	I-4	Salix discolor	II-4	
Carex aquatilis	V-3	Salix petiolaris	I-2	Salix bebbiana	I-4	
Carex rostrata	V-3			Alnus rugosa	I-1	
Naumburgia thyrsiflora	IV-3					
Calamagrostis canadensis-inexpansa-neglecta	IV-2					
Galium labradoricum-trifidum	IV-2					
Potentilla palustris	IV-1					
LOCALLY ABUNDANT						
Equisetum fluviatile	III-2					
Equisetum pratense	III-2					
Phragmites communis	I-5					
Group D (15 stands, 50 species)						
PREVALENT						
Carex atherodes	V-4	Salix candida	II-3			
Naumbrugia thyrsiflora	V-2	Salix petiolaris	II-2			
Carex aquatilis	IV-3	Salix candida	II-2			

. . . cont'd

Table 6 continued.

Major species of ground stratum		Associated upper strata species: Low shrub stratum		Tall shrub stratum	Tree stratum
Group D continued					
PREVALENT (cont'd)					
Calamagrostis canadensis-inexpansa-neglecta	IV-2				
Carex rostrata	IV-2				
Potentilla palustris	IV-2				
*Sparganium eurycarpum	IV-2				
*Typha latifolia	IV-2				
Galium labradoricum-trifidum	IV-1				
LOCALLY ABUNDANT					
Carex lanuginosa	III-3				
Phragmites communis	II-5				
Equisetum fluviatile	II-4				
Group E (11 stands, 51 species)					
PREVALENT					
*Carex lanuginosa	V-4	Salix candida	III-3		
Potentilla palustris	V-4	Betula glandulifera	II-3		
Betula glandulifera	V-3	Betula papyrifera	I-2		
Carex aquatilis	V-3				
Galium labradoricum-trifidum	V-3				
*Salix pedicellaris	V-3				
Calamagrostis canadensis-inexpansa-neglecta	V-2				
Carex atherodes	V-2				

. . . cont'd

Table 6 continued.

Major species of ground stratum		Associated upper strata species: Low shrub stratum		Tall shrub stratum		Tree stratum	
Group E continued							
PREVALENT (cont'd)							
Carex rostrata	V-2						
Naumburgia thyrsiflora	V-2						
*Campanula aparinoides	V-1						
Salix candida	V-1						
Menyanthes trifoliata	IV-3						
LOCALLY ABUNDANT							
Myrica gale	III-3						
Equisetum pratense	II-5						
Group F (8 stands, 65 species)							
PREVALENT							
Equisetum pratense	V-5	Cornus stolonifera	V-3	Salix discolor	IV-4	Populus balsamifera	II-5
Calamagrostis canadensis-inexpansa-neglecta	V-3	Viburnum trilobum	IV-2	Alnus rugosa	IV-2		
Cornus stolonifera	V-2	Ribes hirtellum	IV-1	Salix bebbiana	II-3		
Ribes americanum-hudsonianum	V-2	Ribes americanum	IV-1	Cornus stolonifera	II-3		
Rubus idaeus var. strigosus	V-2	Rosa acicularis	III-1				
Rubus pubescens	V-2	Rubus idaeus var. strigosus	II-1				
Galium triflorum	V-1	Alnus rugosa	II-1				
*Ribes glandulosum	V-1						
Ribes hirtellum-lacustre-oxyacanthoides	V-1						
Rosa acicularis	V-1						

. . . cont'd

Table 6 continued.

Major species of ground stratum		Associated upper strata species: Low shrub stratum		Tall shrub stratum		Tree stratum	
Group F continued							
PREVALENT (cont'd)							
Viburnum trilobum	V-1						
Matteuccia struthiopteris	IV-2						
Amelanchier alnifolia	IV-1						
Arenaria lateriflora	IV-1						
Carex atherodes	IV-1						
Circaea alpina	IV-1						
Galium labradoricum-trifidum	IV-1						
Smilacina stellata	IV-1						
Sonchus arvensis-asper	IV-1						
Group G (8 stands, 73 species)							
PREVALENT							
Equisetum pratense	V-5	Cornus stolonifera	IV-4	Alnus rugosa	III-1	Populus balsamifera	IV-2
Aralia nudicaulis	V-2	Rosa acicularis	IV-1	Cornus stolonifera	II-3	Picea glauca	II-1
Calamagrostis canadensis-inexpansa-neglecta	V-2	Rubus idaeus var. strigosus	IV-1	Salix discolor	II-3	Populus tremuloides	II-1
Cornus stolonifera	V-2	Ribes hirtellum	IV-1	Amelanchier alnifolia	II-3		
Rosa acicularis	V-2	Viburnum edule	II-2	Viburnum trilobum	II-2		
Rubus pubescens	V-2						
*Alnus rugosa	V-1						
Ribes hirtellum-lacustre-oxyacanthoides	V-1						
Smilacina stellata	V-1						
Viburnum edule	V-1						

. . . cont'd

Table 6 continued.

		Associated upper strata species					
		Low shrub stratum		Tall shrub stratum		Tree stratum	
Group G continued							
PREVALENT (cont'd)							
Viburnum trilobum	V-1						
Rubus idaeus var. strigosus	IV-2						
Viola spp.	IV-2						
*Populus balsamifera	IV-1						
Pyrola asarifolia	IV-1						
Ribes americanum-hudsonianum	IV-1						
LOCALLY ABUNDANT							
Matteuccia struthiopteris	III-2						
Group H (5 stands, 57 species)							
PREVALENT							
Equisetum pratense	V-5	Cornus stolonifera	V-2	Cornus stolonifera	IV-2	Picea glauca	III-4
Aralia nudicaulis	V-3	Rosa acicularis	V-1	Prunus virginianum	IV-1	Populus balsamifera	III-2
Rosa acicularis	V-3	Rubus idaeus var.		Alnus rugosa	III-4	Betula papyrifera	II-2
Rubus idaeus var.		strigosus	IV-2	Salix bebbiana	II-3	Acer negundo	II-2
strigosus	V-3	Viburnum trilobum	III-2	Amelanchier alnifolia	II-1	Ulmus americana	I-2
Circaea alpina	V-2	Viburnum edule	III-1	Betula papyrifera	I-2	Fraxinus	
Cornus canadensis	V-2					pennsylvanica var.	
Galium triflorum	V-2					subinterregima	I-1
Rubus pubescens	V-2						
Viola spp.	V-2						
Calamagrostis canadensis-inexpansa-neglecta	V-1						

. . . cont'd

Table 6 continued.

Major species of ground stratum		Associated upper strata species: Low shrub stratum		Tall shrub stratum		Tree stratum	
Group H continued							
PREVALENT (cont'd)							
Cornus stolonifera	V-1						
Matteuccia struthiopteris	V-1						
*Plantago major	V-1						
*Prunus virginiana	V-1						
Ribes hirtellum-lacustre-oxyacanthoides	V-1						
Viburnum edule	V-1						
*Mitella nuda	IV-2						
Arenaria lateriflora	IV-1						
Carex disperma	IV-1						
Ribes americanum-hudsonianum	IV-1						
Viburnum trilobum	IV-1						
Group J (9 stands, 80 species)							
PREVALENT							
Aralia nudicaulis	V-3	Rosa acicularis	IV-2	Salix bebbiana	IV-2	Populus balsamifera	III-2
Calamagrostis canadensis-inexpansa-neglecta	V-3	Cornus stolonifera	IV-1	Salix discolor	III-3	Picea glauca	II-4
*Equisetum arvense	V-3	Rubus idaeus var. strigosus	III-1	Alnus rugosa	II-5	Populus tremuloides	II-4
Galium triflorum	V-2	Ribes hirtellum	II-1	Amelanchier alnifolia	II-2	Betula papyrifera	II-1
Rosa acicularis	V-2			Cornus stolonifera	II-2		
Rubus pubescens	V-2						
Amelanchier alnifolia	V-1						

. . . cont'd

Table 6 continued.

Major species of ground stratum		Associated upper strata species: Low shrub stratum	Tall shrub stratum	Tree stratum
Group J continued				
PREVALENT (cont'd)				
Aster spp.	V-1			
Carex disperma	V-1			
Cornus stolonifera	V-1			
Ribes americanum-hudsonianum	V-1			
Rubus idaeus var. strigosus	V-1			
*Solidago spp.	V-1			
Pyrola asarifolia	IV-2			
Sonchus arvensis-asper	IV-2			
Circaea alpina	IV-1			
Galium labradoricum-trifidum	IV-1			
Ribes hirtellum-lacustre-oxyacanthoides	IV-1			
*Trientalis borealis	IV-1			
Viburnum edule	IV-1			
Viburnum trilobum	IV-1			
LOCALLY ABUNDANT				
Equisetum pratense	II-5			
Petasites palmatus	I-5			
Group K				
PREVALENT				
Calamagrostis canadensis-inexpansa-neglecta	V-3			

. . . cont'd

Table 6 concluded.

Major species of ground stratum		Associated upper strata species: Low shrub stratum		Tall shrub stratum		Tree stratum	
Group K continued							
PREVALENT (cont'd)							
Carex atherodes	V-2	Alnus rugosa	III-4	Alnus rugosa	III-5	Picea mariana	III-5
Equisetum fluviatile	V-2	Rosa acicularis	III-1			Betula papyrifera	III-2
*Caltha palustris	V-1	Myrica gale	II-2			Larix laricina	I-5
Carex disperma	IV-2	Cornus stolonifera	II-1				
Ledum groenlandicum	IV-2	Picea mariana	I-5				
Oxycoccus quadripetalus	IV-2						
*Smilacina trifolia	IV-2						
Fragaria virginianum	IV-1						
*Lycopus uniflora	IV-1						
Potentilla palustris	IV-1						
Rosa acicularis	IV-1						
Rubus idaeus var. strigosus	IV-1						
LOCALLY ABUNDANT							
Cornus canadensis	III-2						
Rubus chamaemorus	II-3						
Vaccinium vitis-idaea	I-5						
Equisetum arvense	I-4						

Table 7. Average environmental attributes* for the terminal groups of the final association analysis.

Group No.	A	B	C	D	E	F	G	H	J	K
Physiographic position	3	6	4	5	3	2	1	1	1	3
Peat depth	4	1	2	1	4	1	-	-	-	4
Peat type (degree of decomp.)	1	4	2	2	2	3	-	-	-	3
Botanical origin (peat)	4	1	2	2	2	2	-	-	-	5
Texture of underlying mineral soil	3	3	3	3	3	3	3	2-3	3	2-3
Specific conductance of soil (mmhos/cm)	0.5	2.2	1.6	1.1	2.4	1.5	1.1	1.2	1.7	1.8
Moisture holding capacity (%)	1040	226	409	457	401	314	169	135	225	362
Available N+P+K (ppm)	907	266	536	647	776	359	248	196	216	109
Water regime	4.8	1.3	3.6	3.5	3.9	5.9	6.5	7.0	6.1	4.8
pH of water	4.9	8.0	6.6	7.1	6.2	7.0	6.8	6.2	6.0	6.4
Specific conductance of water (mmhos/cm)	0.2	0.35	0.7	0.5	0.45	2.1	2.0	1.6	1.8	1.1

*Physiographic position
1 High levee
2 Low levee
3 Closed basin
4 Open basin
5 Floating mat
6 Aquatic

Peat depth
1 Very shallow (0.3 m)
2 Shallow (0.3-1 m)
3 Medium (1-2 m)
4 Deep (> 2 m)

Peat type (degree of decomposition)
1 Fibric peat (< 11% ash)
2 Mesic peat (11-25% ash)
3 Humic peat (26-70% ash)
4 Mineral peat (71-85% ash)

Botanical origin of peat (upper 30 cm)
1 Sedimentary
2 Fen
3 Hypnic mosses
4 Sphagnum moss
5 Forest litter

Mineral soil texture
1 Light (prevailing texture: very fine sandy loam)
2 Medium (prevailing texture: very fine sandy clay loam)
3 (Heavy (prevailing texture: silty clay)

Water regime
1 Water depth > 1 m in August
2 Water depth 30 cm-1 m in August
3 Water depth 0-30 cm in August
4 Water depth at or above surface in mid-June but slightly below surface in August
5 Water table 0-30 cm below surface in August
6 Water table 30 cm-1 m below surface in August
7 Water table > 1 m below surface in August

divisions was involved (Fig. 4, p. 65). The sequence of the initial four divisions is of considerable interest as it illustrates major discontinuities in species composition which are correlated with certain positions in the landscape or complexes of environmental factors.

The first division, resulting in the greatest single reduction in variance, on presence and absence of *Rosa acicularis*, divides parent group 1, consisting of all 98 stands, into two sub-groups:

(1) group 2, consisting of five significant terminal groups, four being forest and tall shrub communities on alluvial levees and one being wooded fen, and

(2) group 3, also consisting of five significant terminal groups, four of which are derived from vegetation on peat and the remaining one consists of communities of submerged and floating aquatics.

The second division, on *Carex rostrata*, separates group 3 into two sub-groups:

(1) group 4, consisting of three significant terminal groups (C, D, E), all being associated with fen peat, and

(2) group 5, including *Sphagnum* bog and aquatic stands.

The third division, on *Potentilla palustris*, separates the wooded fen of Group K from the alluvial levees of Groups F, G, H, and J, whereas the fourth division, on *Potamogeton richardsonii*, separates *Sphagnum* bog (Group A) from aquatic stands (Group B).

At this point, the association analysis has divided the total vegetational variation into five categories with distinct site affinities which have been termed Landscape Units:

I Bog (Group A)

II Aquatic (Group B)

III Fen (Groups C, D, and E)

IV Wooded fen (Group K)

V Alluvial levee (Groups F, G, H, and J)

Two additional significant divisions occur within the broad fen category:

(1) On Betula glandulifera, splitting off stands situated on fen peat of closed basins with impeded drainage (Group E), and

(2) On Sparganium eurycarpum, separating stands mainly located on floating sedge mats (Group D) from those on shallow, anchored peat substrate (Group C).

Further divisions among the category of stands of alluvial levees are more difficult to associate with distinct environmental differences. This may be related to the pronounced uniformity of the physical habitats in this facet of the landscape. Group H, contains mainly forest stands which appear to be overmature and opened up by death of old trees. Plantago major, the species on whose presence the group is removed, is, in fact, an introduced plant that is commonly associated with disturbed localities.

Finally, the absence of Viburnum edule distinguishes Group F, which contains mainly stands associated with topographically low levees that are subject to spring flooding.

Thus most of the significant terminal groups show affinities for distinct positions in the Delta's landscape. Examination of Fig. 4 (p. 65) and the environmental data in Table 7 (p. 77) suggests that the major environmental gradients controlling species composition are moisture regime and nutrient status. Disturbance, however, appears to play a subsidiary role within the more complex vegetation of the alluvial stream levees (see Section 5.3.4.2).

5.3.4 Interrelationships of the terminal groups

In order to extract further information on vegetation and site relationships, the terminal groups were compared with each other in all combinations according to floristic composition and, subsequently, according to environmental features.

5.3.4.1 Floristic comparisons

According to the major species of the ground stratum and the associated woody plants (see Section 5.3.2 and Table 6, p. 68), the groups show considerable floristic intergradation, particularly those within the fens of Landscape Unit III (Groups C, D, E) and the alluvial levees of Landscape Unit V (Groups, F, G, H, J). Floristic composition is much more dissimilar when groups belonging to different landscape units are compared. Group B, consisting of eight aquatic stands, is floristically the most isolated group as it shares no major species with any other group and only very few minor species with the floating fen stands of Group D.

Group A is floristically fairly isolated from all other groups, particularly in the ground stratum whose major species are mainly ericads and narrowleaved sedges. It shares a few species of the ground stratum with the deep peat stands of Groups E and K. The woody strata of Groups A and K are, however, more similar than the ground strata.

Within the fen category, Groups C and D are nearly identical as far as the importance of prevalent species is concerned. Particularly the sedges, *Carex atherodes*, *Carex rostrata*, and *Carex aquatilis*, and the low forb *Naumburgia thyrsiflora* predominate in both groups. However, some plants with apparently restricted amplitudes in respect to the major environmental gradients, produce significant differences among the less abundant species and thus separate the floating mat communities of Group D from the firmer, shallow peats of Group C. The presence of the emergent aquatics, *Sparganium eurycarpum* and *Typha latifolia* distinguishes floating sedge mats, whereas *Equisetum pratense* appears to persist on non-floating, shallow peat but not on floating mats.

Predominant species in the ground cover of the deep peat fens of Group E are the narrowleaved sedge, *Carex lanuginosa*, and the shrubs, *Salix pedicellaris* and *Betula glandulifera*.

The species composition of the four groups (F, G, H, J) associated with alluvial stream levees (Landscape Unit V), with few exceptions, is isolated from the other terminal groups. Within the Landscape Unit, however, species composition is fairly constant. This is not surprising since habitats differ relatively little. Considerable differences exist, however, from group to group in the relative abundance of the major species - presumed to be related to the greater complexity of the forest and tall shrub vegetation, and to variable disturbance by fire, selective logging, and flooding.

5.3.4.2 Environmental comparisons

It has been determined so far that the 10 terminal groups reflect six distinct physiographic positions in the Delta study area. In addition to good agreement between stands in each group and each of these physiographic positions (see Table 7, p. 77 and the example of Appendix B), there is reasonably good agreement with some other attributes of the environment, particularly those which can be regarded as dependent on physiographic position. For instance, deep peat (Class 4) is characteristic of Groups A, E, and K which are associated with closed basins (back swamps). Very shallow to shallow peat (Classes 1 and 2) is characteristic of Groups B, C, and D which are associated with circulating waters of open-drainage basins (rheophilous mires _sensu_ Bellamy 1966). Very shallow peat is also characteristic of Group F which consists of wooded stands of topographically low, and thus periodically flooded, levees. The upper 30 cm of the peat layer almost invariably is similar in composition to the present ground vegetation, indicating that present environmental conditions have existed for a number of years. In the case of minerotrophic fen sites this seems to imply that either the rate of loss by decomposition of old peat is equal to the deposition of new peat, and thus that the relation of the ground water surface to the growing plants has remained unaltered, or that water-tables have gradually risen and maintained an unchanged water-table depth relative to the surface cover (Kulczynski 1949). Since it is known that water levels in the study block have been artificially raised since the late 1930's (see Section 1), the second alternative is more likely.

As mentioned in Section 5.3.3, the observed correlations between broad vegetation types and physiographic position suggest that the variation in the vegetation is mainly controlled by the gradients of water regime and nutrient status. Several diagrams were constructed in which indicators of water regime (e.g., water holding capacity, depth of water-table) for each group were plotted against environmental features, indicative of nutrient status (e.g., conductivity of water, sum of available N + P + K). These diagrams generally resulted in clustering of groups with similar vegetation.

Fig. 5 consists of group-averages for specific conductance of the soil water plotted against mean water regime values for the 10 terminal groups. Soil water conductivity was considered to be more characteristic of the nutrient status of the mainly wet sites in this study than the more conventional soil extract conductivity (cf. Bellamy 1966), particularly since rooting depths in the various sites involved was not known. The nature of the soil water has been shown in numerous studies to be of significance in the development of lowland vegetation (see Literature Review, p. 4).

It is apparent from Fig. 5 that groups of similar floristic character (e.g., the fen vegetation of Groups C, D, and E) are situated in close proximity to each other in respect to the two axes, but are distant from other groups. Individual stand values, however, range fairly widely about the group-averages (Figs. 6 and 7), indicating that additional environmental gradients are important in controlling vegetational variation.

High values on both environmental gradients are characteristic of the groups associated with alluvial stream levees (Landscape Unit V), whereas the lowest position on the nutrient gradient is occupied by the aquatic stands of Group B (Landscape Unit II) and the ombrotrophic bog stands of Group A (Landscape Unit I). Intermediate positions are

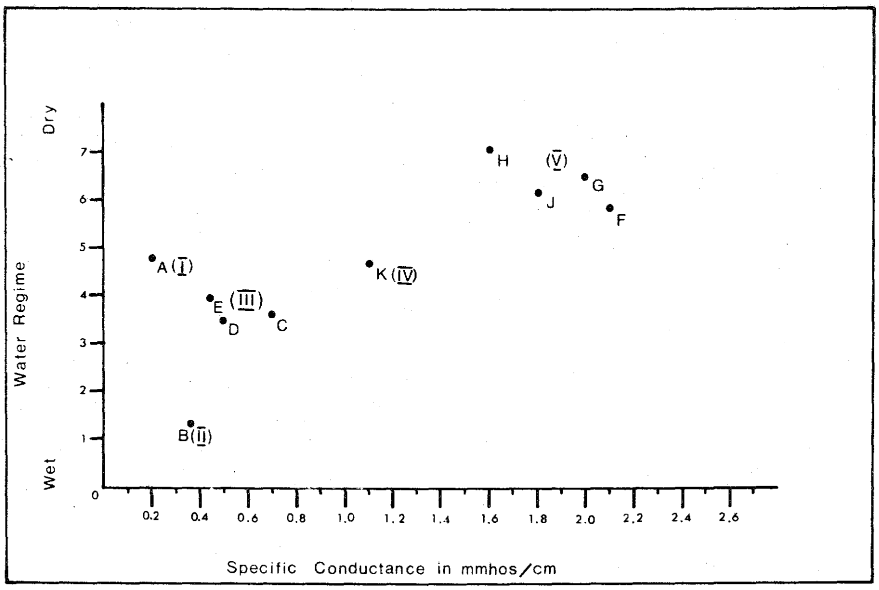


Fig. 5. Distribution of the 10 terminal groups (A-K) from the final association analysis, plotted according to group-averages for water regime and soil water conductivity. Roman numerals refer to Landscape Units to which the groups may be referred.

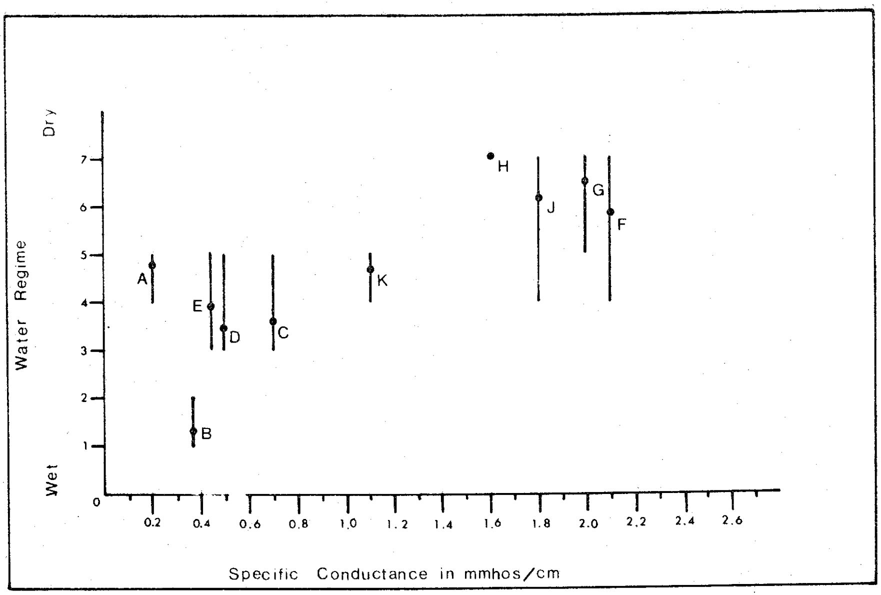


Fig. 6. Range of water regime values for stands in each of the 10 terminal groups of the final association

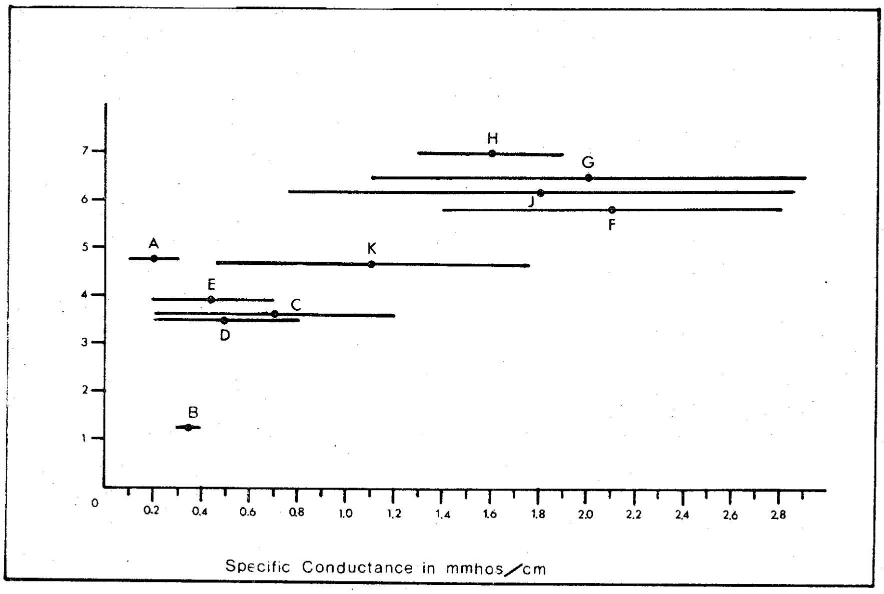


Fig. 7. Mean ±1 standard deviation of soil water conductivity values for stands in each of the 10 terminal groups of the final association analysis.

occupied by the fen vegetation of Landscape Unit III and the wooded fens of Group K (Landscape Unit IV).

In a general way, therefore, Fig. 5 re-establishes the positioning of the 10 end-groups in the hierarchy of the association analysis (see Fig. 4, p. 65). It is considered that the technique of association analysis has fulfilled the function for which it was used in this study, viz., to divide the total vegetational variation into classificatory units that occupy recognizable positions in the landscape, and to suggest major environmental gradients important in controlling species composition. More intensive examination of environmental relationships of stands and species groups can now be undertaken for the main landscape units (Section 6).

5.3.5 Physiognomic and structural characteristics of the terminal groups

In the previous sections it has been shown that the terminal groups of the final association analysis have affinities for distinct positions in the Delta's landscape. Stands within each group have been found to be reasonably similar in terms of floristic composition, and the prevalent species (according to percent presence in stands and average abundance) have been determined (Table 6, p. 68). Some species, owing to relatively wide ecological amplitudes in respect to the environmental gradients present, are abundant in more than one group, whereas others, more exacting in their environmental requirements, are mainly or completely restricted to individual groups (= differential species <u>sensu</u> Braun-Blanquet 1951). There are, however, physiognomic and structural characteristics that produce a visual heterogeneity of the vegetation within the groups; this aspect has not yet been brought out in the discussion.

The present section, therefore, briefly describes and illustrates* community structures that are typical for the terminal groups in each of the five recognized landscape units.

5.3.5.1 Landscape Unit I: Group A

Two types of communities can be discerned in this group:

(1) black spruce bog (Plate 10) and

(2) open ericaceous bog (Plate 11).

(1) Black spruce communities occur mainly in the form of islands on deep _Sphagnum_ peat of closed basins with impeded drainage. The overstory commonly consists of _Picea mariana_ of variable height - but rarely exceeding 5 m - with diameters at breast height (dbh) ranging from 3 to 7 cm. Very closely spaced annular rings indicate that growth in this environment is extremely slow. Slightly larger _Larix laricina_ trees usually occur around the edges of the stands or in gaps in the black spruce canopy. _P. mariana_ seedlings, or seedling-sized plants produced by layering, are abundant in the understory which generally is dominated by various ericaceous shrubs (see Table 6, p. 68), in a dense stratum less than 85 cm tall. Some of the prevalent, or locally abundant, plants show definite relationships with the hummocky ground surface: _Oxycoccus quadripetalus_ occupies dry hummocks in association with _Rubus chamaemorus_, and the insectivorous species _Drosera rotundifolia_ and _Sarracenia purpurea_, whereas _Salix pedicellaris_, _Carex lanuginosa_, and other fen plants are confined to the hollows. The

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*The illustrations for this Section, Plates 10-26 may be found in Appendix C.

Sphagnum mosses which form the ground surface are similarly correlated with microtopography: Sphagnum fuscum and Sphagnum magellanicum occur on the surface of the hummocks, whereas Sphagnum recurvum is restricted to the hollows.

(2) Open ericaceous bog communities frequently surround the black spruce communities. An overstory of living trees is absent, although scattered dead Picea mariana or Larix laricina are often present. The upper vegetation stratum consists of a thicket of shrubs, about 1 m high, in which Chamaedaphne calyculata, Andromeda polifolia, or Betula glandulifera predominate. Other typical species are Equisetum fluviatile, Carex lanuginosa, and Potentilla palustris. The ground surface is nearly level and consists of a mixture of fen litter and Sphagnum recurvum, thus resembling the hollows of the black spruce bog community-type. It appears likely that the open ericaceous bog type is derived from the black spruce type by retrogressive development, probably caused by artificially raised ground water levels (see Section 7.4).

5.3.5.2 Landscape Unit II: Group B

The limited amount of quadrat sampling that was done in the lakes of the Delta showed that dense beds of submerged aquatic vegetation, variously dominated by Potamogeton spp., Ceratophyllum demersum, or Anacharis canadensis are confined to sheltered bays with water depths generally less than 1 m. In deeper water, and particularly in exposed locations, submergents are far less abundant and typically consist of scattered individuals of Potamogeton richardsonii and P. zosteriformis. Nuphar variegatum is similarly restricted to shallow wind-protected water bodies, where the floating leaves of the species may nearly cover the water surface (Plate 12). Two emergent species of Scirpus are locally common: Scirpus validus is distributed in water less than 60 cm deep, whereas Scirpus acutus, the more abundant species, occurs in the form of circular clones in water with a mean depth of 109 cm, but ranging to 150 cm (Dabbs 1970, in press).

5.3.5.3 Landscape Unit III: Group C

Physiognomically, two community-types may be distinguished among the 20 stands of Group C:

(1) willow shrub type, and

(2) shrubless fen meadow.

(1) The willow shrub communities have an open overstory of Salix discolor or Salix petiolaris, approximately 2.5-3 m high (Plate 13). Occasionally Alnus rugosa occurs as an associate. The understory consists of a dense herbaceous layer, 1-1.3 m in height and identical in composition and structure with the shrubless fen meadow vegetation described below. In reference to the reconnaissance vegetation classification (Section 4.3.1), these shrub-dominated stands fall into the mapping category Medium Willow Shrub.

(2) Most of the shrubless fen meadow stands in Group C are dominated by the broadleaved sedges, Carex atherodes, Carex aquatilis, and Carex rostrata, growing luxuriously to a height of about 130 cm (Plate 14). Beneath the canopy of the tall sedges, small herbs such as Naumburgia thrysiflora, Galium labradoricum-trifidum, and Potentilla palustris are sparsely distributed. Equisetum fluviatile and Equisetum pratense were found to be abundant constituents in a number of stands; Phragmites communis var. berlandieri was dominant in two stands.

5.3.5.4 Landscape Unit III: Group D

Although the major species list (Table 6, p. 68), for Group D closely resembles that for Group C, physiognomic differences are pronounced. Only two of the 15 stands in the group for instance are of the *Carex atherodes* - dominated fen meadow type. The remaining stands fall into three physiognomic categories:

(1) Reed communities, dominated by *Phragmites communis* var. *berlandieri*, growing to a height of 3 m. This vegetation type mainly occurs at the outer edge of floating mats or in the form of floating or partially anchored islands in shallow bays (Plate 15). Beneath the dense *Phragmites* canopy, the hummocky surface of the floating mat, which mainly consists of the dead *Phragmites* culms and rhizomes, is only sparsely covered with sedges and small herbs, of which *Carex atherodes*, *Carex lanuginosa*, *Naumburgia thyrsiflora*, *Potentilla palustris*, and *Galium labradoricum-trifidum* are typical.

(2) Fen meadows, dominated by *Equisetum fluviatile*, with a mean height of 120 cm (Plate 16). The tall sedges, *Carex atherodes* and *Carex aquatilis*, and *Sparganium eurycarpum* are common associates. The springy ground surface, consisting of old stalks of *Equisetum fluviatile*, is generally nearly bare except for the scattered occurrence of low herbs such as *Galium labradoricum-trifidum*, *Naumburgia thyrsiflora*, *Sium suave*, *Potentilla palustris*, and *Scutellaria galericulata* var. *epilobiifolia*.

(3) The remaining common community-type on floating mats is visually dominated by the silvery foliage of *Salix candida*, growing to an average height of 1 m (Plate 17). Below and between the clumps of willow, the vegetation strongly resembles that of the open fen meadow communities

of Group C with *Carex atherodes* as the dominant species of the upper herbaceous layer, and *Carex rostrata* and *Carex aquatilis* as abundant associates. But the following differences are apparent: (a) growth of the sedges appears less vigorous, ground cover is reduced, and the average height is only about 80 cm; and (b) *Carex lanuginosa* and the emergent aquatics *Sparganium eurycarpum* and *Typha latifolia* are abundant.

5.3.5.5 Landscape Unit III: Group E

The physiognomy of the 11 stands in Group E is uniformly determined by a shrub layer, 1.0 to 1.5 m high, in which *Betula glandulifera* and *Salix candida* predominate. *Salix pedicellaris* and *Myrica gale* are often associated (Plate 18). Beneath the dense shrub cover, sedges form a field layer with an average height of 40 to 60 cm. The predominant species is *Carex lanuginosa*; *Carex aquatilis*, *Carex atherodes*, *Carex rostrata*, and *Calamagrostis canadensis-inexpansa-neglecta* are also prevalent.

5.3.5.6 Landscape Unit IV: Group K

The five stands on deep mesic or humic fen peat in this group consist of open wooded communities, with overstories dominated by *Picea mariana* (Plate 19) or *Larix laricina* (Plate 20). The trees are of larger stature than those of the *Sphagnum* bogs of Group A: *Picea mariana* has a mean dbh of 13 cm and an average height of 14 m; corresponding measurements for *Larix laricina* are 14 cm and 15 m. Associated woody vegetation is very sparse, consisting of scattered saplings and seedlings of *Alnus rugosa* and *Picea mariana*.

The ground vegetation generally consists of a closed stratum, ca. 50 cm high, dominated by *Calamagrostis canadensis-inexpansa-neglecta*, *Carex atherodes*, and *Equisetum fluviatile*. Associated common small shrubs are *Ledum groenlandicum*, *Rubus idaeus* var. *strigosus*, and *Rosa acicularis*. Near the ground, there is a variable and species-rich layer of low herbs, in which the following species are prevalent: *Caltha palustris*, *Carex disperma*, *Oxycoccus quadripetalus*, *Smilacina trifolia*, and *Lycopus uniflora*.

5.3.5.7 Landscape Unit V: Group F

The eight stands comprising Group F have been shown to be associated with topographically low positions on alluvial stream levees and thus with water-tables that are frequently above the ground surface in the spring, and slightly below the surface during the remainder of the year.

The group consists mainly of tall shrub communities, dominated by *Salix discolor* and *Alnus rugosa* with an average height of 5-6 m (Plate 21). Several of the stands possess a scattered upper canopy of *Populus balsamifera* trees of low vigour (Plate 22). It is presumed that these trees are dying as a result of artificially raised water levels, and that those stands will, in time, become more and more similar to the other tall shrub communities of Group F. Below the tall shrub canopy exists a low shrub layer, averaging 1.5 m in height, that is characterized by *Cornus stolonifera*, *Viburnum trilobum*, *Ribes* spp., *Rubus idaeus* var. *strigosus*, and *Rosa acicularis*. The ground surface is covered by a species-rich herbaceous layer (see Table 6, p. 68) which is dominated by *Equisetum pratense*, *Calamagrostis* spp., *Rubus pubescens*, and *Galium triflorum*. The fern, *Matteuccia struthiopteris*, growing to a height of 80 cm, visually dominates the ground stratum in a number of stands.

5.3.5.8 Landscape Unit V: Groups G and J

Both these groups are associated with mesic sites on alluvial stream levees, and are fairly similar in species composition and in the range of physiognomic types present. In order to avoid unnecessary repetition, the two groups will be discussed together.

Physiognomically most of the 17 stand samples falling into Groups G and J are mixedwoods with *Populus balsamifera* and *Picea glauca* as the major species, but ranging from pure *Populus balsamifera* to nearly pure *Picea glauca* stands (Plates 23 and 24). These forest communities are well-developed and structurally complex with stocking rates averaging 47 m^2/ha, and ranging from 22 to 92 m^2/ha. The dominant trees are large: *Populus balsamifera* has an average diameter at breast height of 29 cm and a mean height of 20 m. The largest individuals with a dbh $>$ 50 cm are frequently senescent as indicated by the presence of broken tops.

The average dbh of mature *Picea glauca* is 38 cm and the average height is approximately 25 m, but a few individuals have reached a dbh of about 70 cm and a height of 33 m. In most stands, the presence of old stumps indicates that the density of white spruce has been reduced by selective cutting. *Abies balsamea* is a major constituent of the tree stratum of only one stand (S-48) situated on a raised stream levee in the interior of the Delta. The only other occurrence of balsam fir is in the form of small seedlings in Stand 30 near the Birch River.

Regeneration of _Populus balsamifera_, ranging from seedlings to small trees, is common, as are immature individuals of other deciduous tree species. However, there is little evidence of _Picea glauca_ regeneration, except on decomposing logs or stumps.

Tall shrubs, ranging from 2.5 to 4.5 m, form a discontinuous intermediate stratum, particularly in gaps in the tree canopy. Predominant species are _Alnus rugosa_, _Salix discolor_, _Salix bebbiana_ and, locally, _Cornus stolonifera_ and _Amelanchier alnifolia_.

The next structural layer consists of a dense, continuous stratum of low shrubs, 1.5 to 2 m high. _Rosa acicularis_, _Viburnum trilobum_, and _Viburnum edule_ predominate; various _Ribes_ spp. and _Rubus idaeus_ var. _strigosus_ are common associates.

The herbaceous field layer, covering the ground surface, is approximately 50 cm tall, and is characterized by _Equisetum pratense_ (Group G) or _Equisetum arvense_ (Group J), _Calamagrostis canadensis-inexpansa-neglecta_, _Aralia nudicaulis_, and _Rubus pubescens_.

In addition to the mature mixedwood stands, Groups G and J also contain eight stands that are apparently fire-successional. Three of these are dominated by even-aged _Populus tremuloides_ with a dbh of 13 cm and a height of 13 m (Plate 25). The stocking rate for the three stands averages 38 m^2/ha. Scattered clumps of _Amelanchier alnifolia_ and _Salix_ bebbiana occur beneath the uniform aspen canopy. The low shrub and ground strata, structurally and compositionally, resemble those of the already described mixedwood stands.

The remaining five stands are tall shrub communities whose overstodies resemble those in Group F: _Salix discolor_, _Salix bebbiana_, and _Alnus rugosa_ are the canopy-forming species with a height of 4 to 6.5 m.

Differences are apparent, however, in the lower strata where species of wetter environments, such as Carex atherodes and Caltha palustris, are generally absent.

There is little evidence of tree regeneration or succession in these stands. Scattered seedlings of Populus tremuloides, Populus balsamifera, and Fraxinus pennsylvanica var. subinterregima are present in most of the aspen and willow stands, but coniferous seedlings were not encountered.

5.3.5.9 Landscape Unit V: Group H

The remaining five stands in this description, Group H are associated with the driest stream levee sites (see Fig. 5, p. 84). Physiognomically, they consist of overmature forest stands that have apparently not been disturbed by logging, fire, or flooding, and are now opening up through natural death of older trees (Plate 26). The overstory is variously dominated by large individuals of Picea glauca with an average dbh of 42 cm and a height of 20 m, Ulmus americana (40 cm dbh, 20 m tall), or Betula papyrifera (20 cm dbh, 15 m tall). Openings formed by the death of older trees have been generally occupied by Alnus rugosa and Salix bebbiana shrubs, or by the deciduous tree species Acer negundo or Fraxinus pennsylvanica var. interregima that have reached a dbh of ca. 15 cm and a height of approximately 7 m. A very dense, and locally almost impenetrable, low shrub stratum - in which Cornus stolonifera, Rosa acicularis, Rubus idaeus var. strigosus, and Viburnum spp. are abundant - averages about 1.5 m in height. The herbaceous field layer is typically dominated by Equisetum pratense and Aralia nudicaulis. Some other prevalent forbs are Circaea alpina, Galium triflorum, Matteuccia struthiopteris, Plantago major, and Mitella nuda.

6. ANALYSIS OF VEGETATIONAL AND ENVIRONMENTAL GRADIENTS

Intensive analysis of vegetation/environment relationships was restricted to the bogs of Landscape Unit I, the fens of Landscape Unit III, and the wooded alluvial levees of Landscape Unit V. It was considered that the aquatic vegetation of Landscape Unit II was insufficiently sampled to permit meaningful gradient analysis to be carried out. Landscape Unit IV (wooded fens) was omitted because of the small number of stands (5) in the group, which also was thought to possibly lead to inconclusive results.

6.1 Basic considerations and choice of techniques

Association analysis has been used in this study for the purpose of classifying the total vegetational variation, contained in the 98 stands, into less heterogeneous groups that are associated with certain positions in the landscape. The divisive technique employed is, however, not as satisfactory at lower levels of vegetational variation, i.e., when working with relatively homogeneous species complements, and, provides little information from which hypotheses regarding causal factors of this variation may be derived.

As pointed out in Section 5.3.1, ordination techniques are useful tools for detecting underlying causal environmental gradients when the total range of those gradients is limited. Of the various ordination techniques available, a form of factor analysis referred to as principal component analysis (PCA) has been used as an efficient tool to (1) simplify complex, multivariate vegetational data into a small number of principal lines of variation, and (2) produce hypotheses of vegetation/environment relationships on the principal lines (Jeglum *et al*. 1969).

Goff and Cottam (1967) and Whittaker (1967) have reviewed the problems of gradient analysis and found factor analysis to be particularly useful where the ranges of environmental gradients are restricted. Austin (1968) has made similar comments. Good examples of the use of the technique are given in recent publications by Orloci (1966, 1967b), Ivimey-Cook and Proctor (1967), Yarranton (1967a, 1967b, 1967c), and Austin (1968).

An attractive feature of principal component analysis is that it permits the use of environmental measurements, in addition to species scores, as attributes of a stand, as demonstrated by Ferrari _et al_. (1957), Dagnelie (1960), and Walker (1968). Interpretation of vegetation/environment relationships is then possible through consideration of the attribute loadings on each extrated factor.

It was, therefore, decided to apply suitable principal component analysis techniques to the main landscape units in order to elucidate underlying gradients that control vegetation pattern in the Cumberland Marshes, and to determine the relative importance of these gradients.

In respect to the choice of the specific analytical technique to be employed, several decisions about data form, statistical parameters, and mathematical expressions had to be made. The relative merits of the diverse possible approaches have been discussed by various authors on theoretical and empirical grounds (see above references) but no clear concensus has emerged. Examination of the literature led the author to believe that a single, universally satisfactory program of principal component analysis is not likely to become available in the near future. Thus it will remain necessary to evaluate techniques empirically, i.e., on the basis of their efficiency in generating working hypotheses about vegetation/environment relationships. As it is outside the scope of this study to contribute to theoretical discussions on this matter, it was decided to employ a program which had been previously used with success, and to apply it to the data on hand.

The particular PCA program selected - obtained through the courtesy of Dr. C. Milner of the I.B.P.-Matador Project, University of Saskatchewan - was written in FORTRAN IV by R. E. Beschel of Queen's University, Kingston, and is based on an earlier one developed by L. Orloci (1966). It was chosen because (1) it permits the use of various statistical parameters in matrix construction (e.g., variance-covariance values, correlation coefficients, dispersion coefficients) and (2) it can be used for both species ordination (R-analysis) and stand ordination (Q-analysis).

In this study, principal component analysis of a correlation matrix was employed because correlation coefficients have been shown by Yarranton (1967a) to be the most efficient parameters to use in the detection of major environmental gradients affecting vegetational variation. Austin (1968) has made similar comments.

6.2 Data treatment and analysis

The species scores used in the principal component analyses consisted of the frequency data obtained for the ground stratum vegetation (see Section 4.5). This set of data was used because the ground stratum forms a continuous mantle over the entire area (with the exception of open water), and thus is more suited for analysis by ordination techniques than the more disjunct woody overstory vegetation. It was further assumed that, because of the generally short life span of individual herbaceous plants, the ground vegetation more directly reflects current ecological conditions than the more long-lived tree and shrub vegetation. The composition of the field layer has been previously found useful in determining specific ecological conditions in forest site and peatland classifications (e.g., Cajander 1909, 1913, 1949; Ilvessalo 1929, Arnborg 1950, Kalela 1954, 1962; Linteau 1955, Rowe 1956b, Mueller-Dombois 1964).

The species scores were employed in the analysis as absolute frequency data in the form of Yarranton's A-matrix (Yarranton 1967a). A few species which occurred in only one or two stands with frequencies below 10 percent were arbitrarily deleted from the analysis in order to avoid unduly large effects that they might have had on the ordinations.

Since in the computation of correlation matrices all variables are standardized to zero mean and unit variance (Austin 1968), available environmental measurements (see Section 4.6.4) could be directly introduced into the R-analysis regardless of their order of magnitude.

For use in the stand ordinations (Q-analyses), environmental measurements were transformed to relative values and grouped into five classes according to decreasing magnitudes. Circles of decreasing diameters, corresponding to these five size-classes, were then superimposed on the stand positions as a visual means of establishing correlations with the spatial distribution of stands in the ordination. These visual displays, though cumbersome, are more useful than calculated simple correlations between component loadings and environmental attributes since they allow non-linear relationships to be considered (cf. Austin 1968).

Abundance data for the woody strata also were superimposed on the stand ordination.

Four PCA runs were performed on Landscape Units I, III, and V with the IBM 360 digital computer at the Saskatoon Campus of the University of Saskatchewan:

(1) Ordination of stands (Q-analysis);

(2) Ordination of species (R-analysis);

(3) Ordination of selected environmental attributes (R-analysis); and

(4) Ordination of species plus selected environmental attributes (R-analysis).

Rotation of factors, to position them at right angles to each other in order to eliminate interactions, was not done since the recognition of factor and gradient interactions is in itself valuable information in understanding vegetation/environment relationships (Walker 1968).

Preliminary examination of the three types of runs (2-4) of the R-analysis was carried out to determine their respective value in explaining vegetational variation. It was found that the spatial distribution pattern of the species derived from (2) and (4) were fairly similar, although shifts occurred in the position of some species. However, the inclusion of environmental attributes in (4) clearly facilitated recognition of underlying environmental gradients and brought out affinities of certain species with particular environmental attributes. The environmental ordination of (3), on the other hand, contributed little correlation with the vegetational ordination.

It was, therefore, decided to restrict detailed examination to the Q-analysis of (1) and the R-analysis of (4). It involved plotting all pair-combinations of the loadings on the first three factors of each analysis and, in the case of the Q-analyses, superimposing selected environmental measurements on the stand positions in the ordinations.

6.3 Landscape Unit I

6.3.1 Stand ordination

This ordination is the Q-expression of a correlation matrix of 9 individuals (stands) and 35 attributes (species).

The loadings on the first four components (F_1-F_4), which together account for 86 percent of the total variance, are presented in Table 8. To facilitate study of the importance of available environmental measurements on each component*, the following data were transformed to relative values by ranking them in order of decreasing magnitude:

(1) Soil data - available N, available P, Ca^{++}, K^+, electrical conductivity, pH, organic matter content, and water holding capacity;

(2) Soil water data - Ca^{++}, Mg^{++}, K^+, Na^+, NO_3^-, $PO_4^{\equiv}$, $SO_4^{=}$, Cl^-, electrical conductivity, and pH.

Examination of the spatial distribution of stands on Factors 1 and 2 (Fig. 8) of the ordination revealed the black spruce-dominated stands (Stands 42, 43, 44, 81 and 99) to be clustered together, and separated from the open ericaceous communities of Stands 66 and 67 and the larch-dominated stands (69 and 70). The positioning of the stands

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*The terms "component" and "factor" are used in the same sense throughout this discussion.

Table 8. Adjusted factor loadings on the first four factors of the principal component analysis (Q-expression of correlation matrix) of the ground stratum vegetation of Landscape Unit I.

Stand	Factor 1	Factor 2	Factor 3	Factor 4
42	0.56	-0.22	-0.21	0.03
43	0.62	-0.23	-0.30	0.13
44	0.57	-0.22	-0.20	0.06
66	-0.28	0.53	-0.13	-0.03
67	-0.47	0.89	-0.47	-0.21
69	-0.21	0.38	0.72	0.63
70	-1.27	-0.87	-0.17	0.07
71	0.06	-0.10	0.67	-0.73
99	0.42	-0.16	0.09	0.04
Percentage of total variance accounted for by each component	35.38	23.91	15.61	11.06

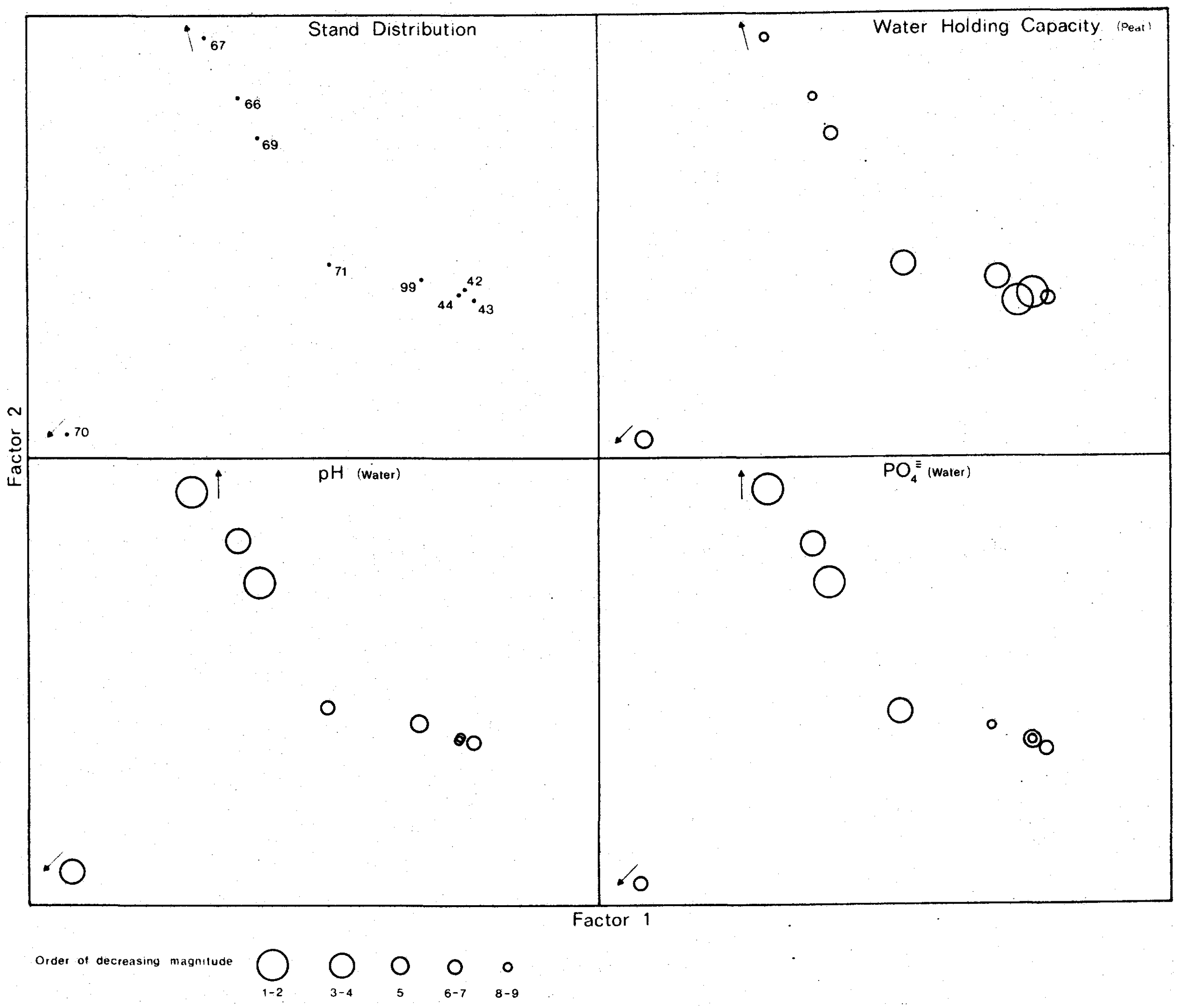

Fig. 8. Stand ordination and superimposed environmental measurements according to Factors 1 and 2 of the principal component analysis (Q-expression) of bogs (Landscape Unit I). Environmental measurements were previously grouped into five classes of decreasing magnitude.

(except Stand 70) along a line diagonal to the two axes indicates strong interaction between the factors. The high loadings of Stand 70 are thought to reflect the fact that its ground surface consists of a mosaic of large hummocks and hollows (fen windows) which greatly differ in species composition of the ground stratum. Thus the stand actually represents a mosaic of microstands (sensu Hanson and Churchill 1961) of bog and fen vegetation.

Of the available environmental measurements, only water holding capacity and organic matter content of the upper 30 cm of peat showed a distinct positive correlation with Factor 1 (Fig. 8). The water holding capacity values, ranging from 500 to 600 percent for the Sphagnum - fen peat mixtures of Stands 66 and 67 to > 1400 percent for the pure, undecomposed Sphagnum surfaces of Stands 42 and 44, reflect the relative capability of those peats to absorb and hold precipitation. Factor 1 is, therefore, at least in part, a gradient of development toward Sphagnum bog surfaces. Factor 2, which removes 24 percent of the total variance, is a combined pH and nutrient gradient, as shown by superimposed relative values for pH and $PO_4^{\equiv}$ of the soil water (Fig. 8). Conductivity, Ca^{++}, and NO_3^- also show imperfect correlations with Factor 2.

Jointly, F_1 and F_2 may be regarded to form a complex gradient (sensu Whittaker 1956) of "relative ombrotrophy", as reflected by accumulation of Sphagnum moss, increasing water holding capacity and organic matter content, and by decreasing pH values and nutrient content.

Factor 3 showed little interaction with the first two factors of the ordination. Judging from the available environmental data, it represents, at least in part, a salinity gradient as shown by the distribution of Na^{+} and Cl^{-} values of the soil water (Fig. 9). Less distinct, but similar, correlations were shown by electrical conductivity and summed ion values.

It was not possible to associate any environmental gradient with the fourth extracted component.

6.3.2 Ordination of species and environmental attributes

This ordination consists of the R-expression of a correlation matrix of 35 species and 12 environmental attributes in 9 stands. The loadings on the first three factors, accounting for approximately 70 percent of the total variance, are presented in Table 9.

The spatial distribution of attributes on Factors 1 and 2, which together remove 56 percent of the total variance, shows three distinct clusters of species (Fig. 10):

(1) The first cluster, possessing negative loadings on both components, consists of Campanula aparinoides, Carex atherodes, Cornus stolonifera, Lycopus uniflorus, Menyanthes trifoliata, Naumburgia thyrsiflora, Petasites sagittatus, Scolochloa festucacea, and Stellaria longifolia - mainly species that are common in the ground stratum of minerotrophic fen and shrub communities (Groups C, D, and F of the final association analysis). Associated with these species are the positions for pH, conductivity, Ca^{++}, and other ions of the soil water, indicating the preference of these species for nutrient-rich sites.

(2) The second cluster, with high positive loadings on F_2 and low negative loadings on F_1, contains Betula glandulifera, Campanula

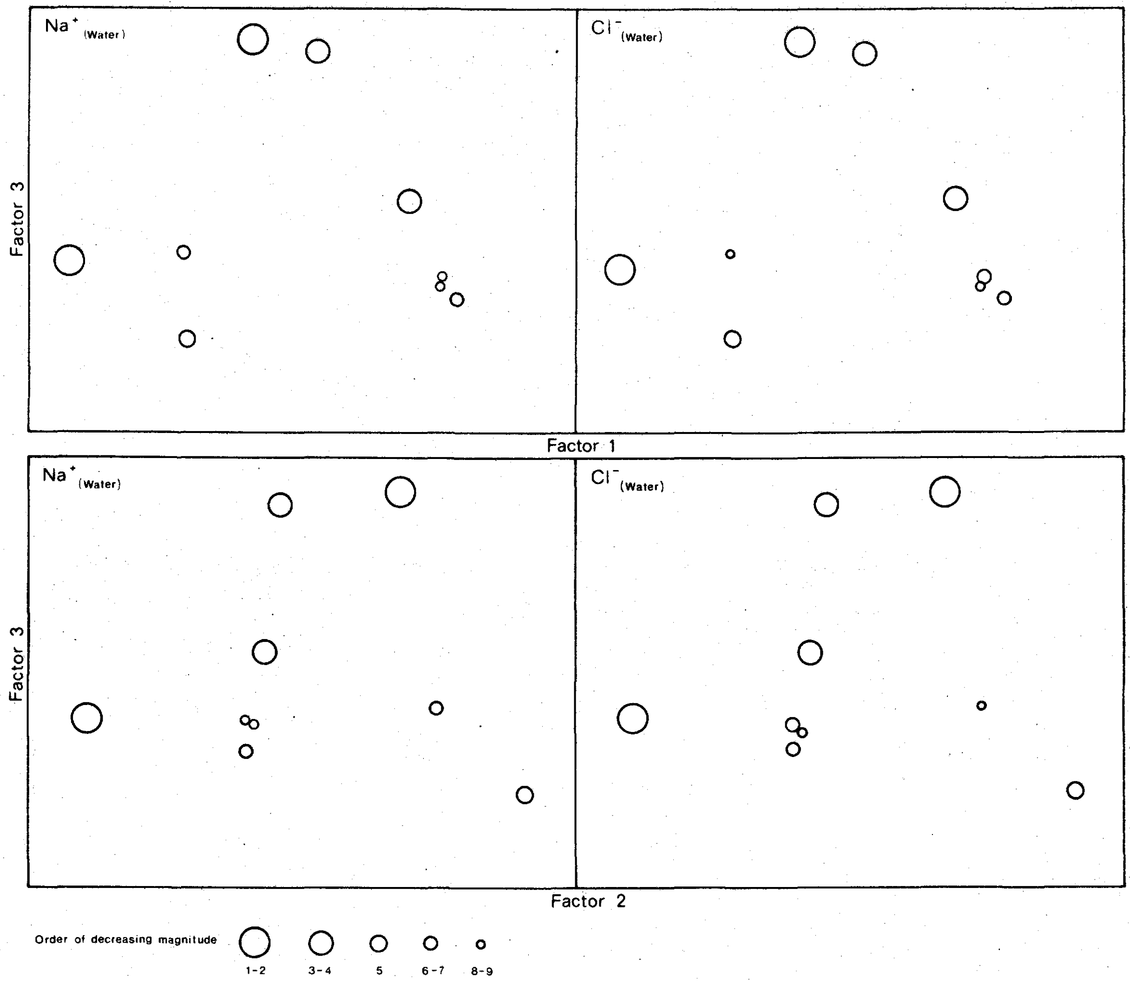

Fig. 9. Environmental measurements superimposed on the ordination of stands according to Factors 1-3 of the principal component analysis (Q-expression) of the ground stratum vegetation of bogs (Landscape Unit I). Environmental measurements were previously grouped into five classes of decreasing matnitude.

Table 9. Normalized attribute loadings on the first three factors of the principal component analysis (R-expression of correlation matrix) of the ground stratum vegetation of Landscape Unit I.

Attribute	F_1	F_2	F_3
Andromeda polifolia	0.07	0.05	-0.27
Betula glandulifera	-0.18	-0.06	0.10
Calamagrostis canadensis-inexpansa-neglecta	-0.06	0.05	-0.26
Calla palustris	-0.18	-0.16	0.08
Campanula aparinoides	-0.17	-0.16	0.14
Campanula rotundifolia	-0.03	0.21	0.14
Carex aquatilis	-0.17	0.17	0.05
Carex atherodes	-0.18	-0.16	0.05
Carex deweyana	-0.02	-0.01	-0.19
Carex lanuginosa	-0.07	0.24	0.09
Chamaedaphne calyculata	0.17	-0.02	0.10
Cornus stolonifera	-0.17	-0.16	0.14
Drosera rotundifolia	-0.02	-0.01	-0.19
Equisetum fluviatile	-0.16	0.17	0.04
Eriophorum chamissonis	0.10	0.03	0.09
Galium triflorum	-0.03	0.21	0.14
Kalmia polifolia	0.19	-0.14	-0.01
Larix laricina	-0.07	0.05	-0.24
Ledum groenlandicum	0.19	-0.15	-0.09
Lonicera villosa var. solonis	0.08	-0.07	-0.05
Lycopus uniflorus	-0.17	-0.16	0.14
Menyanthes trifoliata	-0.18	-0.06	0.10
Naumburgia thyrsiflora	-0.17	-0.16	0.14
Oxycoccus quatripetalus	0.19	-0.14	0.04
Petasites sagittatus	-0.17	-0.16	0.14
Picea mariana	0.17	-0.13	-0.04
Potentilla palustris	-0.11	0.19	0.20
Rubus chamaemorus	0.18	-0.16	0.08
Salix pedicellaris	-0.11	0.02	-0.21
Salix petiolaris	-0.04	0.26	0.16
Sarracenia purpurea	0.08	-0.01	0.08
Scolochloa festucacea	-0.17	-0.16	0.07
Smilacina trifolia	-0.04	-0.03	-0.31
Stellaria longifolia	-0.16	-0.15	0.02
Vaccinium vitis-idaea var. minus	-0.05	0.01	-0.33
Ca^{++}	-0.18	-0.04	-0.07
Mg^{++}	0.08	0.12	-0.05
Na^{+}	-0.20	-0.07	-0.15
K^{+}	-0.18	-0.10	0.00
NO_3^{-}	-0.14	-0.10	-0.04
$PO_4^{\equiv}$	-0.09	0.18	-0.16
$SO_4^{=}$	-0.11	-0.11	0.01
Cl^{-}	-0.20	-0.05	0.03
Conductivity	-0.20	-0.05	0.03
pH	-0.15	0.16	-0.07
Organic matter	0.12	-0.06	0.10
Water holding capacity	0.10	-0.24	-0.08
Percentage of total variance accounted for by each component	35.09	20.94	13.61

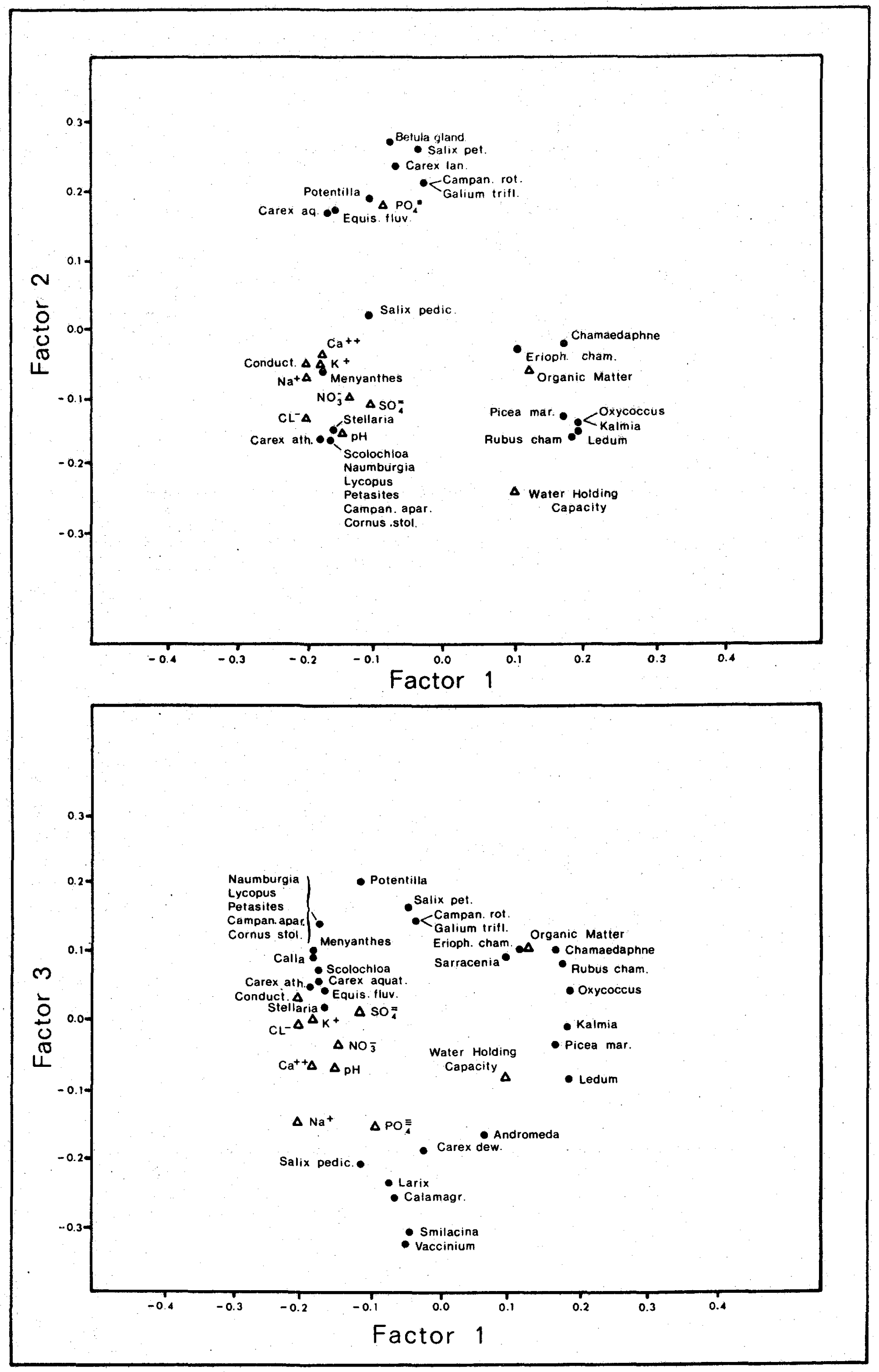

Fig. 10. Ordination of species and environmental attributes according to Factors 1-3 of the principal component analysis (R-expression) of the ground stratum vegetation of bogs (Landscape Unit I). Attributes with loadings $< \pm 0.1$ on both axes were omitted.

rotundifolia, Carex aquatilis, Carex lanuginosa, Equisetum fluviatile, Galium triflorum, Potentilla palustris, and Salix petiolaris - predominantly species that are most abundant on floating mats and in deep peat fens of closed basins (Groups D and E of the final association analysis; see Table 6, p. 62). The only environmental attribute closely associated with this cluster is $PO_4^{\equiv}$ of the soil water.

(3) The third cluster, possessing positive loadings on F_1 and negative loadings on F_2, is made up of Chamaedaphne calyculata, Eriophorum chamissonis, Kalmia polifolia, Ledum groenlandicum, Oxycoccus quadripetalus, Picea mariana, and Rubus chamaemorus. Positively associated environmental parameters are organic matter content and water holding capacity of the upper 30 cm of peat, whereas pH and ion concentrations are negatively associated with this cluster. Therefore, these species are ecologically most adapted to the nutrient-poor sites of Sphagnum bogs, and thus characterize the end-point of the developmental gradient leading toward ombrotrophic conditions.

When the attribute positions are plotted on Factors 1 and 3 (Fig. 10), the clusters are less distinct but the tendency persists for the same species and environmental attributes to hold together.

6.4 Landscape Unit III

6.4.1 Stand ordination

The 46 stands and 42 species of Landscape Unit III, consisting of the fen vegetation of Groups C, D, and E from the final association analysis, were subjected to Q-type principal component analysis of a correlation matrix. The factor loadings of the stands on the first four factors, accounting for approximately 41 percent of the total variance, are listed in Table 10. All combinations of these components were plotted and environmental attributes were superimposed on the stand positions. Subsequent examination did not reveal apparent relationships between stand positions on F_4 and the available environmental measurements. The following discussion is, therefore, restricted to the first three components.

The first component, F_1, removing 15 percent of the total variance, is thought to represent a pH gradient as shown by the superimposed values for HCO_3^- and pH (Fig. 11). The second component, F_2, accounting for 10 percent of the total variance, appears to be related, at least in part, to a gradient of salinity or nutrient availability, as shown by the values for electrical conductivity, Ca^{++}, NO_3^-, $PO_4^{\equiv}$ (Fig. 12) and, less distinctly, for Mg^{++}, Cl^-, and Na^+.

Other environmental attributes, e.g., K^+, organic matter content, and water holding capacity of the soil did not show apparent trends in respect to F_1 and F_2. The distribution of water regime classes (see Table 7, p. 77), likewise gave no clear-cut patterning on the ordination, probably because those measurements were too crude. Total peat depth showed a weak negative correlation with F_1.

The third component, F_3, which removes only 9 percent of the total variance, showed no discernable relationship with conductivity, pH, individual ions, nor with water regime (Fig. 13). It showed some correlation with peat depth since depths < 1 m tended to possess positive loadings, whereas depths > 1 m tended to have negative loadings on F_3. Physiographic position also showed imperfect correlation with F_3.

Table 10. Adjusted factor loadings on the first four factors of the principal component analysis (Q-expression of correlation matrix) of the ground stratum vegetation of Landscape Unit III.

Stand	Factor 1	Factor 2	Factor 3	Factor 4
4	0.38	0.25	-0.15	0.25
5	0.17	0.33	0.45	0.43
6	0.10	-0.42	0.84	0.23
7	0.32	-0.44	0.30	-0.22
8	0.22	0.31	0.06	-0.10
9	0.24	0.16	0.13	-0.20
13	0.26	0.18	0.06	0.20
19	-0.04	-0.08	0.15	0.11
20	0.25	0.04	-0.23	0.00
22	0.31	0.18	-0.26	0.10
24	0.30	0.19	-0.25	0.12
25	0.17	-0.00	0.20	0.06
26	0.20	-0.19	0.17	-0.05
27	-0.43	0.11	0.01	0.08
29	0.31	0.10	-0.02	0.20
32	0.06	0.21	0.18	-0.00
33	-0.46	0.00	0.44	-0.07
34	-0.61	-0.18	0.00	0.11
35	-0.72	-0.10	-0.42	0.13
36	-0.46	0.24	-0.40	-0.12
37	-0.49	-0.45	0.10	-0.04
38	-0.38	1.35	0.42	-1.05
39	-1.32	-0.09	-0.01	0.08
40	0.91	0.23	-0.06	-0.13
50	0.21	0.07	-0.09	-0.05
51	0.05	0.00	0.12	-0.03
52	0.11	0.04	0.17	0.17
53	0.26	0.12	-0.00	0.11
54	0.08	0.03	0.51	0.22
55	0.32	0.13	-0.10	0.12
56	0.22	0.11	0.19	0.17
57	0.31	0.13	-0.41	0.01
58	0.20	0.07	0.04	0.13
59	0.32	0.13	-0.35	0.03
60	0.05	-0.04	0.08	0.11
61	0.01	-0.73	0.17	-0.54
62	0.12	-0.32	0.16	-0.10
63	-0.14	-0.48	0.41	-0.04
64	0.37	-0.23	-0.54	-0.40
65	0.28	-0.03	-0.40	-0.09
88	-0.58	-0.13	-0.45	0.41
89	-0.40	0.00	-0.45	0.38
93	0.09	0.01	-0.01	0.22
96	0.15	-0.19	-0.28	-0.88
97	0.28	-0.02	-0.45	-0.14
98	0.22	0.03	-0.02	0.08
Percentage of total variance accounted for by each component	14.72	10.21	8.93	7.60

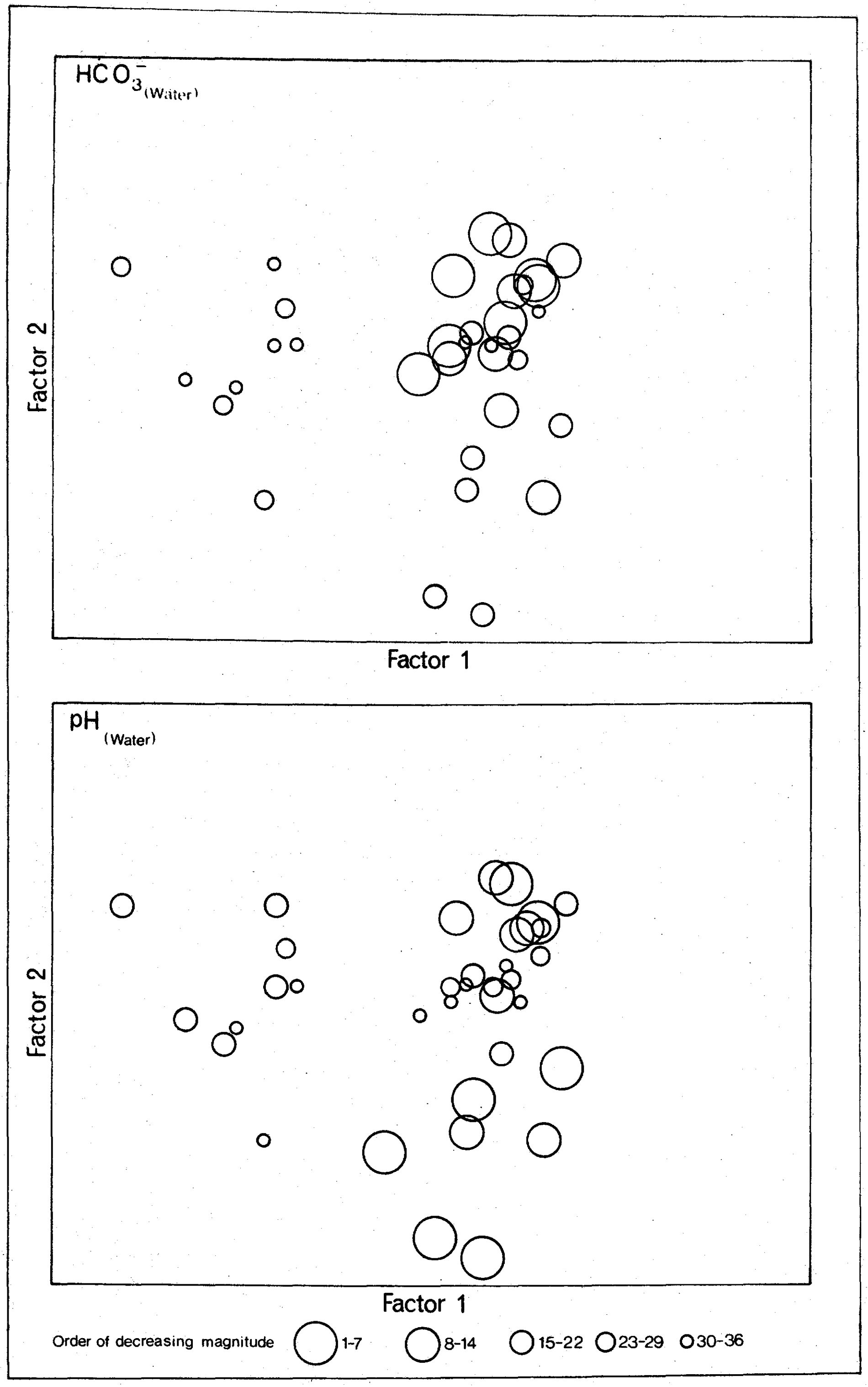

Fig. 11. Environmental measurements superimposed on the ordination of stands according to Factors 1 and 2 of the principal component analysis (Q-expression) of the ground stratum vegetation of fens (Landscape Unit III). Environmental measurements were previously grouped into five classes according to decreasing magnitude.

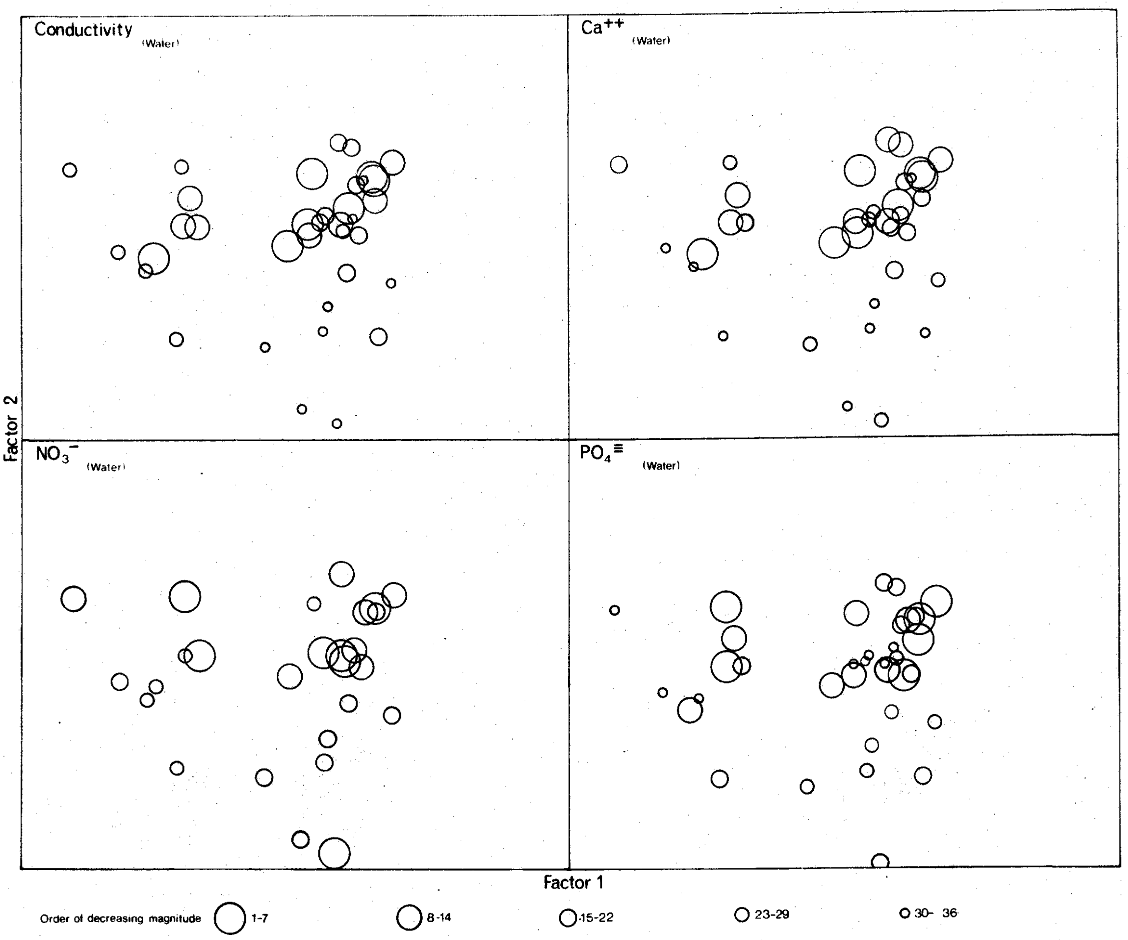

Fig. 12. Environmental measurements superimposed on the ordination of stands according to Factors 1 and 2 of the principal component analysis (Q-expression) of the ground stratum vegetation of fens (Landscape Unit III). Environmental measurements were previously grouped into five classes of decreasing magnitude.

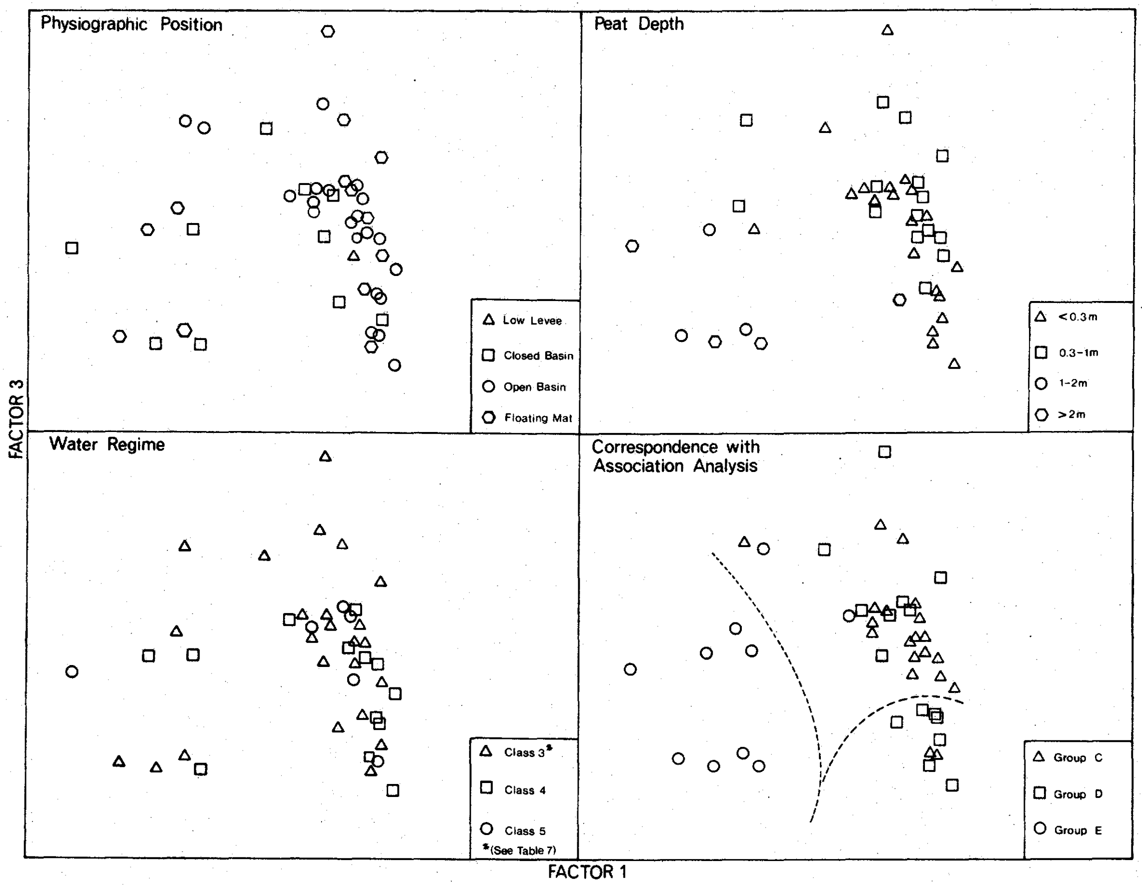

Fig. 13. Environmental categories and groups of the final association analysis superimposed on the ordination of stands according to Factors 1 and 3 of the principal component analysis (Q-expression) of the ground stratum vegetation of fens (Landscape Unit III).

The distribution of stands on the first three axes showed that stands falling into the three groups of the final association analysis (Groups C, D, and E) tended to be clustered together on the diagrams (e.g., Fig. 13). This suggests that environmental factors, other than those measured are important in controlling vegetation pattern.

It, therefore, appears that, among the stands sampled, the major environmental gradients which directly affect the composition and distribution of fen community-types are pH and nutrient status of the hydro-edaphic complex (*sensu* Bellamy 1962), while differences in relative wetness are of lesser importance in affecting vegetational variation in this generally moisture-saturated environment. Nutrient availability and pH, however, are governed, in turn, by the nature and circulation of the water available to plant growth. Thus in closed basins (back swamps), where the water source is local runoff, nutrient status and pH tend to be lower than in open basin locations where nutrient-richer waters are circulating, and where acid products of decomposition are continually flushed out.

6.4.2 Ordination of species and environmental attributes

This ordination represents the R-expression of a correlation matrix of 42 species and 20 environmental attributes in 36 stands. The loadings on the first three components, accounting for approximately 32 percent of the total variance, are listed in Table 11.

The spatial distribution of attributes on Factors 1 and 2 which, together, represent 22.5 percent of the total variance, is in the form of four fairly distinct clusters (Fig. 14):

(1) The first cluster, possessing negative loadings on both

Table 11. Normalized attribute loadings on the first three factors of the principal component analysis (R-expression of correlation matrix) of the ground stratum vegetation of Landscape Unit III.

Attribute	F_1	F_2	F_3
Acorus calamus	0.09	-0.03	-0.07
Alnus rugosa var. americana	0.00	0.11	0.27
Aster	0.00	0.05	0.15
Betula glandulifera	-0.15	-0.07	0.28
Calamagrostis canadensis-inexpansa-neglecta	0.01	-0.04	0.00
Calla palustris	0.06	-0.14	-0.08
Campanula aparinoides	-0.13	-0.23	-0.04
Carex aquatilis	-0.09	-0.18	0.01
Carex atherodes	0.18	0.08	-0.04
Carex lanuginosa	-0.18	0.08	0.02
Carex rostrata	0.12	0.02	0.04
Cicuta bulbifera	0.04	-0.08	-0.09
Equisetum arvense	-0.05	-0.02	0.19
Equisetum fluviatile	0.06	0.05	-0.04
Equisetum pratense	-0.05	0.04	0.22
Galium labradoricum-trifidum	-0.18	-0.15	-0.04
Galium triflorum	0.06	0.08	-0.01
Hippuris vulgaris	0.07	-0.10	-0.08
Hypericum virginicum var. fraseri	0.03	-0.18	-0.07
Impatiens capensis	0.04	-0.09	-0.03
Menyanthes trifoliata	-0.28	0.00	-0.06
Myrica gale	-0.10	-0.04	0.33
Naumburgia thyrsiflora	0.03	-0.20	-0.06
Oxycoccus quadripetalus	-0.11	-0.14	0.12
Petasites palmatus	0.02	0.12	0.26
Phragmites communis var. berlandieri	0.05	-0.08	-0.06
Potentilla palustris	-0.20	-0.18	0.05
Ranunculus circinatus var. subrigidus	-0.10	0.02	-0.03
Rumex orbiculatus	-0.07	0.02	-0.03
Salix candida	-0.08	-0.10	-0.06
Salix discolor	0.11	0.09	0.05
Salix pedicellaris	-0.23	-0.09	0.02
Salix petiolaris	0.09	0.08	-0.01
Scolochloa festucacea	-0.02	0.02	0.01
Scutellaria galericulata var. epilobiifolia	0.06	-0.19	-0.10
Sium suave	0.05	-0.04	-0.10
Solidago spp.	-0.02	0.09	0.29
Sonchus arvensis-asper	-0.04	-0.11	-0.00
Sparganium eurycarpum	0.09	-0.12	-0.09
Triglochin maritima	-0.28	0.13	-0.15
Typha latifolia	0.07	-0.13	-0.12
Utricularia intermedia	0.07	-0.12	-0.07

. . . cont'd

Table 11 concluded.

Attribute	F_1	F_2	F_3
Ca^{++} (water)	-0.24	0.20	-0.15
Ca^{++} (soil)	-0.18	0.07	0.19
Mg^{++} (water)	-0.00	0.17	-0.16
Na^{+} (water)	-0.27	0.16	-0.16
K^{+} (water)	-0.01	0.05	-0.02
K^{+} (soil)	-0.10	-0.24	0.09
HCO_3^- (water)	0.15	0.17	-0.09
NO_3^- (water)	-0.03	-0.07	0.04
$PO_4^{\equiv}$ (water)	-0.01	-0.01	0.09
$SO_4^{=}$ (water)	0.04	0.00	-0.12
Cl^- (water)	-0.26	0.19	-0.16
Available P (soil)	-0.07	-0.20	0.12
Available N (soil)	-0.06	-0.04	0.30
Conductivity (water)	-0.24	0.21	-0.16
Conductivity (soil)	-0.24	0.16	-0.03
pH (water)	0.15	-0.10	-0.05
pH (soil)	0.10	0.02	0.11
Organic matter (soil)	-0.12	-0.18	-0.11
Water holding capacity (soil)	-0.13	-0.19	-0.14
Water regime	0.00	0.14	0.12
Percent of total variance accounted for by each component	12.55	10.05	9.74

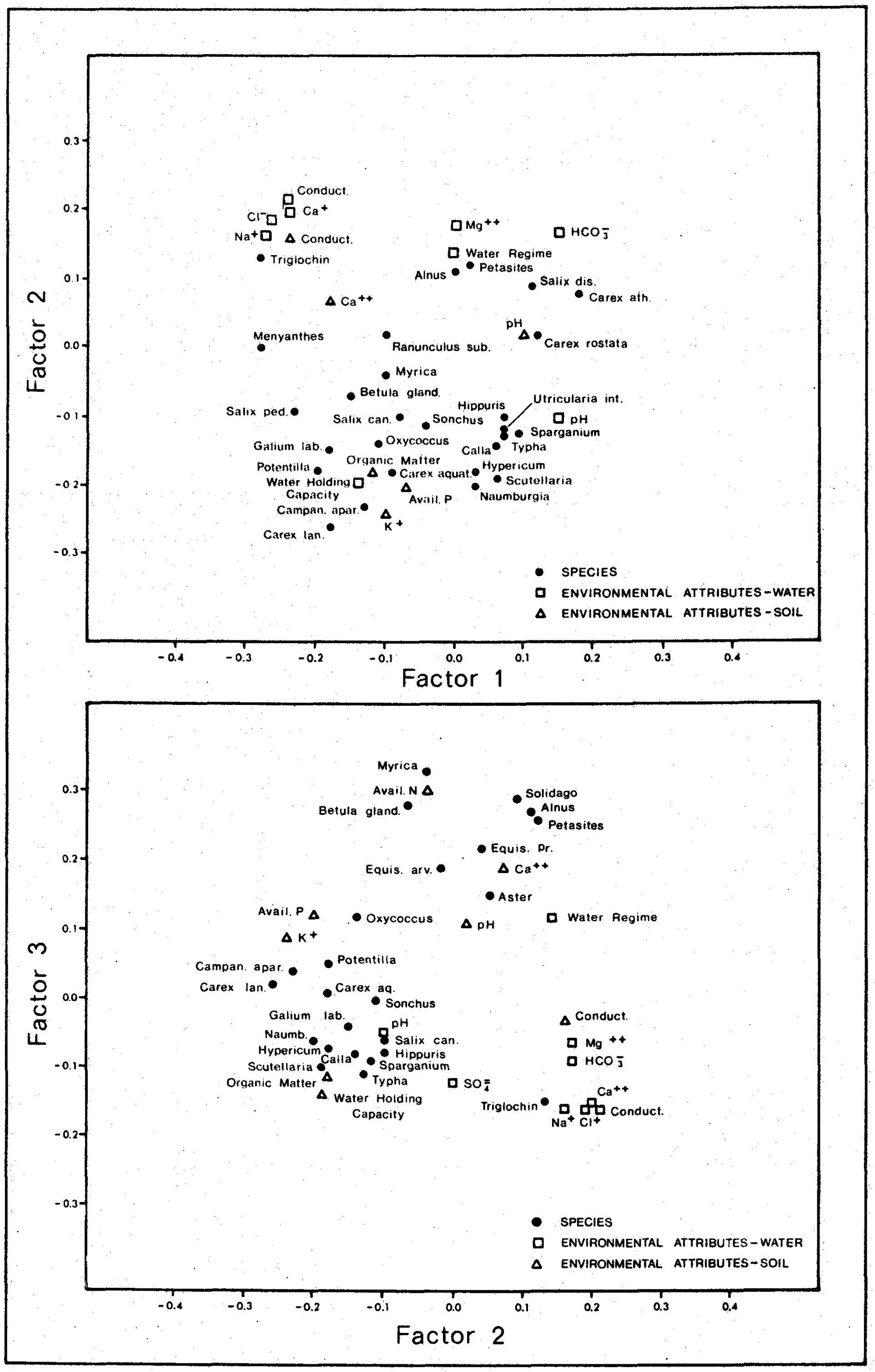

Fig. 14. Ordination of species and environmental attributes according to Factors 1-3 of the principal component analysis (R-expression) of the ground stratum vegetation of fens (Landscape Unit III). Attributes with loadings $< \pm 0.1$ on both axes were omitted.

components, consists of Betula glandulifera, Campanula aparinoides, Carex aquatilis, Carex lanuginosa, Galium labradoricum-trifidum, Menyanthes trifoliata, Myrica gale, and Oxycoccus quadripetalus. All of these, except C. aquatilis and O. quadripetalus, are most prevalent on the deep peat sites of closed basins (Group E of the final association analysis; see Table 6, p. 68). Associated environmental attributes are water holding capacity, organic matter content, available soil P and soil K^+.

(2) The second cluster, with positive loadings on F_1 and negative ones on F_2, is made up of the submergent aquatics, Hippuris vulgaris and Utricularia intermedia; the emergents, Sparganium eurycarpum and Typha latifolia; and the small herbs, Calla palustris, Hypericum virginicum var. fraseri, Naumburgia thyrsiflora, and Scutellaria epilobiifolia - species particularly characteristic of floating mat sites. The only environmental attribute positioned with this cluster is pH of the water.

(3) The third cluster, possessing positive loadings on both axes, consists of Alnus rugosa, Carex atherodes, Carex rostrata, Petasites palmatus, and Salix discolor - plants prominent on the relatively nutrient-rich, shallow fen peat and low levee sites (Groups C and F of the final association analysis, respectively). Associated environmental attributes are soil pH, and HCO_3^- and Mg^{++} of the soil water.

(4) The fourth cluster, negative on F_1 and positive on F_2, consists of the environmental attributes, conductivity (soil and water), Ca^{++} (soil), Na^+ and Cl^- (water), and the halophytic species Triglochin maritima. This plant occurred in only two stands (S-88 and S-89) which were characterized by abnormally high concentrations of Na^+ and Cl^-.

Environmental gradients thought to be related to the first three components are as follows:

F_1 is a pH gradient as illustrated by the positive loadings of soil pH and pH and HCO_3^- of the water.

F_2 is a combined moisture and salinity gradient as shown by positive loadings for conductivity, Na^+, Cl^-, Ca^{++}, Mg^{++}, and water regime, and by the negative loadings for organic matter and water holding capacity. Species loadings are in accordance with this complex gradient: Positive loadings are possessed by *Alnus rugosa*, *Salix discolor*, and *Petasites palmatus* - species characteristic of alluvial stream levees, i.e., sites drier and nutrient-richer than the fen stands included in this ordination. Conversely, negative loadings apply to *Campanula aparinoides*, *Carex aquatilis*, *Carex lanuginosa*, and *Naumburgia thyrsiflora* - species prevalent on wet and relatively nutrient-poor peat and floating mat sites.

F_3 is related to soil nutrient availability, as shown by the positive loadings for the major soil nutrients, available N, available P, K^+, and Ca^{++}, and by the negative loadings on the non-nutrient ions, Na^+, Cl^-, HCO_3^-, and $SO_4^=$.

6.5 Landscape Unit V

6.5.1 Stand ordination

This ordination is the Q-expression of a correlation matrix of 30 stands and 73 species, consisting of the alluvial stream levee vegetation of Groups F, G, H, and J from the final association analysis.

The loadings on the first four factors, accounting for approximately 38 percent of the total variance, are given in Table 12. To

Table 12. Adjusted factor loadings on the first four factors of the principal component analysis (Q-expression of correlation matrix) of the ground stratum vegetation of Landscape Unit V.

Stand	Factor 1	Factor 2	Factor 3	Factor 4
1	-0.04	-0.37	-0.04	-0.12
2	0.04	-0.46	0.08	-0.50
3	0.32	-0.49	0.49	-0.27
10	-0.04	0.35	-0.01	0.00
11	0.05	-0.17	-0.10	-0.07
12	-0.03	-0.21	-0.08	0.15
14	0.24	-0.20	0.17	0.18
15	-0.11	-0.16	0.02	-0.08
16	-0.19	0.19	-0.21	-0.18
17	-0.11	-0.05	-0.31	-0.21
18	0.19	-0.16	-0.14	-0.08
21	0.33	-0.28	0.13	-0.05
23	0.38	-0.06	0.12	0.13
28	0.14	-0.18	0.11	-0.21
30	-0.16	-0.18	-0.56	0.15
31	-0.16	-0.18	-0.56	0.15
41	-0.06	0.55	-0.66	-0.21
45	0.02	0.14	-0.06	-0.04
46	0.02	0.25	-0.27	-0.14
47	0.77	0.18	0.28	0.12
48	-0.69	0.74	0.72	-0.57
49	1.22	0.76	0.04	0.23
68	-0.11	0.27	-0.13	-0.16
80	-0.41	0.22	0.12	0.14
81	-0.24	0.14	-0.22	0.10
82	-0.34	0.11	0.17	0.10
83	-0.00	0.03	0.09	-0.06
84	-0.39	-0.19	0.29	0.51
85	-0.30	-0.08	0.24	0.19
86	-0.45	0.19	0.22	0.80
Percent total variance accounted for by each component	13.18	9.58	8.40	6.80

facilitate study of the possible importance of available environmental measurements on each axis, available data were transformed to relative values as follows:

(1) Soil data (available N, available P, Ca^{++}, Mg^{++}, Na^{+}, K^{+}, pH, conductivity, organic matter content, water holding capacity) were ranked in order of decreasing magnitude as outlined in Section 6.2.

(2) To rate the stands according to relative wetness, the position of the water-table on July 7, 1967, was selected because measurements were available for most stands on that date and, for the remaining ones, could be estimated with sufficient confidence from subsidiary information.

(3) To position stands according to overstory composition along a successional gradient, the following assumption was made: Primary plant succession on the alluvial levee deposits involves a change from shrub and tree species that are capable of withstanding repeated flooding and silt deposition, to species which are intolerant to these conditions, and require stable sites for their establishment and growth. Thus based on general knowledge of the autecology of tree and shrub species in the Saskatchewan Delta and elsewhere (e.g., Ritchie 1956, Rowe 1956b, Anon. 1961, Maini 1968, _inter alios_), the major canopy-forming species were placed in an approximate order of successional position (similar to the "climax adaptation values" of Curtis and McIntosh 1951). To rank the 30 stands, relative density and average tree diameters were used as indicators of the relative stability which each stand had experienced, and thus of its position relative to all other stands along a successional gradient (see Appendix D). Evidence

of past disturbance by fire, or through selective cutting for white spruce, was also considered in ordering the stands.

Judging from the environmental data available, the first factor is, at least partly, a moisture gradient, as shown by the diagrams for relative position of the water-table and for water holding capacity of the soil - which itself is closely related with organic matter content (Fig. 15). Positive loadings on F_1 are associated with wet stands of low levee positions, whereas the drier stands of higher levees tend to have negative loadings. However, in part, F_1 also represents a gradient pertaining to nutrient availability, as illustrated by the superimposed relative values for Ca^{++} and available N of the soil (Fig. 16).

The second component incorporates the remainder of the moisture gradient, but mainly represents a nutrient gradient as shown by the diagrams for available soil N and P, and Ca^{++} (Figs. 16 and 17). Soil pH also was correlated with F_2, whereas soil conductivity, Mg^{++}, and the highly soluble Na^{+} and K^{+} ions gave more variable results. Factor 2, therefore, appears to represent a gradient from high to low nutrient availability and pH of the soil. Leaching of nutrients from the upper soil horizons and decreasing pH values are phenomena associated with podzolic soil development leading from the original alluvial-lacustrine deposits toward gray wooded profiles. It is, therefore, essentially a successional gradient.

Factor 3 appeared to be, at least in part, a pH gradient with negative loadings characteristic for stands having soil pH values < 7 and positive loadings associated with soil pH values > 7 (Fig. 17).

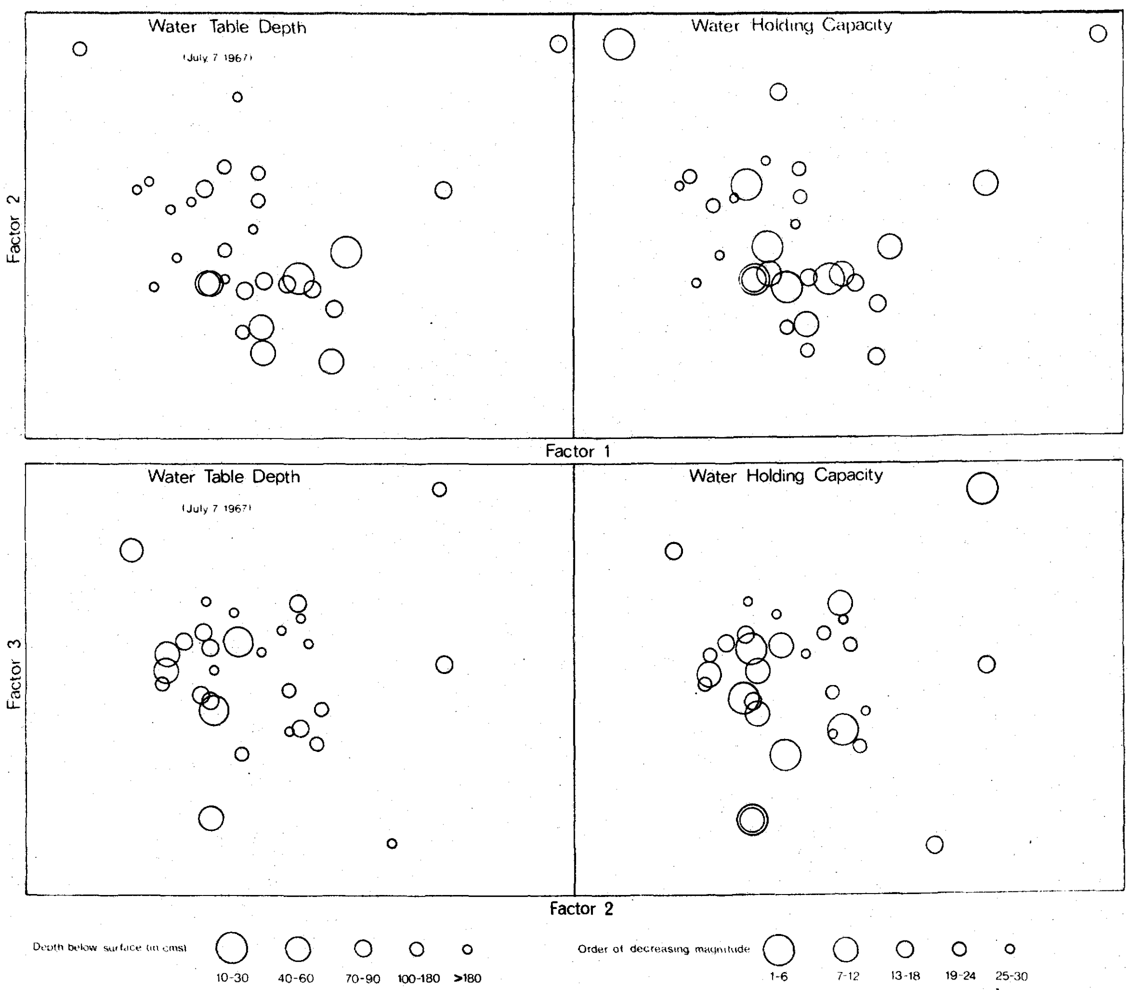

Fig. 15. Environmental measurements superimposed on the ordination of stands according to Factors 1-3 of the principal component analysis (Q-expression) of the ground stratum vegetation of wooded stream levees (Landscape Unit V). Environmental measurements were previously grouped into five classes according to magnitude.

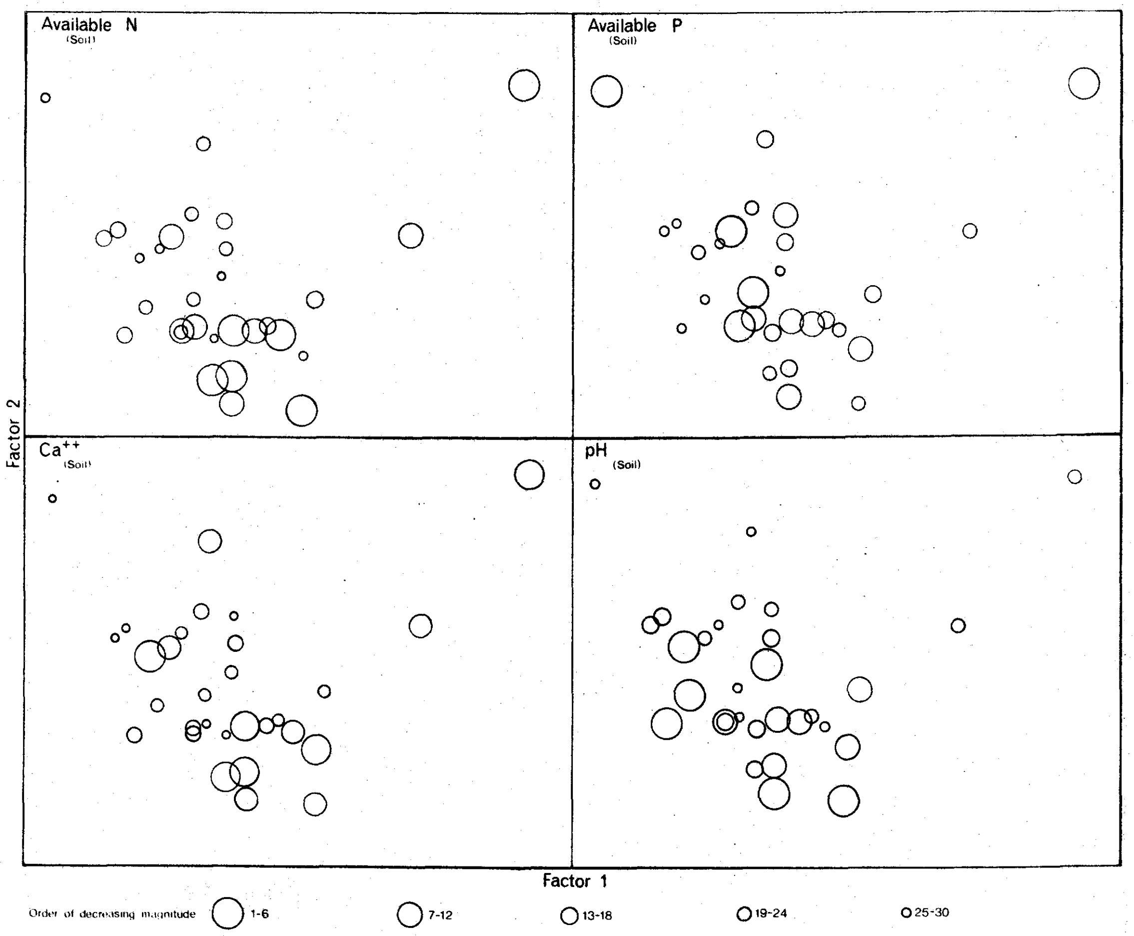

Fig. 16. Environmental measurements superimposed on the ordination of stands according to Factors 1 and 2 of the principal component analysis (Q-expression) of the ground stratum vegetation of wooded stream levees (Landscape Unit V). Environmental measurements were previously grouped into five classes of decreasing magnitude.

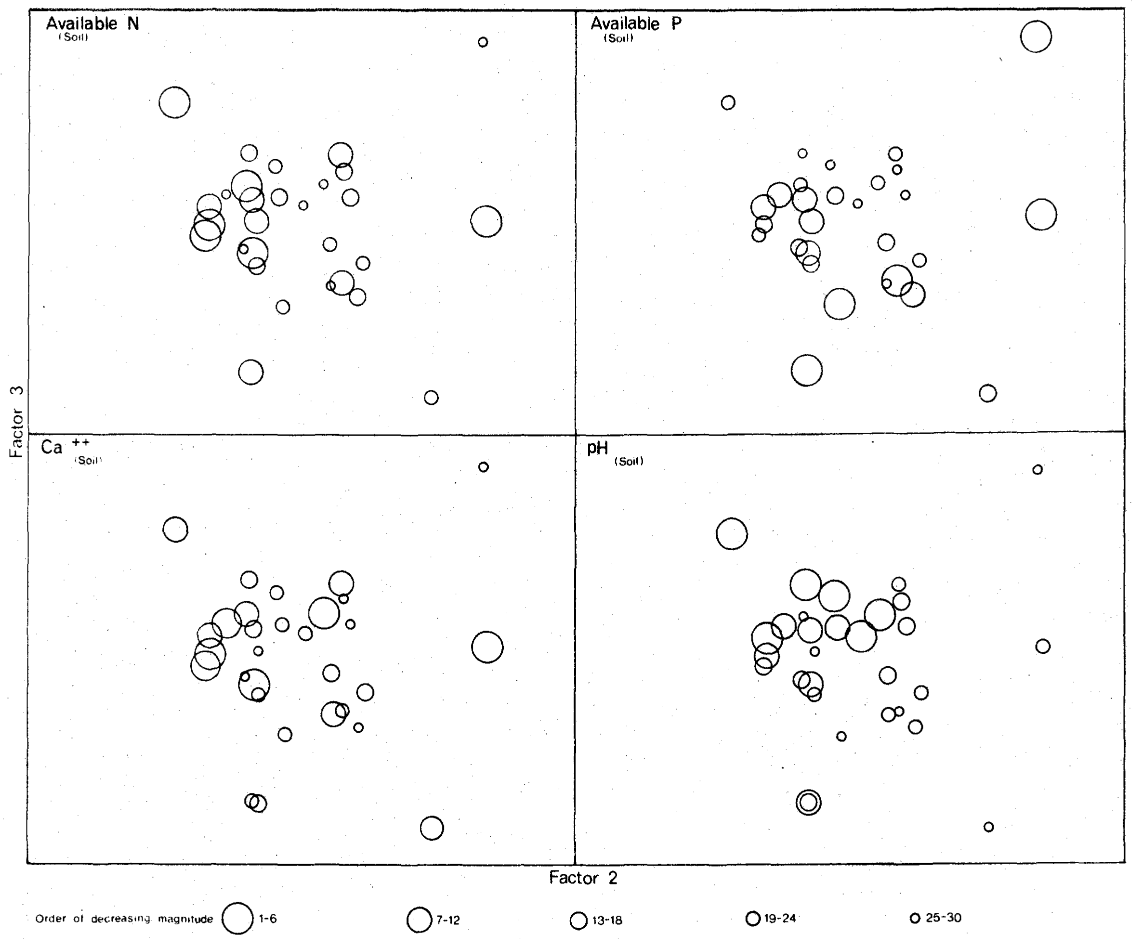

Fig. 17. Environmental measurements superimposed on the ordination of stands according to Factors 2 and 3 of the principal component analysis (Q-expression) of the ground stratum vegetation of wooded stream levees (Landscape Unit V). Environmental measurements were previously grouped into five classes of decreasing magnitude.

Moisture regime and nutrient availability (except for Ca^{++}) showed no involvement with F_3. Beyond this level, it proved impossible to associate ecological gradients with the extracted factors of the principal component analysis.

To test whether the stand ordination reflected relative site maturity, the successional stand sequence derived from the overstory composition (see Appendix D) was superimposed on the ordination (Fig. 18). The diagrams indicate pronounced interaction between F_1 and F_2, and an inverse relationship between successional status and the relative values for moisture status and nutrients. Thus it appears that the main environmental influences controlling vegetation variation in the understory of the mixed forest and tall shrub stands of the alluvial levees are moisture status and nutrient availability, i.e., interacting gradients inversely related to stability of site and maturity of the vegetation.

6.5.2 Correspondence of stand ordination and classification by association analysis

To examine the relationship between the two analytical techniques used in this study, classification of the stands according to the four terminal groups (F, G, H, J) of the final association analysis was superimposed on the stand ordination (Fig. 19).

The diagrams show a fairly distinct separation of Groups F and H on components F_1 and F_2, whereas Groups G and J are not clearly separated from each other, and tend to occupy an intermediate position between the other groups. No clear-cut separation of the groups was apparent on components F_3 and F_4. It is suggested, therefore, that the

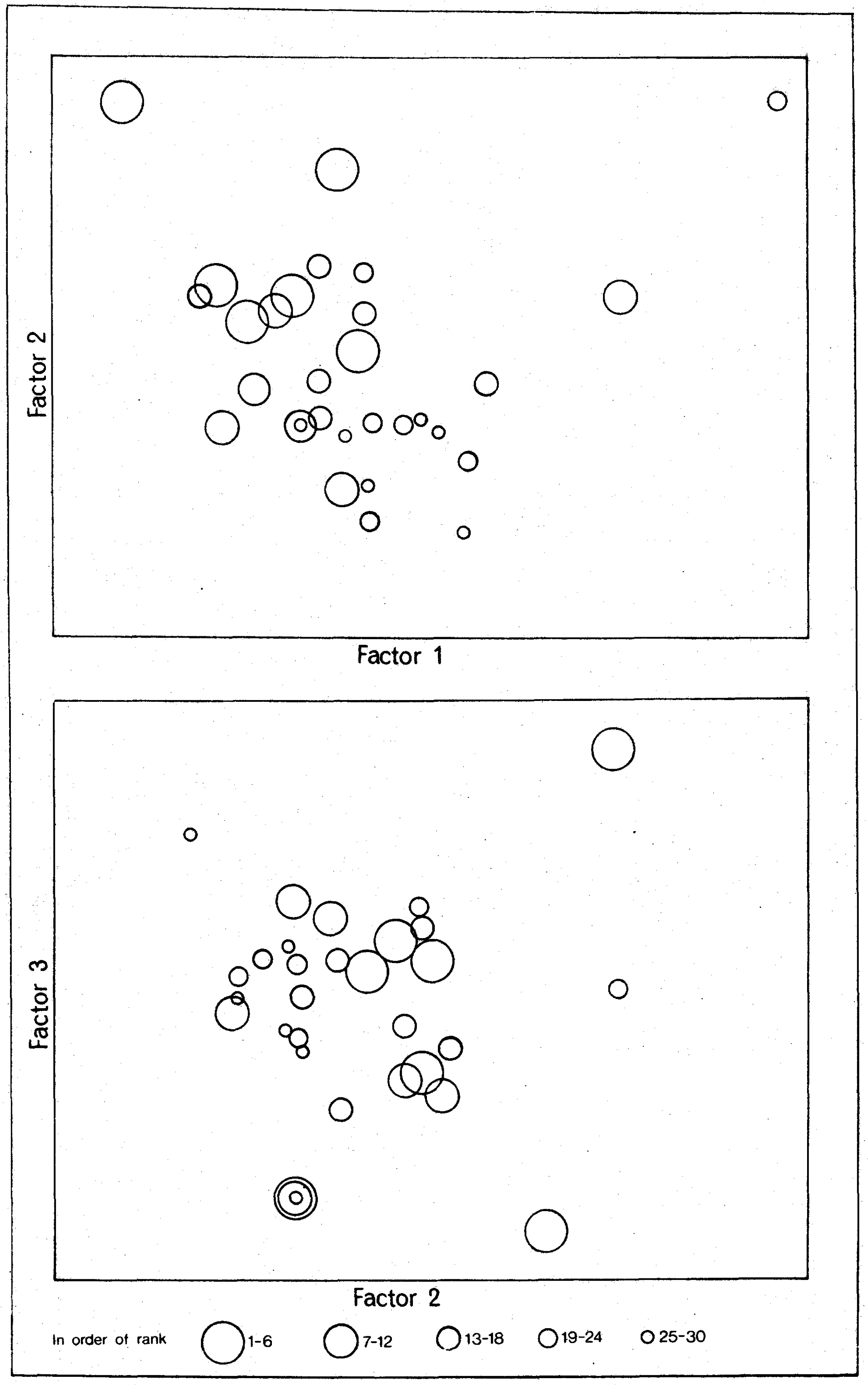

Fig. 18. Relative site maturity superimposed on the ordination of stands according to Factors 1-3 of the principal component analysis (Q-expression) of the ground stratum vegetation of wooded stream levees (Landscape Unit V). Stands were previously ranked according to apparent increase in environmental stability, as reflected by relative density and size of the canopy-forming trees and shrubs (see Appendix D).

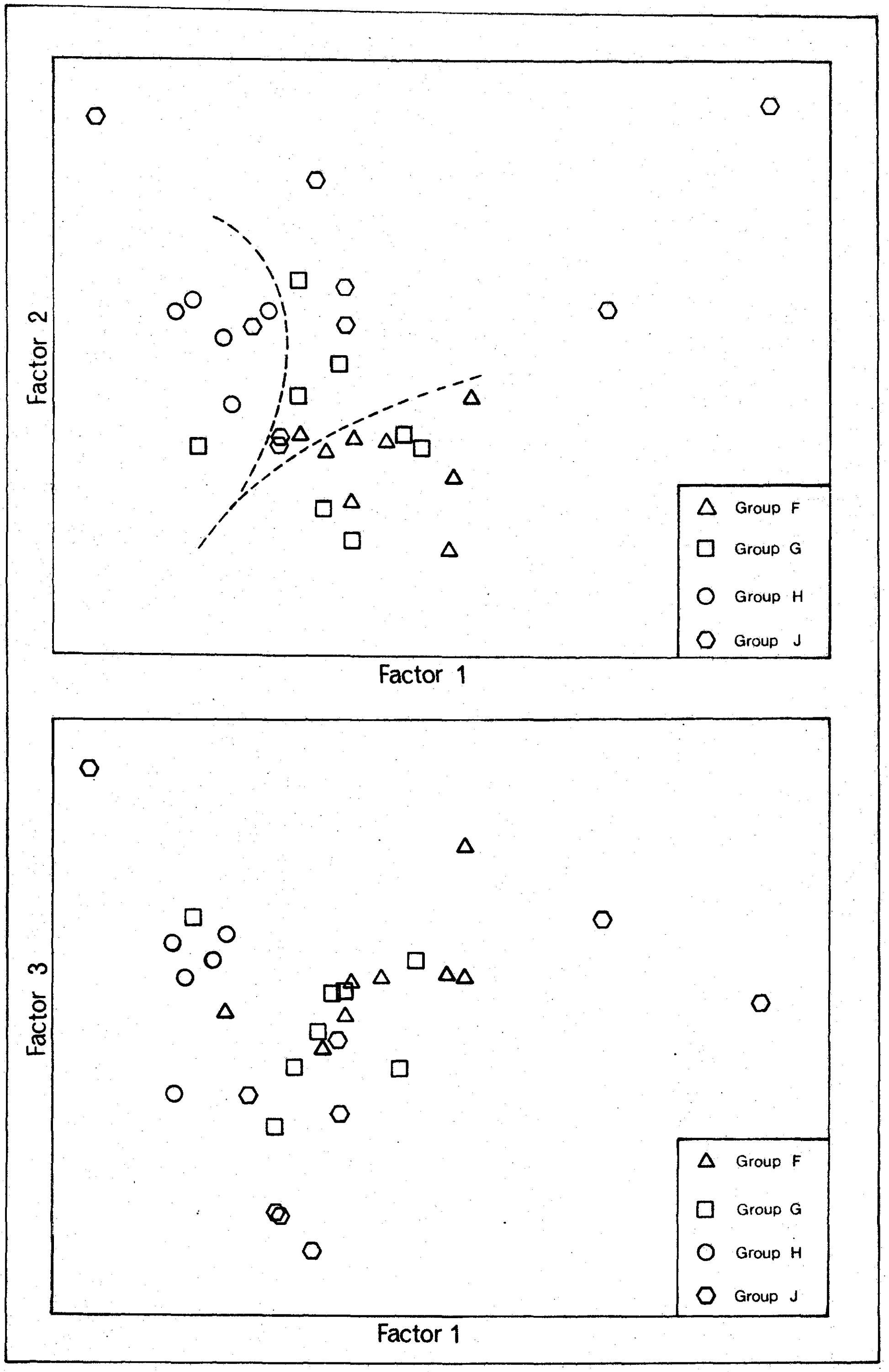

Fig. 19. Groups of the final association analysis superimposed on the ordination of stands according to Factors 1-3 of the principal component analysis (Q-expression) of the ground stratum vegetation of wooded stream levees (Landscape Unit V).

classificatory program of the association analysis responded to the same lines of vegetational variation that determined the first two factors of the principal component analysis. The environmental gradients associated with those factors have previously been identified as moisture regime and nutrient status.

6.5.3 Ordination of species and environmental attributes

This ordination represents the R-expression of a correlation matrix of 52 species* and 12 environmental attributes in 30 stands.

The first component in this ordination appears to reflect a moisture gradient, as shown by the high positive loading for water-table depth and the negative loadings for water holding capacity of the top soil layer (A) and for organic matter content (Table 13 and Fig. 20). Positioned near water-table depth are the following species which, according to the species-presence lists, are abundant only in the driest stands on alluvial levees: *Fragaria* spp., *Mitella nuda*, *Prunus virginiana*, *Rubus acaulis*, *Viburnum edule*, and *Viola* spp. Negative loadings are associated with *Calamagrostis canadensis-inexpansa-neglecta*, *Carex atherodes*, and *Naumburgia thyrsiflora*, i.e., species most abundant in environments wetter than those of Landscape Unit V.

F_2 appears to be a combined pH and nutrient gradient, as shown by the factor loading for pH which is the highest positive value for any attribute, the positive loadings for conductivity, available N, Na^+, Ca^{++}, and water holding capacity of the "B" soil Layer (31-90 cm below

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*Twenty-one minor species which occurred with less than 20 percent frequency in one or two stands only were deleted from the ordination.

Table 13. Normalized attribute loadings on the first four factors of the principal component analysis (R-expression of correlation matrix) of the ground stratum vegetation of Landscape Unit V.

Attribute	F_1	F_2	F_3
Acer negundo	0.17	0.15	0.00
Alnus rugosa var. americana	-0.06	0.08	-0.17
Amelanchier alnifolia	0.01	0.00	0.21
Anemone canadensis	0.03	0.05	0.02
Aralia nudicaulis	0.12	0.18	0.23
Arenaria lateriflora	0.14	0.15	-0.07
Aster	-0.18	0.06	0.19
Calamagrostis canadensis-inexpansa-neglecta	-0.17	0.06	-0.21
Carex atherodes	-0.20	0.11	0.05
Carex disperma	-0.12	-0.02	0.21
Circaea alpina	0.10	-0.11	-0.15
Cirsium arvense	-0.11	0.09	-0.04
Cornus canadensis	0.10	-0.15	0.16
Cornus stolonifera	-0.19	-0.07	0.02
Epilobium angustifolium	0.03	-0.16	-0.01
Equisetum arvense	-0.06	0.00	0.31
Equisetum pratense	0.05	-0.10	-0.23
Fragaria spp.	0.13	0.09	0.06
Galium labradoricum-trifidum	-0.04	0.15	-0.09
Galium triflorum	0.12	-0.12	0.02
Impatiens capensis	0.09	-0.03	-0.01
Matteuccia struthiopteris var. pensylvanica	-0.03	0.03	-0.10
Mentha arvensis var. villosa	-0.12	0.07	-0.12
Mertensia paniculata	0.04	-0.14	-0.05
Mitella nuda	0.17	0.06	0.08
Naumburgia thyrsiflora	-0.11	0.10	0.03
Plantago major	0.12	0.00	0.11
Populus balsamifera	0.06	0.08	-0.07
Prunus virginiana	0.17	0.10	0.05
Pyrola asarifolia	-0.01	-0.28	0.07
Ranunculus macounii	-0.10	0.04	-0.01
Ribes americanum-hudsonianum	-0.11	0.11	-0.10
Ribes hirtellum-lacustre-oxyacanthoides	-0.05	-0.06	-0.12
Ribes glandulosum	0.05	-0.11	-0.05
Ribes triste	-0.03	0.08	0.08
Rosa acicularis	-0.10	-0.15	0.03
Rubus acaulis	0.17	0.06	0.11
Rubus idaeus var. strigosus	0.13	0.03	-0.07
Rubus pubescens	-0.14	-0.05	0.05
Rumex orbiculatus	-0.02	0.01	0.07
Scutellaria galericulata var. epilobiifolia	-0.05	0.00	-0.13
Smilacina stellata	-0.02	0.11	0.04
Solidago	-0.19	0.14	-0.02
Sonchus arvensis-asper	-0.23	0.17	0.09
Stachys palustris var. pilosa	-0.10	0.06	-0.01
Symphoricarpos occidentalis	-0.17	0.10	0.11

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Table 13 concluded.

Attribute	F_1	F_2	F_3
Trientalis borealis	0.04	-0.08	0.22
Ulmus americana	0.13	0.14	-0.10
Viburnum edule	0.20	0.10	0.10
Viburnum trilobum	-0.01	-0.26	-0.00
Vicia americana	-0.16	0.07	0.21
Viola	0.22	0.10	0.01
Ca^{++}	-0.03	-0.01	0.02
Mg^{++}	-0.20	0.07	0.17
Na^{+}	-0.18	0.13	0.14
K^{+}	-0.02	-0.27	0.02
Available N	-0.16	0.11	-0.11
Available P	-0.10	-0.29	0.00
pH	0.07	0.19	-0.11
Conductivity	-0.11	0.09	0.07
Organic matter	-0.15	-0.26	-0.13
Water holding capacity (A-layer)*	-0.14	-0.23	-0.14
" " " (B-layer)	-0.07	0.13	-0.08
Water table depth	0.23	0.08	0.18
Percentage of total variance accounted for by each component	14.56	11.04	9.75

*A-layer = 0-30 cm below surface.
B-layer = 31-90 cm below surface.

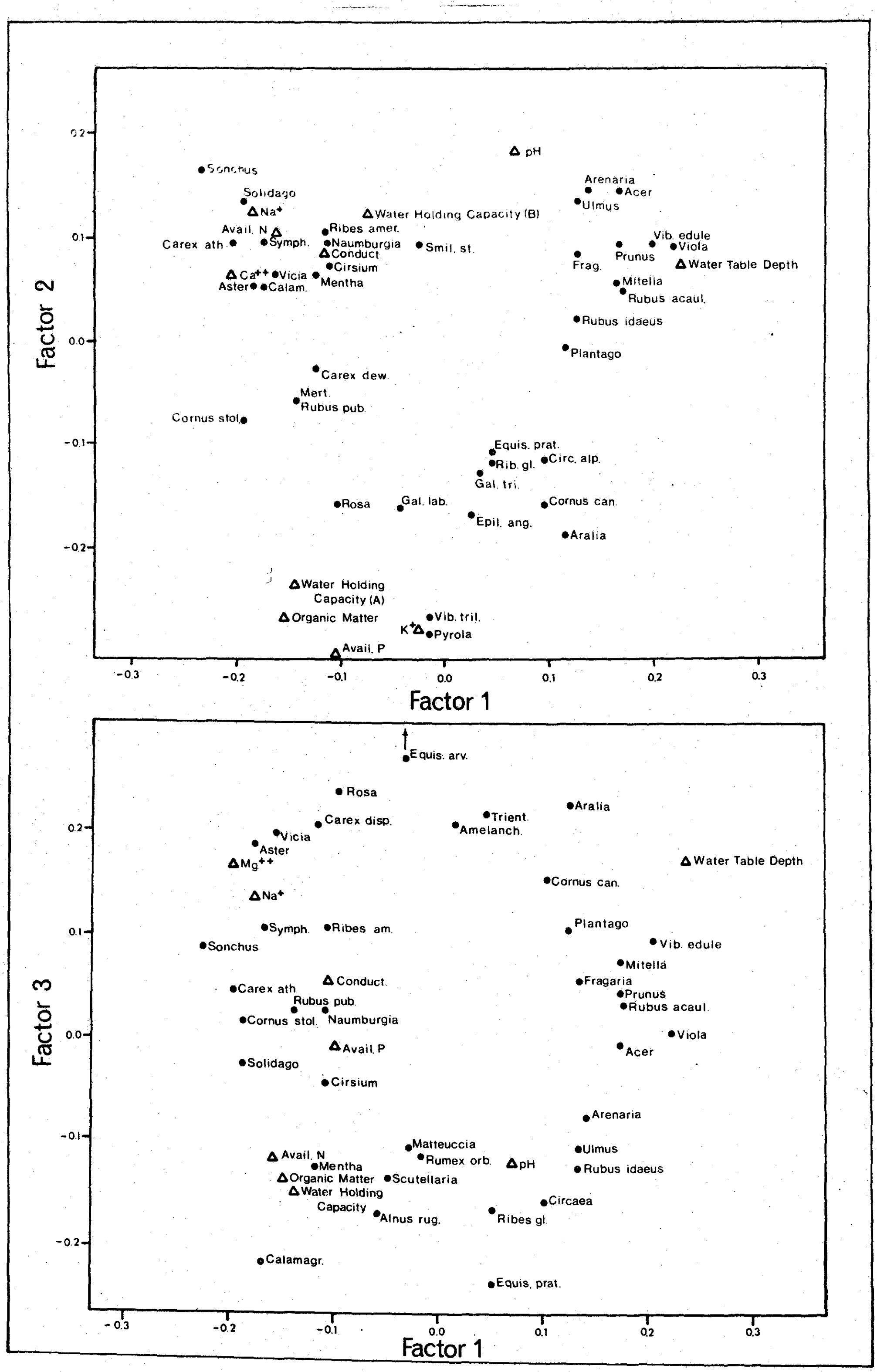

Fig. 20. Ordination of species and environmental attributes according to Factors 1-3 of the principal component analysis (R-expression) of the ground stratum vegetation of wooded stream levees (Landscape Unit V). Attributes with loadings $< \pm 0.1$ on both axes were omitted.

ground surface). The latter measurement is thought to reflect heavy soil texture and, therefore, relative impermeability to leaching of soluble ions. Sonchus arvensis-asper, a genus commonly associated with soil disturbance - which itself reflects increased nutrient availability and higher pH values - has the highest loading of any species on F_2, whereas Pyrola asarifolia, a plant most common in mature coniferous forests has the highest negative loading.

On F_1 versus F_2, Aster spp., Ribes americanum-hudsonianum, Symphoricarpos occidentalis, and Vicia americana are positioned in close proximity to environmental attributes that reflect high nutrient availability. These species may, therefore, be regarded as indicators of high nutrient status for the forest communities on the alluvial levees of the Delta. Other species, closely placed with the above, are Calamagrostis canadensis-inexpansa-neglecta, Carex atherodes, Mentha arvensis, and Naumburgia thyrsiflora - species most prevalent in the shallow peat fens adjacent to the alluvial levees. The presence in that cluster of Solidago spp., Circium arvense, and Solidago spp. in addition to Sonchus arvensis-asper, suggests that disturbance (probably through fire and logging) may be an important influence by which availability of nitrogen and calcium is increased.

It was not possible to associate F_3 with any recognizable environmental gradient.

7. ENVIRONMENTAL MEASUREMENTS AND STRATIGRAPHY OF FIELD-TRANSECTS

This section presents water level data for major lakes and field-transects in the study block, periodic ground temperature records, and the results of the stratigraphic analysis of peat cores. Those data provide further insight into the dynamics of vegetation/environment relationships in the Saskatchewan River Delta.

7.1 Seasonal and annual changes in lake water levels

Water level measurements for five major lakes in the study block, recorded during the field seasons of 1965, 1966, and 1967 are listed in Table 14.

It is apparent from Table 14(A) that, for the three years under observation, seasonal fluctuations between spring and summer levels were small, averaging about 6 cm (0.2 ft), and ranging from 3-21 cm (0.1-0.7 ft). This stability of water levels within each open-water season is mainly the result of the controlled inflow of water from the Saskatchewan River through the Dragline Canal. It is known that lake levels have been held fairly stable from spring to fall since the completion of the intake-structure on the Dragline Canal in 1962 (H. Moulding, Ducks Unlimited, pers. comm.), and to a lesser extent since the construction of the canal itself in 1939. Spring water levels for the three years show a marked increase from 1965 to 1966, ranging from 18-51 cm (0.5-1.7 ft), and a further smaller increase of up to 21 cm (0.7 ft) from 1966 to 1967.

Table 14(B) lists maximum and minimum levels recorded for each lake for all three field seasons. The total fluctuation ranges from 37 cm (1.2 ft) for Junction Lake to 88 cm (2.9 ft) for Cut Beaver Lake;

Table 14. Water level data from five major lakes in the Saskatchewan River Delta study area, recorded during the open water seasons of 1965 to 1967.

A. Spring (9-15 June) and summer (2-5 August) water levels.

	Water levels in feet above sea level								
	1965			1966			1967		
Lake	Spring	Summer	Change ft/cm	Spring	Summer	Change ft/cm	Spring	Summer	Change ft/cm
Cut Beaver	876.0	875.4	-0.6(-18 cm)	877.7	878.0	+0.3(+9 cm)	878.0	877.9	-0.1(-3 cm)
Muskeg	875.6	875.8	+0.2(+ 6 cm)	876.1	876.2	+0.1(+3 cm)	876.8	876.4	-0.4(-12 cm)
Deep	874.8	875.2	+0.4(+12 cm)	875.9	876.1	+0.2(+6 cm)	876.6	876.3	-0.3(-9 cm)
Junction	874.9	875.6	+0.7(+21 cm)	874.6	874.8	+0.2(+6 cm)	874.6	874.8	+0.2(+6 cm)
Egg	872.5	873.1	+0.6(+18 cm)	873.4	873.1	-0.3(-9 cm)	873.5	873.3	-0.2(-6 cm)
Mean seasonal change			+0.3(+ 9 cm)			+0.1(+3 cm)			-0.2(-6 cm)

B. Maximum and minimum water levels recorded for the periods, 4 June-18 August 1965, 16 May-2 August 1966, and 24 May-6 September 1967.

Lake	Maximum recorded level (ft-ASL)	Date	Minimum recorded level (ft-ASL)	Date	Total fluctuation ft	Total fluctuation cm
Cut Beaver	878.0	24/5/67 9/6/67	875.1	3/7/65	2.9	88
Muskeg	876.8	9/6/67 23/6/67	875.5	3/7/65	1.3	40
Deep	876.7	24/5/67	874.8	15/6/65	1.9	58
Junction	875.6	20/7/65	874.4	6/7/66	1.2	37
Egg	873.8	24/5/67	872.4	3/7/65	1.4	43
Mean total fluctuation					1.7	60

it averages 60 cm (1.7 ft.

7.2 Seasonal position of the ground water-table

The position of the ground water-table was measured every two weeks during the field seasons of 1965 to 1967 at several locations along each field-transect (see Section 4.6.2), except for Transect 9 which was read in 1967 only. Several problems were encountered that interfered with the interpretation of the results:

(1) Some of the standpipes were dislodged by frost action during the winters of 1965-66 and 1966-67 and had to be re-established. Thus exact year-to-year comparison could not be made;

(2) Several pipes could not be located during surveying of the field-transects in winter (see Section 4.6.5). Therefore, their exact elevation in relation to other pipes could not be determined; and

(3) Moving ground water occasionally caused pipes to become clogged with silt so that true water-table positions could not be read until the obstruction had been removed.

Because of these difficulties, some sets of water level records had to be discarded. Information was found to be reasonably reliable for Transects 2, 4, and 7 (see Figure 2, p. 12) for 1966, and for Transect 9 for 1967. Detailed examination was, therefore, restricted to those data; other records were evaluated to the extent that confidence could be placed in them.

Transects 2, 4, and 7 extend from alluvial stream levees across shallow fen peat deposits and floating mats to shallow lakes that are interconnected by natural or artificial channels. The level nature of the terrain is evident from the profile diagrams for the transects:

T-2 has a vertical drop of 0.9 m (3 ft) over a horizontal distance of 1,460 m (4,800 ft), T-4 drops 1.4 m (4.5 ft) over 580 m (1,900 ft), and T-7 falls 1.1 m (3.6 ft) over 670 m (2,200 ft).

The available data on seasonal water-table positions suggest the following events:

(1) The position of the water-table gradually decreases from spring to autumn in all locations. This drop is greater within the mineral substrate of the stream levees than within the peat deposits (Fig. 21). Floating mats rise and fall in accordance with lake level fluctuations and thus the proximity of the water to the surface of the mat may remain unchanged through the season.

(2) During May and June, melt water is often held in slight depressions on the surface of the still frozen peat deposits (see Section 7.3 below). As the ice gradually melts, the supernatant water drains downward, and by mid-July, the peat surfaces are generally dry.

(3) Ground water-table changes within stream levees do not respond directly to fluctuations in the water levels of lakes and adjacent fens (Fig. 21), probably because of relatively low permeability of the fine-textured alluvium. In the spring, percolating melt water brings the ground water levels under the forest and tall shrub cover of the levees to within 31-62 cm (1-2 ft) of the ground surface, i.e., to a point above the corresponding water level positions in the adjacent fens. But from July on, levees have water-tables as low or even lower than the corresponding lake levels.

Transect 9 is situated on deep peat within a closed basin formed by the levees of old drainage channels. It extends from a low levee near the south shore of Cut Beaver Lake across an expanse of bog birch

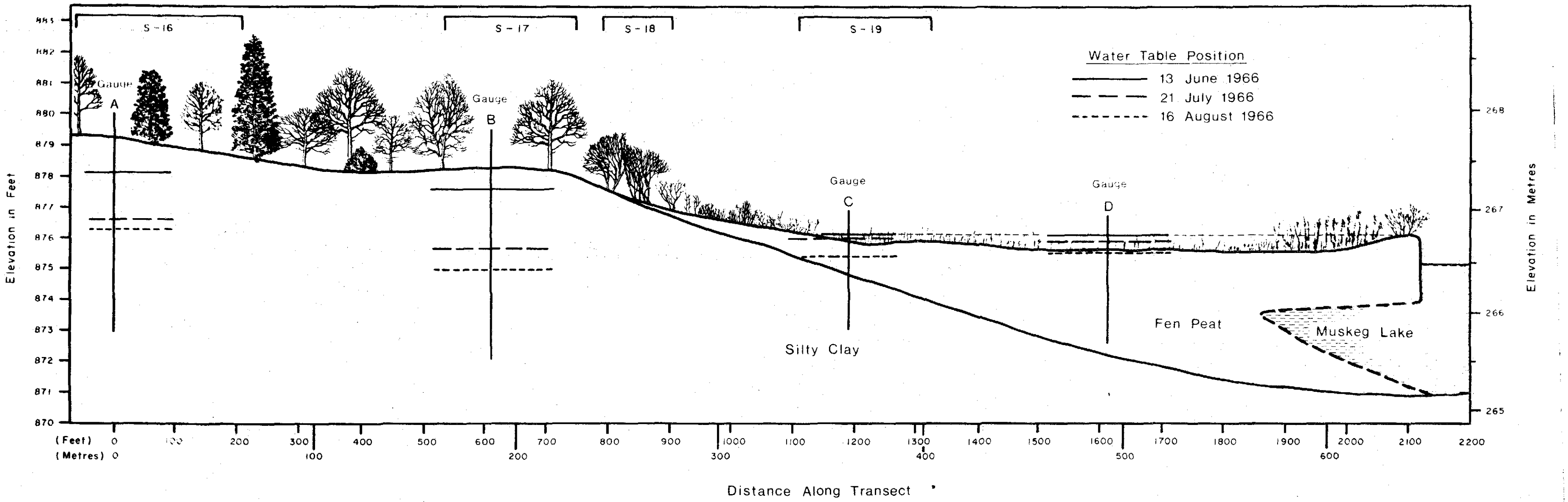

Fig. 21. Seasonal position of the ground water-table at four measuring stations on Transect 7 (1966).

and ericaceous shrub vegetation into a slightly raised black spruce bog (see Fig. 23, p.145). The transect is 670 m (2,200 ft) long and has a rise of approximately 45 cm (1.5 ft).

During May and early June 1967, the water-table along the entire transect was at or slightly above the surface. A very gradual drop occurred through the summer so that by early September, the water-table at the highest point, within the black spruce community (Stand 43), was 30 cm below ground level and at the lowest point, within the bog birch community (Stand 67), measured approximately 8 cm below ground level.

7.3 Soil temperature

Soil temperature is an important environmental variable because it influences the metabolic activity of roots and soil organisms and the availability of moisture (Fraser 1957). Water absorption is decreased by low soil temperatures through physiological adjustments within the plants and through decreased vapour pressure (Kramer 1949, as quoted in Heinselman 1963). Pronounced differences in the seasonal march of ground temperatures may occur in organic and mineral soils within the same climatic zone as a result of differing properties of these substrates. This in turn will significantly affect the vegetation pattern in the area.

Temperature records of the substrate (see Section 4.6.3) at depths of 15 and 60 cm below the ground surface were averaged for stands falling into the following landscape facets:

(a) Alluvial levees with mixed forest cover (8 stands);

(b) Alluvial levees with tall shrub cover (4 stands);

(c) Fen peat with low shrub cover (7 stands); and

(d) Sphagnum peat with black spruce cover (2 stands).

The average temperatures for each time period were plotted and curves of best fit were drawn through the points (Fig. 22). These depths were chosen because they are believed to bracket the rooting zones of most plant species in the area.

The period for which temperature records were available, 26 May to 28 August, or 7 September, covers the major portion of the growing season, although some growth occurs beyond those dates. The diagrams serve as a means of comparing the seasonal march of temperatures in three common substrates, viz., alluvium, fen peat and Sphagnum peat, and beneath four overstory types, viz., mixed forest, black spruce forest, and shrub cover.

Examination of Fig. 22 shows the curves for (a), (b), and (c) to be essentially similar. At the 15 cm depth, ground temperatures rise rapidly from 3.2-5.5°C for 26 May to a maximum of near 14°C for 8 July - paralleling the period of greatest daily insolation. From that point, temperatures drop very gradually throughout the rest of the monitored period. It appears, therefore, that to a depth of at least 15 cm, moist fen peat heats up as rapidly as the alluvial soils of the stream levees.

The curves for (a), (b), and (c), at the 60 cm depth are also fairly similar. Here the temperature increase is, however, more gradual than at the shallower depth and the maximum of 8.3-9.7°C is not reached until 22 July or later.

Thin ice lenses at a depth of 30-45 cm persisted locally in fen peat deposits until early July. This phenomenon appeared to be confined to topogenous sites (i.e., where ground water was not moving) and

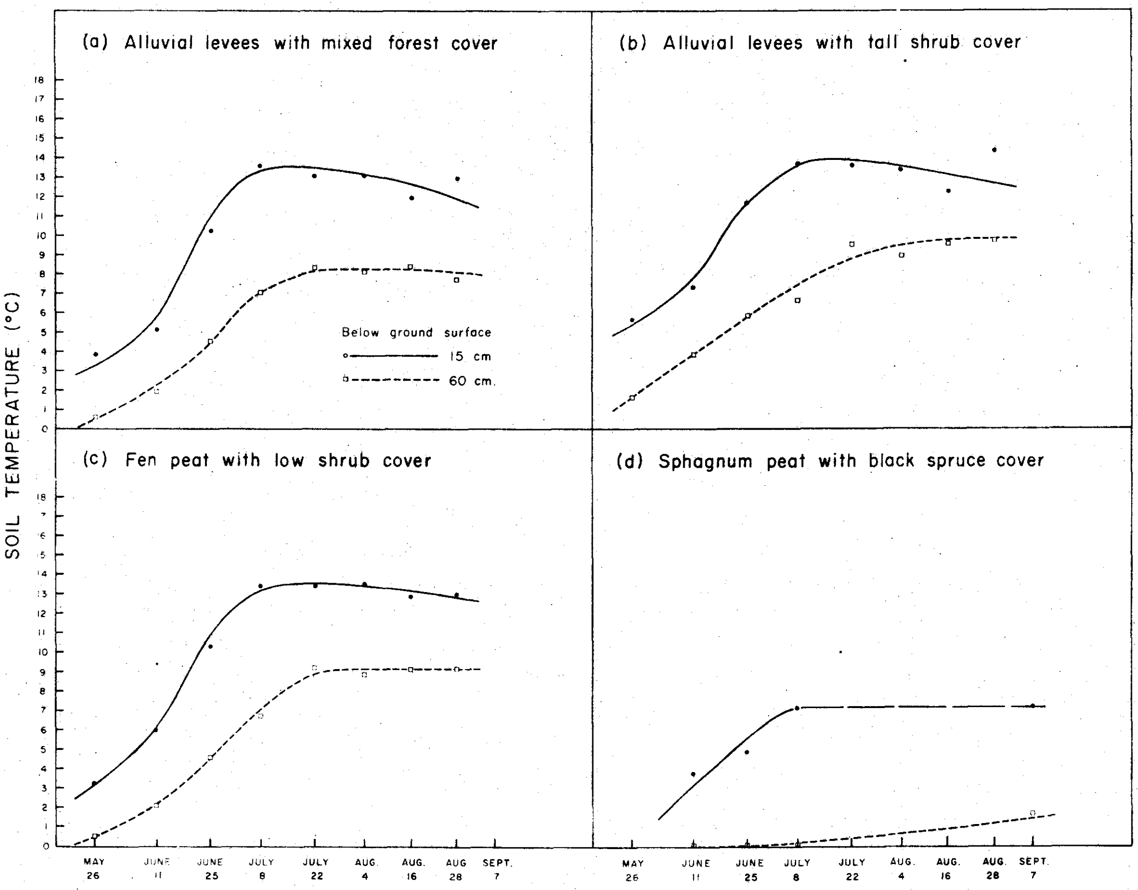

Fig. 22. Average ground temperature graphs at 15 cm and 60 cm below surface for four selected landscape facets.

where, in addition, radiation was severely restricted by dense shrub cover.

The ground temperature graphs for Sphagnum peat with black spruce cover, (d), differ significantly from the three former diagrams. Here the temperature rise at the 15 cm depth until 8 July 1967 is more gradual and only rises to 7.2°C. Unfortunately, it was not possible to carry out further measurements until 7 September when the temperature was again found to be 7.2°C.

At the 60 cm depth, the temperature remained at or near zero until 8 July, and then rose very gradually to 1.7°C on 7 September. A continuous frost layer was encountered at approximately 18 cm in mid-June and at ca. 45 cm on 8 July. On 7 September 1967, ice lenses (ca. 10 cm thick) were still present at a depth of 75 cm.

The low temperatures and the greater temperature differential between the two depths is thought to reflect the considerably lower heat conductivity of the highly porous Sphagnum peat surfaces as compared to mineral soils and denser fen peats (see Baver 1956, p. 373).

The presence of continuous frost at least as late as mid-July in the slightly raised black spruce-Sphagnum bogs (see Fig. 24, p. 147), suggests that, by this means, local precipitation is held within the rooting zone of the bog vegetation and prevented from mixing with the nutritionally somewhat richer ground water of the surrounding deep peat fens. Thus the low heat conductivity of the Sphagnum moss is thought to directly contribute to the perpetuation of the ombrotrophic character of the black spruce bogs.

7.4 Stratigraphy of field-transects

Macroscopic analysis of peat cores was undertaken on six field-transects, as outlined in Section 4.7. Identification of botanical constituents to the genus level was relatively simple in the case of poorly decomposed (fibric) peat but became more difficult with increasing decomposition. The botanical origin of humic bottom muck could not be positively established.

The analysis showed a major difference in peat stratigraphy between (1) those field-transects that extend from stream levees to open delta lakes (Transects 1, 2, 3, and 7) and (2) Transect 9 (see Fig. 2, p. 12) which extends across part of a closed basin or backswamp. These two types will be discussed in turn below.

7.4.1 Stratigraphy of open basin peat deposits

Peat deposits adjacent to the shallow delta lakes were found to be derived from fen and aquatic vegetation and less than 1.5 m thick. Since no significant differences in the stratigraphy of the four transects became apparent, detailed description is confined to Transect 1 (Fig. 23). Additional data are presented in Appendix E.

The transect profile of Fig. 23 shows that a large part of the peat deposits, extending between the open expanse of Egg Lake and the levee of the Saskatchewan River, forms a floating mat approximately 45 cm thick. (It is interesting to note that on the air photo mosaic taken in early June 1968, the floating portion is recognizable by a polygonal surface pattern.) Most of the floating mat consists of buoyant fibric peat, whereas denser mesic peat lies at the surface near the edge of the alluvial levee. Appendix E further shows that the

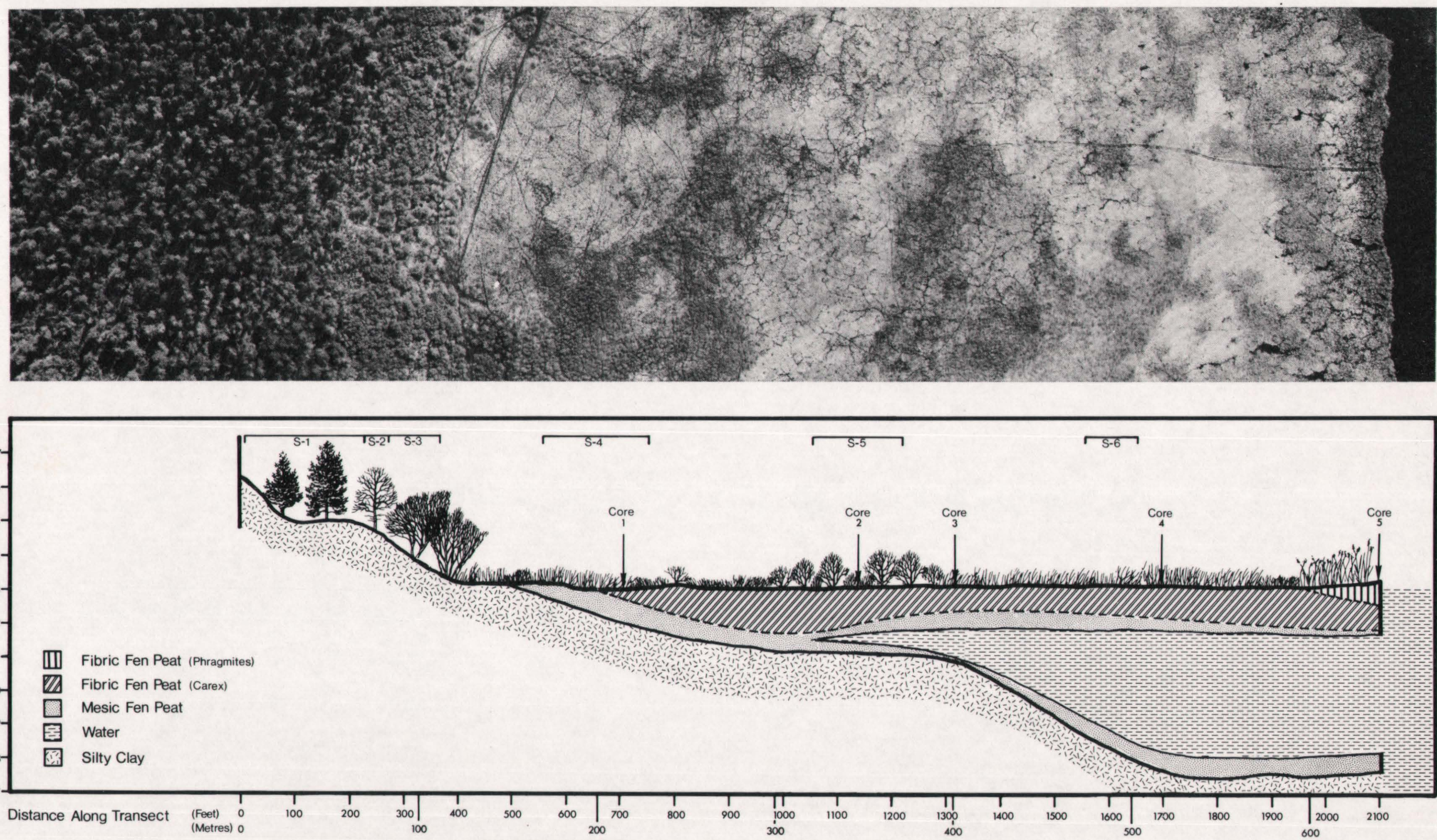

Fig. 23. Airphoto mosaic and profile diagram of Transect 1, showing the location of vegetation stands, examined peat cores, and the composition of the organic and mineral substrates.

least decomposed (and probably youngest) peats occur near the outer edge of the transect and that, for a given depth, decomposition increases toward the levee.

The fibric and mesic peat layers predominantly consist of Carex remnants with admixtures of Equisetum, hypnic mosses, and woody materials. The spatial distribution of dead culms and rhizomes of Phragmites communis is interesting. The present distribution of the species in the study block is generally in bands of varying width along the outer edge of the floating mat. It rarely occurs further landward. However, within the fibric fen peat deposits, Phragmites remnants occur on the surface at the outer edge of the mat but, for some distance landward, are found at lower levels of the organic mat, mixed with other fen plants.

7.4.2 Stratigraphy of closed basin peat deposits

Three cores were examined along Transect 9: Core 16 in the vicinity of the levee of an old stream channel near the south shore of Cut Beaver Lake, Core 17 approximately midway, and Core 18 in the raised black spruce stand in the centre of the backswamp (Fig. 24 and Appendix E).

The transect surface is lowest at the edge of the basin, it rises gradually toward the centrally located black spruce community (Stand 43). The organic layer is much deeper than in open basin locations, ranging from 120 cm near the edge to 315 cm at the centre of the basin.

Fibric peat of fen origin predominates beneath the bog birch and low willow community (Stand 67) near the levee, whereas about 240 cm of fibric peat of Sphagnum origin occurs beneath the raised black

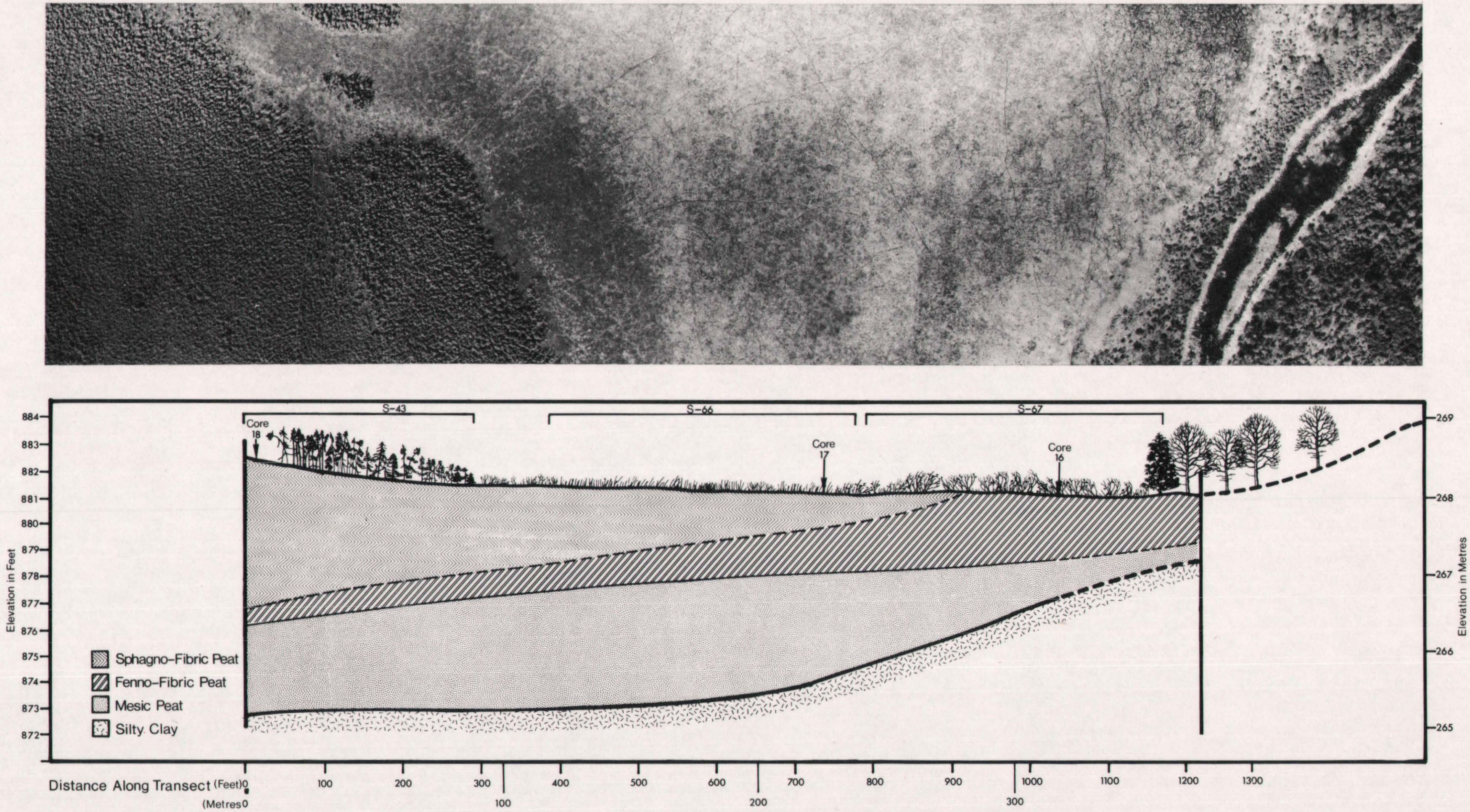

Fig. 24. Airphoto mosaic and profile diagram of Transect 9, showing the location of vegetation stands, examined peat cores, and the composition of the organic and mineral substrates.

spruce community. Examination of individual core sections showed the peat near the surface to consist of raw Sphagnum and, with increasing depth, to very gradually decrease in fiber content. In the middle section of the transect, under the ericaceous shrub community of Stand 66, the Sphagnum layer is much shallower, and at the surface consists of a mixture of poorly decomposed Carex, Eriophorum, and Sphagnum (mainly Sphagnum recurvum). Woody fossils, including Picea mariana and Larix laricina twigs and needles are frequent within the sphagno-fibric layer.

The botanical origin of the underlying mesic peat layer was difficult to ascertain but it appeared to consist of layered mictures of fen plants, hypnic and sphagnic mosses, and silt. Immediately above the clay base, a thin deposit of unidentifiable humic peat - possibly of aquatic origin - was evident.

This stratigraphy suggests that the process which led to the present character of this landscape facet was one of basin-filling in which aquatic vegetation gave way to fen vegetation, and, finally to Sphagnum mosses.

Repeated flooding and silt deposition was of importance during the early stages of development. The water-table within the deepening peat layer apparently showed several long-term fluctuations which resulted in transformations between fen and Sphagnum growth (Kulczynski 1949).

Eventually, however, the peat surface lost contact with the terrestical water supply and developed into a continental raised bog (sensu Kulczynski 1949). It appears, however, that, as a result of an artificially induced, raised water-table during the past 30 years, a retrogression to fen conditions has occurred at the edges of the

Sphagnum bog, viz., the portion of Transect 9 now occupied by ericaceous shrub (Stand 66). It is thought that the existence of a frost layer within the *Sphagnum* peat throughout the growing season (Section 7.3) is instrumental in maintaining the ombrotophic character of the central black spruce bog (Stand 43).

8. VEGETATION IN THE LANDSCAPE

To complete the ecological account of the vegetation, an attempt was made to integrate the vegetation and site relationships, as analyzed and described in Sections 5-7, at the landscape level.

Vegetation zonations in the study area, in the broad view, reflect moisture regime gradients. For example, along spatial transects extending from alluvial levees to open lake water, the typical zonation - from (1) mixed forest through (2) willow shrub and anchored sedge fen, to (3) floating mat and aquatic communities - clearly relates to increasing wetness. However, this increase in moisture availability is paralleled by a decline in nutrient availability away from the levees, as rooting in the mineral substrate is prevented through peat accumulation. This nutrient gradient is particularly apparent in closed basins with impeded drainage where the vegetation zonations reflect the fact that the margins receive some nutrients from the surrounding levees and the centres, far removed from that effect, are very nutrient-poor. Consequently, ombrophilous species such as *Sphagnum recurvum*, *Sphagnum magellanicum*, and *Sphagnum fuscum* are able to invade these peat surfaces. Hummock-building by these mosses further removes the peat surface from the influence of mineral soil water, and creates the present nutrient-poor, ombrotrophic character of those sites.

It is thus evident that nutrient status and the type and degree of peat accumulation are both dependent on landform and water circulation or drainage patterns, as has been previously demonstrated by Kulczynski 1948, Heinselman 1963, Bellamy 1966, 1969, and others.

The dynamics of vegetation/environment relationships in the landscape of the Cumberland Marshes may be conveniently portrayed through the following three main physiographic divisions, encompassing landform and water circulation:

(1) drained alluvial levees,

(2) open drainage basins, and

(3) closed drainage basins.

The preceding analysis (Sections 5-7) has provided the basis for classifying the vegetational and environmental spectrum into a total of nine ecologically significant vegetation/site categories (Table 15) within these physiographic divisions. These vegetation/site categories also correspond with the landscape units of the final association analysis and, to some extent, with mapping units of the reconnaissance vegetation map (Table 15).

8.1 Drained alluvial levees

The levees along the rivers and streams of the Cumberland Marshes have, in most places, been built up sufficiently high above the flood plain that they are only rarely subject to flooding and thus are generally well drained. Furthermore, they are little affected by water level fluctuations in the adjacent marshes (see Section 7.2). The forests on these levees are quite variable in terms of overstory composition (as pointed out in Section 5.3.5), but this diversity mainly stems from past disturbance rather than from pronounced site differences. A gradient of relative site maturity, however, underlies the variation in forest composition since older, more mature sites tend to possess lower pH and soil nutrient levels than younger sites (see

Table 15. Main physiographic divisions, vegetation/site categories, and correspondence with landscape units and the reconnaissance vegetation map.

Main physiographic divisions	Vegetation/site categories (according to final association analysis, principal component analyses, and peat core analysis	Correspondence with landscape units according to final association analysis	Approximate correspondence with units of the preliminary vegetation map
1. Drained alluvial levees	Levee forests	Stream levee (V)	White Spruce-Hardwoods Forest
	Tall shrub communities on levee deposits		Tall Willow-Alder Shrub
2. Open drainage basins	Emergent and submergent aquatic communities of lakes	Aquatic (II)	Bulrush Swamp
			Water-lily Pad
			Water-lily-Bulrush Mixture
	Fen communities on shallow anchored root mats of open basins	Fen (III)	Medium Willow Shrub
			Broadleaved Sedge-Reedgrass Meadow
	Fen communities on floating mat of open basin lakes		Low Willow Shrub
			Broadleaved Sedge-Reedgrass Meadow
			Narrowleaved Sedge-Cattail Meadow
			Phragmites Swamp

. . . cont'd

Table 15 concluded.

Mean physiographic divisions	Vegetation/site categories (according to final association analysis, principal component analyses, and peat core analysis	Correspondence with landscape units according to final association analysis	Approximate correspondence with units of the preliminary vegetation map
3. Closed drainage basins	Fen communities on deep peat deposits of closed basins		Narrowleaved Sedge-Cattail Meadow Bogbirch Shrub
	Black spruce and larch communities on deep peat deposits of closed basins	Wooded Fen (IV)	Black Spruce-Tamarack Forest
	Black spruce communities on deep *Sphagnum* peat of closed basins	Bog (I)	Black Spruce-Tamarack Forest
	Ericaceous shrub-bogbirch communities on deep fen *Sphagnum* peat		Bogbirch Shrub

Section 6.5.1). This process of podzolic soil development will probably accelerate as a consequence of the upstream Gardiner and Squaw Rapids hydro-electric dams which will eliminate further flood-deposition of alluvium on all but the lowest (and youngest) levee sites.

Tall willow and alder shrub communities are typical cover on lower and wetter levee sites; they grade into the fen vegetation of the contiguous lake and marsh basins.

8.2 Open drainage basins

Water circulating through shallow lakes and marshes, interconnected by natural and artificial channels, is derived from local runoff, augmented (since about 1940) by nutrient-rich waters from the Saskatchewan River (see Section 3). Thus minerotrophic conditions prevail throughout the open drainage basin system and water levels have been raised through this modified water regime.

The constant, slow movement of water through the system and the seasonal fluctuations in the lake levels have created conditions favouring the accumulation of shallow deposits of poorly-decomposed fen peat (see Fig. 23, p. 145) which rests on the gently sloping clay bottom in the topographically higher locations near the levees, but has become buoyed up in the lower, lakeward positions.

In response to this landform and water circulation pattern, the typical vegetation zonation that has developed consists, near the levees, of willow shrub that gradually declines in stature with increasing peat depth away from the levees. Beyond this shrub zone exists a band of, generally shrubless, fen meadows on shallow firm root mats that are usually inundated during the early part of the growing season, owing to the presence of frost within the peat layer (see Section 7.2), retarding drainage toward the lake. Carex atherodes reaches its greatest abundance in these wet, minerotrophic sites, forming almost pure stands and growing to a height of 130 cm (Plate 14, p. 195).

The third zone consists of buoyant root mats, ranging from 100 to 3,000 m in width, which float up and down with the fluctuating lake levels and thus possess a relatively unchanging moisture regime. While the herbaceous cover on floating mats consists mainly of the same species as those characterizing the anchored fen peat deposits, emergents such as Sparganium eurycarpum, Typha latifolia, and Acorus calamus are abundant in locations where there are breaks in the mat, whereas low willow shrub occurs in locations where the mat is apparently thicker.

It is not evident to what extent, the variable composition of the floating mat vegetation stems from minute differences in habitat conditions or from the vagaries of historical events. It is apparent that some species can survive for indefinite periods under environmental conditions which would totally preclude their establishment. For instance, vast stands of Salix petiolaris are still alive in the eastern part of the Cumberland Marshes after having been constantly immersed for seven years in 1 m of water, through impoundment by the Ducks Unlimited Dam (Fig. 1, p. 11). Apparently the Phragmites communis communities at the outer edge of the floating mats originated as emergent clones growing into shallow water or wet mudflats at the edge of the lakes, prior to the artificial increase in water levels from about 1940 on, and have since remained in a more or less static condition. The fact that buried layers of Phragmites culms and rhizomes occur below the sedge peat further landward (see Section 7.4.1) suggests Phragmites as the pioneer in the formation of the fen peat deposits in open basin lakes, and its seral replacement by sedges as the main peat-forming plants.

Experimental research, beyond the scope of this study, would be required to reach a definite understanding of the mechanisms by which the extensive floating mats have originated and are maintained.

8.3 Closed drainage basins

Numerous depressional locations, more or less completely surrounded by raised levees of flowing or cut-off stream channels, occur within the flood plain complex of the Cumberland Marshes. Drainage is strongly impeded and the source of water for these closed basins is runoff from the surrounding levees and from within the basins themselves. In terms of the classes of hydrotopography used by Swedish scientists (Sjörs 1948) these are "topogenous sites", i.e., they possess immobile horizontal mineral soil water surfaces. Since few of the basins are totally separated from adjacent marshes and streams, probably some slight exchange of ground water occurs in most cases.

These physiographic conditions have led to the gradual accumulation of deep peat deposits, apparently through the process of basin-filling, involving a succession of aquatic and marsh plants, and a concomitant rise in the water-table - possibly caused by building-up of the encircling levees through silt deposition during floods. Growth of Sphagnum mosses over the fen peat deposits occurred in some of the closed basins when the peat surface lost contact with the mineral soil water - perhaps during a prolonged drought cycle. The ensuing ombrotrophic conditions favoured the development of the black spruce bog islands within the larger closed drainage basins (e.g., Fig. 24, p. 147).

The present vegetation zonation in a typical closed drainage basin consists of a narrow band of shrub and sedge fen immediately adjacent to the levees, whereas the major portion of the basin is covered by dense, low *Betula glandulifera* and *Salix candida* shrub over a field layer dominated by *Carex lanuginosa*. These species, although present in other communities as well, reach their greatest prevalence in these sites, which the principal component analysis has shown to be characterized by relatively low pH values. Where *Sphagnum* moss has accumulated above the fen peat deposits, there are now stands of stunted black spruce with an understory of ericaceous shrubs and bog plants, such as *Drosera rotundifolia* and *Sarracenia purpurea*. Temperature measurements in these stands (Section 7.3) have suggested that cold temperatures within the shallow rooting zone of those bogs, and the presence of frost until early September may be important factors in storing rain and melt water for plant growth, but also in preventing the somewhat richer soil waters of the surrounding deep peat fen from coming into contact with the bog plants. Persistent soil frost may, therefore, have been important in maintaining the ombrotrophic character of these bog islands despite higher water-tables throughout the Cumberland Marshes during the past 30 years.

9. DISCUSSION

9.1 On methods and results of the study

The purpose of this study was to answer questions about the nature and interrelationships of major components of the landscape of the Cumberland Marshes, particularly the structure and composition of the vegetation, the character of the physical sites in which extensive vegetation types occur, the principal environmental gradients that control species distribution, and the processes that have developed the present landscape. Because of the complexity of the natural systems studied, reproduction, in the abstract, of the structure and function of particular landscape components necessarily entailed considerable oversimplification.

It is believed that because of prior extensive ground checks, interpretation of aerial photographs, and reconnaissance vegetation mapping, the selected study locations have encompassed the spectrum of vegetation and site types in the area reasonably well. But because the study locations were selected subjectively, the results, in a strict sense, apply only to the set of data on hand. It is, therefore, quite possible that an increased sample size would have led to the discovery of additional community-types and in changes in the ranking of some species. But it is unlikely that the deduced vegetation/environment relationships would have been significantly affected.

Species-presence lists were employed in the initial vegetation analysis because the total species complement of a stand reflects the sum-total of recent environmental influences to a greater extent than categories based on dominants. This was considered particularly important in the area studied, where the woody vegetation is probably still adjusting to a modified water regime. This use of species-presence lists in the association analysis proved reasonably successful as a means of classifying stand-samples into groups with affinities for distinct positions in the landscape.

Some fault can, however, be found in the direct use, in the principal component analysis, of frequency data as quantitative measurements for ground stratum species. Walker (1968) and, very recently, Swan (1970) have pointed out that frequency data (or any other quantitative vegetation measurements) are of a truncated nature, i.e., they provide estimates of the degree of presence of a species, but regard all zero values as absolute. In other words, zero values do not indicate the degree of absence of species or, conversely, their likelihood of being present. The large number of zeros in each of the correlation matrices, therefore, possibly may have distorted the true degree of similarity between stands. This fact may account for the prevalence of low factor loadings in the principal component analyses, and thus for some of the difficulties encountered in attempting to recognize environmental gradients governing vegetational variation.

Both the association analysis and the principal component analysis were made credible as analytical tools by the fact that their results showed considerable correspondence. The differences that did occur are thought to stem from two influences: (1) inherent weaknesses in the techniques such as the problem of misplaced stands in the association analysis (see Section 5.2.1) and the truncated frequency data in the principal component analysis; and (2) the built-in indeterminacy of vegetation, i.e., widely differing ecological amplitudes of species and historical events - such as the effects of past disturbance - affecting present plant distribution.

The monothetic-divisive "DIVINF" program (Lance and Williams 1968) - previously used with success by Walker (1968) - has been shown to be a stable tool for the classification of the vegetation spectrum dealt with in this study, as the hierarchy established by the preliminary analysis (Section 5.2) remained "stable with the addition of new information" (Lambert and Williams 1966) in the final analysis (Section 5.3). Contrary to Walker (1968), the abundance of major species was not found to be a sound criterion to judge the ecological value of divisions of the association hierarchy. For instance, Groups C and D of the final association analysis, which were divided on presence and absence of Sparganium eurycarpum, shared the same prevalent species but occupied distinctly different physiographic positions in the landscape, viz., shallow, anchored fen peat deposits and floating mats, respectively. Less abundant species thus are often better indicators of environmental characteristics than those species which are abundant through much of the vegetation spectrum and which, therefore, must possess wide tolerances for the range of environmental gradients present.

The application of principal component analysis to three of the five landscape units that had been distinguished in the course of the association analysis, viz., bogs, fens, and alluvial stream levees, showed moisture regime, nutrient status, and pH to be the most significant gradients controlling distribution of species and communities. The interactions of these factors with each other and with such physical characteristics as nature and depth of the substrate, soil frost, and water circulation, have been brought out by the principal component analysis.

The contention of some Scandinavian and Canadian forest ecologists (e.g., Cajander 1909, Kalela 1954, Linteau 1955, Rowe 1956a) that the composition and structure of undergrowth vegetation can be used as site indicators has been corroborated by the principal component analysis of wooded stream levee vegetation (Landscape Unit V) through correspondence between ordinations based on (1) ground stratum species and (2) relative site maturity.

Quantitative measurement of attributes of the physical environment that control plant distribution is always difficult since the investigator is forced to select, from a vast number of parameters that could be measured, those which he, a priori, considers of significance. Reference to the findings of other studies is of value in selecting specific attributes for inclusion in the sampling program, but there is an inherent danger of disregarding environmental factors that are of primary importance in the particular systems studied. It is, furthermore, not always certain that determinations, such as nutrient-ion content of soil or water samples, truly reflect availability to the plants. Therefore, measured ranges of environmental attributes can, at best, be considered as relative indicators of site characteristics.

The best characterization of physical sites in this study resulted from the recognition of categories according to landform and drainage patterns, since the gradients of moisture and nutrient status and pH, which have been found to interact in producing the existing vegetational variation, are all dynamically dependent on those features of the landscape. Many other environmental factors, such as type and degree of peat accumulation and soil frost phenomena, are similarly related to, and may be fully understood only, in reference to physiographic features of the landscape.

In consequence, considerably more ecologically significant information can be obtained from reconnaissance maps which in addition to the chorology of the vegetation also include notations on landform and drainage patterns, and other apparent features of the landscape.

9.2 On similarity and contrast with the vegetation of neighbouring areas

The vegetation of the Cumberland Marshes is, in general appearance, quite similar to the lowland vegetation described for other parts of the southern boreal forest of western Canada. For instance, papers by Moss (1953a, 1953b, 1955) describe many communities for northwestern Alberta which closely resemble the fen, bog, and moist forest communities dealt with in this study. Jeglum's (1968) vegetation classification for the Candle Lake area of Saskatchewan, approximately 200 km west of Cumberland House, contains a number of dominance types that occurred in the present study as well. For instance, his Broad-leaved Sedge Fen group is identical with the Broadleaved Sedge-Reedgrass Meadow category of the reconnaissance vegetation map that accompanies this report, in which _Carex atherodes_, _Carex rostrata_, _Carex aquatilis_, and _Calamagrostis_ spp. predominate. Jeglum's _Populus balsamifera_ (I-34) and _Picea glauca_ (I-35) Moist Forest dominance-types are quite similar in composition to the balsam poplar and white spruce-dominated communities described in this study. However, it appears that the flora in the Cumberland House area is richer in species, as indicated by the occurrence of 14 tree species (Dirschl and Dabbs 1969), whereas only eight trees were found at Candle Lake.

The black spruce bogs of this study (Group A of the final association analysis) closely resemble the *Picea mariana-Ledum groenlandicum-Sphagnum fuscum* dominance-type (H-31) of Jeglum's classification, but bogs dominated by *Pinus banksiana* were not discovered in the Cumberland Marshes. There is, however, a major difference in the respective position of these bog communities in the landscape. In the level topography of the Saskatchewan River Delta, bogs occur in the form of black spruce islands (cf. Sjörs 1963) within deep peat deposits of undrained interior basins, a position also recorded for peatlands in Minnesota by Heinselman (1963). In the topographically steeper Candle Lake area, on the other hand, Treed Bog is typically positioned as sloping terraces between fen drainageways and the upland.

Other differences related to (1) the generally more minerotrophic conditions in the Cumberland Marshes and (2) the much more widespread occurrence of floating mats. Thus, much of the floating mats in the Cumberland Marshes is covered with fens, in which *Carex atherodes*, *Carex rostrata*, and *Carex aquatilis* are prevalent. Jeglum (1968) found these species to be common only in firm root mats.

Another point of contrast is the occurrence of *Phragmites communis* which at Candle Lake apparently occurs only as an emergent in shallow, protected waters of lakes, ponds, and sluggish streams, whereas in the Cumberland Marshes it is mainly found in the form of floating root mats. Artificially maintained high lake levels in the Cumberland Marshes probably account for this difference since emergent *Phragmites communis* is eliminated by deep immersion over a number of years (Walker 1965). The thick mats formed by the undecomposed culms and rhizomes of dense clumps of *Phragmites* are thought to have become separated from the mineral bottom and buoyed up when water levels rose. Formation of buoyant mats ("plaurs") of Phragmites communis, in this manner, has been described for lakes and bays on the Baltic coast of Sweden by Björk (1967).

Many of the wetland species encountered in this and Jeglum's studies in the southern boreal forest were also found to be common in wetlands of the aspen grove and grassland zones of Saskatchewan by B. Walker (1968) and in the Delta Marsh on the south shore of Lake Manitoba by J. Walker (1965), attesting to the general unity of the flora of the region. However, some striking differences in species-abundance are apparent. For instance, the grass Scolochloa festucacea which occurred sparsely in only two of the stands sampled in this study, and in only a few of Jeglum's sampling locations, is much more prevalent farther south. In the Delta Marsh, it was found to be of prime importance in the re-colonization of bare mudflats that had been exposed by falling water levels, and in prairie sloughs it is a leading dominant of moderately saline, shallow marsh habitats, particularly where mowing has taken place.

The remarkably wide ecological amplitude of Carex atherodes, determined in the present analysis, has been previously noted by a number of workers. Moss (1953b) observed this species to be a leading dominant throughout the reedswamp-marsh-wet meadow-low grassland sere in northwestern Alberta. At Delta Marsh, it was also found to be widespread, particularly where water was above the soil surface for part of the growing season. B. Walker (1968) considered it the most prevalent wetland species within the aspen grove and grassland regions of Saskatchewan, while at Candle Lake, it formed a leading dominant on non-floating root mats, but was also common in floating mat communities and shrub fens. In the present study, C. atherodes was found prevalent on shallow, anchored fen peat, forming luxuriant, almost pure stands in locations where spring-flooding commonly occurred; it was also widespread in floating mat and shrub fen communities.

Natural vegetation changes in lowlands of the southern boreal forest appear to be unidirectional (except where man-made interference has taken place) and to proceed at a much slower rate than in wetlands of the aspen grove and grassland region, where the vegetation undergoes rapid, cyclic changes in response to more variable moisture supplies.

9.3 On contribution of the study and future research needs

The findings of this study have added to the limited knowledge of the ecology of northern deltas and wetlands: understanding urgently needed to predict and evaluate the effects on those wetlands of ongoing and impending large-scale engineering projects. The construction of hydro-electric power dams on major rivers is altering the natural, seasonal regime of high and low flows with which those wetlands are in equilibrium. For example, the recent W. A. C. Bennett Dam on the Peace River has brought about greatly lowered water levels in Lake Athabasca and the contiguous Peace-Athabasca Delta, producing widespread adjustment in the vegetation and having detrimental effects on fish and wildlife populations (Dirschl 1970, Peace-Athabasca Delta Committee 1970). A number of similar dams are in the planning or construction stages.

Even more severe ecological effects can be foreseen from the implementations of a variety of engineering schemes, involving the southward diversion of water from the Mackenzie and Saskatchewan-Nelson drainage basins which have been proposed or are being investigated (see Quinn 1970).

In addition to the scientific interest which the northern deltas and wetlands deserve as unique ecosystems, the utilization of their fish and wildlife resources has been the traditional economic base for the native peoples of the north. Lack of ecological understanding and short-sighted land use policies can easily destroy these resources, as well as the potential value of these environments as recreational areas for the Canadian people who are becoming rapidly aware of the need for preservation of natural environments.

It is, therefore, important that ecological inventory and mapping be extended to all major deltas and other wetland areas within the Mackenzie and the Saskatchewan-Nelson drainage basins so that, as an integral part of the planning for hydro-engineering projects, the ecological implications can be weighed against the direct economic benefits.

Other research needs that have become apparent as a result of this study are: (1) research to determine the primary productivity of major wetland communities and of the pathways and rates of energy and nutrient transfer within these ecosystems, (2) detailed chronological investigations, through techniques such as radioactive carbon-dating, in order to determine the rates at which peat-forming processes occur, and (3) experimental water manipulations in representative wetlands in order to verify vegetation/environment relationships that have been empirically deduced in this and other ecological studies.

10. SUMMARY

The Cumberland Marshes, a portion of the Saskatchewan River Delta situated in east-central Saskatchewan, consist of approximately 2,760 square kilometers (1,070 square miles) of shallow lakes, fens, bogs, and meandering streams with raised levee banks covered by shrub and moist forest vegetation. Water regime and vegetation have been slightly modified through forest and wildlife utilization schemes, but the area has, in the main, been preserved as a natural ecosystem. No previous research into the landscape ecology of the Cumberland Marshes has been undertaken.

This study attempted an initial ordering of the present landscape pattern and sought to identify past and ongoing developmental processes. Its specific objectives were to describe the more extensive vegetation types, to characterize the sites in which they occur, to identify the principal environmental gradients that control the vegetation pattern, and to investigate developmental processes through analysis of peat cores.

To achieve an overview of the landscape of the Cumberland Marshes and of the distribution of its major components, a reconnaissance vegetation map of the entire area was prepared through interpretation of aerial photographs, employing a physiognomic-floristic classification based on 190 ground checks. Subsequently a representative block of 660 km^2 (255 square miles) was selected for detailed field study.

Nine field-transects, extending across typical vegetation and physiographic zonations, were established and permanently marked. Elevational profiles of the ground surface were surveyed during the

winter. Thirty-seven homogeneous stands of vegetation were selected for sampling along these transects; another 61 stands were chosen elsewhere in the study block so as to include all common vegetation types in the sampling program.

Quantitative data were collected for herbs, low and tall shrubs, and trees in all 98 stands. Frequency of occurrence of herbaceous ground stratum species was recorded in 30 or 40 quadrats, 0.5 x 0.5 m in size and distributed systematically over the area of each stand. Woody strata were sampled with the point-centre quarter method. Tree and shrub diameters, and average height of major species were also recorded. Subsequently, number of individuals per hectare, stocking rate, relative density, and relative dominance were computed from the measurements. A species-presence list was also compiled for each stand.

Environmental observations and measurements included: (1) biweekly recording of lake water levels and of soil temperatures and water-table depths in several locations along the field-transects during three consecutive growing seasons, (2) determination of conductivity and pH of soil samples, and (3) analysis of major ions in soil water and soil samples.

Initial classification of the vegetation data was carried out through the technique of association analysis, employing a monothetic-divisive program that had been previously used for the analysis of wetland vegetation in Saskatchewan. It resulted in 10 terminal groups that were considered to fall into five broad categories, termed Landscape Units:

I	Bog	IV	Wooded fen
II	Aquatic	V	Alluvial levee
III	Fen		

Lists of major species of the ground stratum, and of associated species of the woody strata were compiled for all groups; group-averages for the environmental attributes were also computed. Examination of the hierarchy of divisions, and the environmental features associated with the terminal groups, suggested that the environmental gradients most instrumental in controlling vegetational variation are moisture regime and nutrient status, whereas disturbance plays a subsidiary role within the complex vegetation of the alluvial stream levees. The groups show considerable floristic intergradation, particularly those within the fens of Landscape Unit III and the wooded levees of Landscape Unit V. Floristic composition is much more dissimilar when groups from different landscape units are compared. Physiognomic and structural characteristics produce a visual heterogeneity of the vegetation within most groups that is not always reflected in the environment.

The association analysis technique proved valuable in this study as a means of classifying the total vegetational variation into groups of stands which, although still fairly heterogeneous, are correlated with certain physiographic positions in the landscape. At lower levels of vegetational variation, the divisive technique used was not as satisfactory and provided little information from which hypotheses about causal factors could be derived.

Ordination techniques, including principal component analysis, have been previously found useful in detecting underlying causal environmental gradients when the total range of those gradients is limited. Principal component analysis of a correlation matrix - derived from frequency data of the ground stratum vegetation - was carried out with the stand-samples of Landscape Unit I (bogs), Landscape Unit III (fens), and Landscape Unit V (alluvial stream levees). Both Q-type analyses (stand ordinations) and R-type analyses (ordinations of species and selected environmental attributes) were undertaken. To facilitate visual examination, environmental data were transformed to relative values and superimposed (as circles of different diameters) on the stand positions plotted from the factor loadings on the first three extracted components.

For the nine stands of bog vegetation, it was concluded that variation in the vegetation is primarily determined by a complex gradient of "relative ombrotrophy" as reflected by accumulation of Sphagnum moss, increase in water-holding capacity and organic matter content, and by decreasing pH values and nutrient content.

The principal component analysis of the 46 stands of fen vegetation also suggested pH and nutrient status of the hydro-edaphic complex as the major gradients affecting composition and distribution of community-types and major species. Differences in moisture status appeared to be of lesser importance in affecting vegetational variation in this generally moisture-saturated environment.

From the analysis of the 30 moist forest and tall shrub stands on alluvial levees it was concluded that the main environmental gradients, affecting composition of the understory, are moisture availability, nutrient status and, to a lesser extent, soil pH. An inverse relationship between relative site maturity, and the relative values for pH and nutrient availability indicated that incipient podzolization of the alluvial-lacustrine soils primarily controls the composition of the understory of the forest and shrub communities of the stream levees. The composition of the overstory, however, has often been greatly modified by disturbance.

Periodic water-table measurements along transects showed a gradual drop from spring to fall in all locations. Frost within the peat layer often holds melt water on the surface of fen sites. Water-table changes within stream levees do not respond directly to fluctuations in the water levels of lakes and adjacent fens, probably because of the low permeability of the fine-textured alluvium.

Thin ice lenses at a depth of 30-45 cm persisted until early July in topogenous sites with dense shrub cover. In other fen sites, soil temperatures were above freezing by the end of May. In _Sphagnum_ peat, temperatures remained considerably lower throughout the growing season, and ice lenses were still encountered at 75 cm below surface in early September. Continuous frost until at least mid-July in the black spruce bogs is thought to prevent contact with the somewhat richer ground water of the surrounding deep peat fens during most of the growing season. Thus the low heat conductivity of the _Sphagnum_ moss may help to maintain the ombrotrophic character of the bogs.

Frozen peat cores were collected from five field-transects and macroscopically examined according to botanical origin, degree of decomposition, and colour. Diagrams of the stratigraphy of the transects were subsequently prepared.

Peat deposits of open basins with moving ground waters were less than 1.5 m deep and were derived from fen and aquatic vegetation. Floating mats consisted of poorly decomposed fen peat; denser, mesic peat occurred closer to the levees. For a given depth, decomposition increased toward the levee. _Phragmites communis_ is now nearly confined to the outer portion of the floating mat, but the occurrence of dead culms and rhizomes at lower levels of the fen peat layers suggests that the species has initiated the encroachment of the organic mat into the lake basins and has later been replaced by sedges and other fen plants.

The stratigraphy of a representative transect across part of a closed basin with impeded drainage, showed much deeper peat, ranging to 315 cm in the centre of the basin. Fibric fen peat occurred at the edge of the basin while the centre was occupied by 240 cm of raw Sphagnum moss, covered by a black spruce bog community. Mesic peat, consisting of layered mixtures of fen plants, hypnic and sphagnic mosses, and silt occurred nearer the bottom. Immediately above the clay base, a thin layer of unidentifiable humic peat - possibly of aquatic origin - was evident.

Spatial and dynamic relationships of vegetation pattern and environment in the Cumberland Marshes were portrayed by means of three broad physiographic divisions, encompassing landform and drainage pattern: (1) drained alluvial levees, (2) open drainage basins, and (3) closed drainage basins. Vegetation/site types, recognized through the use of association and principal component analyses, that are typical for each of these physiographic divisions were described.

Most of the vegetation types, described for lowlands at Candle Lake in the southern boreal forest of Saskatchewan by Jeglum (1968) also occur in the Cumberland Marshes. There are, however, some pronounced differences in their respective position in the landscape, which are attributed to the extremely level topography of the Cumberland Marshes, and the more minerotrophic conditions caused by nutrient-rich waters from the Saskatchewan River flowing through the system. Similarities also exist with the wetland vegetation of the aspen grove and grassland zones to the south, signifying the essential unity of the region's flora. However, there are some striking differences in the abundance and local distribution of some major species. Natural vegetation changes in the lowlands of the southern boreal forest are mainly unidirectional and slow, whereas the vegetation of the aspen grove and grassland zones undergoes rapid, cyclic changes in response to a more variable moisture supply.

This study has contributed to the limited knowledge that exists about the ecology of northern deltas and wetlands. Such knowledge is urgently required in order to evaluate and predict the effects of proposed vast power dam and river diversion projects on major northern rivers, and to permit environmental implications to be considered along with direct economic benefits. Ecological inventory of major wetlands in the Mackenzie and Saskatchewan-Nelson river drainage basins is considered an urgent requirements, along with intensive research into primary productivity and chronology of wetland ecosystems, and experimental studies to test the empirical findings of this and other ecological studies of these wetlands.

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APPENDIX A. Example of the tables constructed for each of the end-groups in the preliminary association analysis. Environmental characterizations for each of the seven stands in the Disturbed Levee Group.

Environmental characteristics	Stand number 30	41	45	46	47	48	49	Average
Physiognomy	Mature mixed forest	Mature mixed forest	Aspen regeneration	Tall willow shrub	Aspen regeneration	Open mixed forest	Tall willow shrub	Mixed forest or regeneration following disturbance
Disturbance	Selective logging	--	Fire	Fire	Fire	Selective logging	Fire	Fire or logging
Site	Levee	Levee	Levee	Levee	Levee	Levee	Levee	Levee
Substrate	Duff / SiC*	Duff / VSCL**	Duff / SiC	Duff / SiC	Duff / SiC	Duff / SiC	Duff / SiC	Duff / SiC
Conductivity (mmhos/cm)	1.0	1.0	1.1	1.4	1.7	1.2	1.9	1.3
pH	7.5	7.0	7.5	7.3	6.7	7.0	7.5	7.2

*Silty clay.

**Very fine sandy clay loam.

APPENDIX B. Example of the procedure used in extracting prevalent species for each end-group in the final association analysis: ground stratum of 11 stands in Group E.

Species	Percent frequency Stand No. 19	27	34	35	36	37	38	39	40	88	89	No.	%	Sum of freq.	Mean freq. in stands present	Presence class	Abundance class
Abies balsamea											3	1	9	3	3	I	1
Acorus calamus		3					3					2	18	6	3	I	1
Agastache foeniculum							3					1	9	3	3	I	1
Agrostis scabra			8	10					13			3	27	31	10	II	1
Alnus rugosa var. americana							38					1	9	38	38	I	2
Aster							8	15	13			3	27	36	12	II	1
Betula glandulifera	5	78	43	30	85		75	80	83	1	43	10	91	523	52	V	3
Calamagrostis canadensis-inexpansa-neglecta	90	33	80	25	25	38	40	23	15	13		10	91	382	38	V	2
Caltha palustris					5		3	3				3	27	11	4	II	1
Campanula aparinoides	15	8	48	70	3	78	10	95	37	13		10	91	377	38	V	2
Carex atherodes	100	90	3	3	33		55	25	80		3	9	82	362	40	V	2
Carex aquatilis	38	25	43	18	30	98	53	43	55	50	90	11	100	543	49	V	3
Carex disperma							3					1	9	3	3	I	1
Carex lanuginosa	25	8	90	93	98	85	13	90	100	73	50	11	100	725	66	V	4
Carex limosa										40		1	9	40	40	I	2
Carex rostrata	40	35	1	35	8	13	55	30	18			9	82	235	26	V	2
Cornus stolonifera							3					1	9	3	3	I	1
Equisetum arvense							38					1	9	38	38	I	2
Equisetum fluviatile	58	3	93	3		3					93	6	55	253	42	III	3
Equisetum pratense		73					80	90	95			4	36	338	84	II	5
Fragaria virginiana							40	5				2	18	45	23	I	2
Galium labradoricum-trifidum	25	70	53	58	5	63		93	63	70	30	10	91	530	53	V	3
Impatiens capensis				10		28	3					3	27	41	14	II	1

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APPENDIX B concluded.

Species	Percent frequency Stand No. 19	27	34	35	36	37	38	39	40	88	89	No.	%	Sum of freq.	Mean freq. in stands present	Presence class	Abundance class
Menyanthes trifoliata			15	93	25			98	3	97	77	7	64	408	58	IV	3
Myrica gale			10	8	100	8	100		100			6	55	326	54	III	3
Naumburgia thyrsiflora	73	43	78	18	15	85	3	35	18	10	13	11	100	391	36	V	2
Oxycoccus quadripetalus				15	15							2	18	30	15	I	1
Petasites palmatus							20					1	9	20	20	I	1
Petasites sagittatus										1		1	9	1	1	I	1
Potamogeton natans						3						1	9	3	3	I	1
Potentilla fruticosa							3					1	9	3	3	I	1
Potentilla palustris	28	90	85	80	70	30	20	85	93	73	50	11	100	704	64	V	4
Ranunculus circinatus var. subrigidus										3	33	2	18	36	18	I	1
Rumex orbiculatus		3	10			5				10		4	36	28	7	II	1
Salix bebbiana	1											1	9	1	1	I	1
Salix candida	48	12	25	13	10	3	1	50	28	20	7	11	100	218	20	V	1
Salix discolor	10	5		3	13		23	15	1			7	64	70	10	IV	1
Salix pedicellaris	3	48	63	45	1	25		65	73	43	43	10	91	409	41	V	3
Salix petiolaris	1											1	9	1	1	I	1
Salix serissima	1						3	15	3			4	36	22	6	II	1
Scolochloa festucacea		23										1	9	23	23	I	2
Scutellaris galericulata	3	10				13						3	27	26	9	II	1
Sium suave				3				10	3			3	27	16	5	II	1
Smilacina stellata							10					1	9	10	10	I	1
Solidago			3				33	3				3	27	39	13	II	1
Stellaria longifolia						5		5				2	18	10	5	I	1
Triglochin maritima										13	1	2	18	14	7	I	1
Typha latifolia			13									1	9	13	13	I	1
Utricularia intermedia						28						1	9	28	28	I	2

APPENDIX C

Set of 17 photographic plates (Plates 10-26), illustrating typical community-types, described in the text, in oblique and horizontal view.

Plate 10. Black spruce (Picea mariana) community on deep Sphagnum peat, situated in an interior basin with impeded drainage (backswamp). Ground vegetation is dominated by Ledum groenlandicum and other ericaceous shrubs.

Plate 11. Ericaceous shrub community adjacent to a black spruce (Picea mariana) stand on deep Sphagnum peat. Predominant shrubs are Chamaedaphne calyculata, Andromeda polifolia, and Betula glandulifera.

Plate 12. Oblique view of Highbank Lake, showing the typical clonal distribution of Scirpus acutus and the dense cover of floating Nuphar variegatum leaves.

Plate 13. Willow shrub community on fen peat, dominated by <u>Salix discolor</u> and <u>Salix petiolaris</u>.

Plate 14. Fen meadow, dominated by Carex atherodes on a substrate of shallow fen peat, and situated adjacent to the alluvial levee of an abandoned stream.

Plate 15. Phragmites communis in the form of floating islands in Bloodsucker Lake.

Plate 16. Almost pure stand of Equisetum fluviatile on a floating mat of poorly decomposed fen peat.

Plate 17. Floating mat community, dominated by _Salix candida_, associated with various sedges and the emergent aquatics _Sparganium eurycarpum_ and _Typha latifolia_.

Plate 18. Low shrub community, dominated by Betula glandulifera and Salix candida, on deep fen peat of a closed basin. Prevalent in the field layer are the sedges, Carex lanuginosa, Carex aquatilis, Carex atherodes, and Carex rostrata.

Plate 19. Black spruce community on deep, mesic fen peat with an open ground stratum of Calamagrostis spp., Carex atherodes, and Equisetum fluviatile.

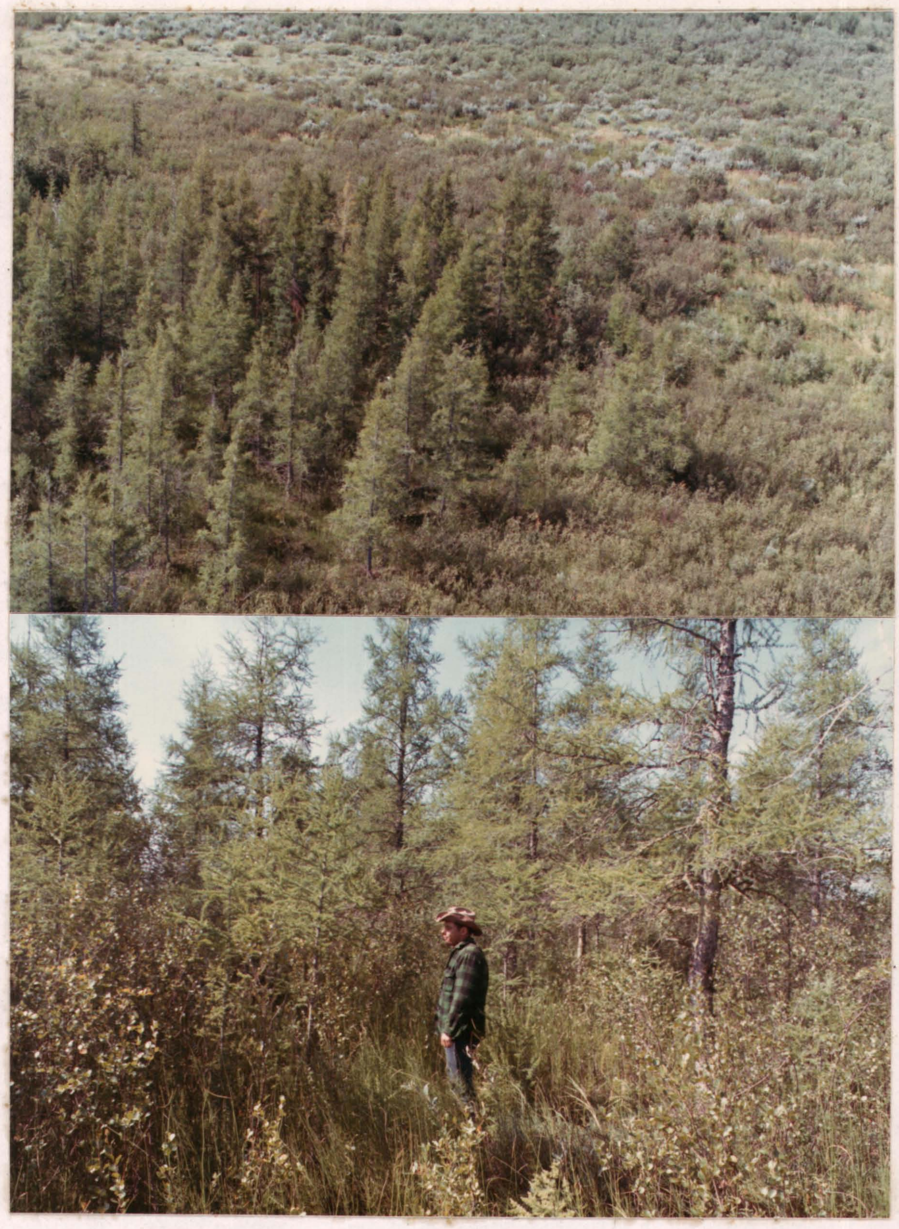

Plate 20. Larch (Larix laricina) community on deep, mesic fen peat with an understory of Calamagrostis spp., Carex spp., and Ledum groenlandicum and Betula glandulifera shrubs.

Plate 21. Tall shrub community, dominated by Salix discolor and Alnus rugosa, situated on a seasonally flooded, low stream levee.

Plate 22. Scattered balsam poplars (Populus balsamifera) on a seasonally flooded, low levee. The trees are dying as a result of artificially raised water levels and are being replaced by willow and alder shrubs.

Plate 23. Mature mixedwoods on the raised alluvial levee of the Saskatchewan River. White spruce (Picea glauca) and balsam poplar (Populus balsamifera) are the dominant trees. Associated are tall and low shrubs, and a species-rich field layer which nearly prevents white spruce regeneration.

Plate 24. Above: Pure stand of mature white spruce (Picea glauca) on sandy soil. Note the sparse understory vegetation.

Below: Pure stand of mature balsam poplar (Populus balsamifera) with a dense understory of various shrubs and herbs.

Plate 25. Fire-successional stand of aspen (Populus tremuloides) on the levee of an interior stream. Beneath the even-aged tree canopy exists a very dense stratum of low shrubs and herbs. There is little evidence of tree regeneration.

Plate 26. Overmature mixedwood community on the levee of the Saskatchewan River. Openings in the canopy, through death of old trees, are occupied by tall shrubs or be regeneration of Acer negundo and Fraxinus pennsylvanica var. subinterregima trees.

APPENDIX D. Ranking of the 30 stands of wooded stream levee vegetation (Landscape Unit V) according to apparent environmental maturity of site. Based on size and relative density of canopy-forming shrubs and trees.

				Tolerant to flooding							Intolerant to flooding				
Rank	Stand No.	Absolute density (Ind./ha)	Measurement	Salix discolor	Alnus rugosa	Salix bebbiana	Populus balsamifera	Fraxinus pennsylvanica	Acer negundo	Ulmus americana	Populus tremuloides	Betula papyrifera	Picea glauca	Abies balsamea	Remarks
			A*												
1	10	1420	B	75	25										
			A												
2	12	1579	B	61	36										
			A					<7.5							
3	14	687	B	65	33			2							
			A												
4	18	605	B	54	9	38									
			A				<7.5								
5	3	1426	B	65	16		2								
			A				<7.5								
6	31	1500	B	75		23	2								
			A												
7	21	472	B	50		48									
			A												
8	49	1550	B	47		53						tr			
			A												
9	47	2220	B	5		93									Fire damage evident.
			A				<7.5								Some over mature balsam
10	28	2143	B	7	44	42	6								poplars present.
			A				12.5								Immature balsam poplar
11	2	1148	B				100								stand.

* A = mean diameter at breast height of trees in cm.
B = relative density of individual trees or shrubs.

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APPENDIX D continued.

Rank	Stand No.	Absolute density (Ind./ha)	Measurement	Tolerant to flooding: Salix discolor	Alnus rugosa	Salix bebbiana	Populus balsamifera	Fraxinus pennsylvanica	Acer negundo	Ulmus americana	Intolerant to flooding: Populus tremuloides	Betula papyrifera	Picea glauca	Abies balsamea	Remarks
			A				13.4								Immature balsam
12	11	2561	B				100								poplar stand.
			A												
13	17	1161	B				100								
			A				33.8		10.0						
14	23	405	B				95		5						
			A				41.3		10.7						
15	86	1189	B				18		82						
			A				30.5		17.5	11.3			27.5		
16	15	455	B				80		5	10			5		
			A				11.8				12.1				
17	45	2789	B				26				74				Evidence of past fire.
			A				12.3				14.1				
18	68	2674	B				22				78				
			A				13.2				13.1				
19	46	1191	B				27				73				Evidence of past fire.
			A				32.0			15.0	15.0	42.5			
20	81	297	B				64			3	6	28			
			A				50.7		19.0	22.5					
21	84	768	B				48		48	5					
			A				60.0	14.2	17.8	30.6					
22	85	891	B				7	27	45	20					Balsam poplars are overmature
			A				30.6		15.0	19.9		17.2	32.0		
23	1	450	B				16		3	17		14	42		" " " "
			A				28.4					22.2	41.9		Selective logging for white
24	30	315	B				39					20	35	tr	spruce has taken place.

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APPENDIX D concluded.

				Tolerant to flooding							Intolerant to flooding				
Rank	Stand No.	Absolute density (Ind./ha)	Measurement	Salix discolor	Alnus rugosa	Salix bebbiana	Populus balsamifera	Fraxinus pennsylvanica	Acer negundo	Ulmus americana	Populus tremuloides	Betula papyrifera	Picea glauca	Abies balsamea	Remarks
			A								50.0	26.2	47.5		
25	80	270	B								5	85	10		
			A				30.0					15.0	27.5		
26	83	835	B				16					2	82		
			A				20.0		15.0				31.3		
27	82	455	B				11		2				86		
			A				29.0					15.0	62.5		
28	41	312	B				13					8	80		No evident disturbance.
			A									13.6	38.7		
29	16	297	B									13	87		" " "
			A									15.3	29.6	19.1	Overmature stand, light
30	48	418	B									27	50	23	cutting of white spruce.

APPENDIX E. Results of macroscopic peat core analyses.

E.1 Fiber content and color of peat core segments from open basin transects.

E.1.1 Transect 1

Depth (cm) below surface		Near levee → Core 1 UR[a]	Core 1 R[b]	Core 2 UR	Core 2 R	Core 3 UR	Core 3 R	Core 4 UR	Core 4 R	Core 5 UR	→ Near lake Core 5 R
0-15	A[c]	5/10	3/10	5/10	4/10	8/10	7/10	9/10	7/10	9/10	8/10
	B[d]	10YR2/2	10YR3/1	10YR2/2	10YR2/1	10YR3/1	10YR3/1	10YR3/2	10YR3/2	10YR4/2	10YR5/3
16-30	A	4/10	3/10	5/10	4/10	6/10	4/10	6/10	5/10	7/10	6/10
	B	10YR4/2	10YR3/2	10YR3/2	10YR3/2	10YR4/2	10YR3/2	10YR3/1	10YR3/2	10YR3/2	2.5YR3/2
31-45	A	3/10	3/10	Water		5/10	4/10	4/10	3/10	6/10	5/10
	B	10YR3/1	10YR3/1			10YR4/2	10YR4/1	10YR2/1	10YR2/1	10YR3/2	10YR3/4
46-60	A	Clay bottom		Clay bottom		Water		Water		Water	
	B										
61-90	A										
	B										
91-105						Clay bottom					
106-150											
121-135											
136-150											
151-170	A									2/10	<1/10
	B							Clay bottom		7.5YR4/0	7.5YR4/0
171-185										Clay bottom	

[a]Unrubbed peat sample (see Table 4, p. 52).

[b]Rubbed peat sample.

[c]Fiber content by volume.

[d]Munsell colour code.

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APPENDIX E continued.

E.1.2 Transect 2

Depth (cm) below surface		Near levee →									Near lake
		Core 10		Core 9		Core 8		Core 7		Core 6	
		UR[a]	R[b]	UR	R	UR	R	UR	R	UR	R
0-15	A	6/10	5/10	7/10	6/10	8/10	8/10	8/10	8/10	9/10	8/10
	B	10YR3/1	10YR3/1	10YR3/1	10YR3/2	10YR3/1	10YR3/2	10YR3/2	10YR3/1	10YR2/1	10YR3/1
16-30	A	5/10	5/10	6/10	6/10	8/10	7/10	8/10	7/10	7/10	6/10
		10YR3/4	10YR4/2	10YR3/2	10YR3/2	10YR3/2	10YR2/2	10YR3/2	10YR3/1	10YR3/2	10YR3/3
31-45	A	5/10	4/10	5/10	4/10	6/10	5/10	7/10	5/10	6/10	4/10
	B	10YR3/1	10YR3/2	10YR3/3	10YR4/2	10YR3/1	10YR3/2	10YR3/1	10YR3/2	10YR3/4	10YR4/4
46-60	A	5/10	4/10	5/10	4/10	5/10	5/10	5/10	5/10	Water	
	B	10YR3/3	10YR3/2	10YR3/4	10YR3/4	10YR4/2	10YR3/2	10YR3/1	10YR3/2		
61-75	A	4/10	4/10	4/10	4/10	Water		2/10	3/10		
	B	10YR3/2	10YR3/2	10YR3/2	10YR3/2			10YR3/1	10YR4/2		
76-90	A	Clay bottom		5/10	5/10			Water			
	B			10YR3/2	10YR3/2						
91-105	A			6/10	6/10						
	B			10YR4/1	10YR4/1						
106-135	A			Clay bottom							
	B										
121-135	A										
	B										
136-150	A					4/10	3/10				
	B					10YR4/2	10YR4/2				
151-165	A					4/10	3/10	7/10	4/10	5/10	3/10
	B					10YR4/1	10YR3/2	10YR4/3	10YR3/2	75YR4/0	10YR4/1
166-180	A					3/10	3/10	6/10	4/10	3/10	2/10
						10YR4/1	10YR4/1	10YR4/3	10YR3/2	75YR0/2	10YR4/1
181-195	A					Clay bottom		Clay bottom		2/10	2/10
										10YR4/1	10YR4/1
196-210	A									Clay bottom	
	B										

. . . cont'd

APPENDIX E continued.

E.1.3 Transect 3

Depth (cm) below surface		Near levee													Near lak
		Core 34		Core 33		Core 31		Core 30		Core 29		Core 27		Core 26	
		UR	R	UR	R	UR	R	UR	R	UR	R	UR	R	UR	R
0-15	A	5/10	5/10	7/10	6/10	8/10	8/10	8/10	8/10	8/10	5/10	8/10	8/10	8/10	6/10
	B	10YR3/1	10YR3/2	10YR3/2	10YR3/2	10YR3/2	10YR3/2	10YR3/1	10YR3/2	10YR3/2	10YR3/3	10YR3/1	10YR3/3	10YR3/1	10YR3
16-30	A	5/10	5/10	4/10	4/10	6/10	3/10	7/10	5/10	7/10	5/10	8/10	8/10	8/10	6/10
	B	10YR3/2	10YR3/4	10YR3/1	10YR3/2	10YR2/1	10YR3/2	10YR3/2	10YR3/4	10YR3/2	10YR3/3	10YR3/1	110YR3/3	10YR3/1	10YR3
31-45	A	4/10	3/10	4/10	4/10	6/10	5/10	5/10	5/10	5/10	5/10	8/10	8/10	6/10	6/10
	B	10YR3/3	10YR4/4	10YR3/3	10YR3/4	10YR2/2	10YR2/2	10YR3/2	10YR3/4	10YR3/2	10YR4/3	10YR3/1	10YR3/3	10YR3/1	10YR3
46-60	A	4/10	3/10	Water		5/10	5/10	5/10	5/10	Water		6/10	6/10	7/10	7/10
	B	10YR3/2	10YR4/4			10YR3/4	10YR4/3	10YR3/1	10YR4/2			10YR3/1	10YR3/3	10YR3/1	10YR3
61-75	A	Water				4/10	3/10	Water				Water		Water	
	B					10YR3/2	10YR3/2								
76-90	A					Water									
	B														
91-105	A														
	B														
106-120	A														
	B														
121-135	A									4/10	4/10				
	B									10YR3/1	10YR3/2				
136-150	A									Clay bottom					
	B														
151-165	A							5/10	5/10					2/10	5/10
	B							10YR3/1	10YR3/2					10YR4/1	10YR4
166-180	A					3/10	3/10	2/10	2/10					3/10	2/10
	B					10YR3/1	10YR3/2	10YR4/1	10YR4/1					10YR5/2	10YR5
181-195	A	2/10	<1/10	3/10	3/10	2/10	2/10	4/10	4/10			Clay bottom		Clay botto	
	B	10YR3/2	10YR4/1	10YR3/2	10YR3/2	10YR4/1	10YR4/1	10YR3/1	10YR4/2						
196-210	A	Clay bottom		Clay bottom		Clay bottom		Clay bottom							

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APPENDIX E continued.

E.1.4 Transect 7

Near levee ⟶ Near lake

Depth (cm) below surface		Core 11 UR	Core 11 R	Core 13 UR	Core 13 R	Core 14 UR	Core 14 R	Core 15 UR	Core 15 R
0-15	A	8/10	8/10	8/10	5/10	8/10	8/10	6/10	4/10
	B	10YR3/2	10YR3/3	10YR2/1	10YR3/4	10YR3/1	10YR3/3	10YR3/1	10YR3/2
16-30	A	7/10	6/10	6/10	5/10	3/10	3/10	Water	
	B	10YR3/2	10YR3/3	10YR2/1	10YR3/3	10YR4/2	10YR4/2		
31-45	A	6/10	5/10	4/10	5/10	Water		1/10	<1/10
	B	10YR3/1	10YR3/2	10YR3/4	10YR3/3			10YR4/2	10YR4/2
46-60	A	5/10	5/10	4/10	4/10	3/10	3/10	1/10	<1/10
	B	10YR3/2	10YR3/2	10YR3/2	10YR3/1	10YR5/3	10YR5/3	10YR4/2	10YR4/7
61-75	A	Water		4/10	4/10	2/10	2/10	Clay bottom	
	B	↓		10YR3/2	10YR3/2	10YR4/1	10YR4/1		
76-90	A			3/10	2/10	Clay bottom			
	B			10YR4/1	10YR4/1				
91-105				Clay bottom					
106-120									
121-135									
136-150									
151-165		Clay bottom							

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APPENDIX E concluded.

E.2 Fiber content and color of peat core segments from a closed basin transect (Transect 9)

Depth (cm) below surface		Edge of basin ——> Centre of basin					
		Core 16		Core 17		Core 18	
		UR	R	UR	R	UR	R
0-15	A	9/10	7/10	9/10	8/10	9/10	9/10
	B	10YR4/2	10YR4/3	10YR5/3	10YR6/3	10YR4/3	10YR4/4
16-30	A	7/10	7/10	8/10	8/10	9/10	8/10
	B	10YR4/2	10YR4/3	10YR4/3	10YR4/3	10YR4/4	10YR5/3
31-45	A	6/10	6/10	8/10	7/10	9/10	9/10
	B	10YR4/2	10YR3/2	10YR4/2	10YR4/3	10YR4/4	10YR6/4
46-60	A	5/10	5/10	6/10	5/10	9/10	9/10
	B	10YR4/2	10YR4/2	10YR3/2	10YR4/3	10YR5/4	10YR6/4
61-75	A	5/10	5/10	4/10	4/10	9/10	8/10
	B	10YR4/2	10YR4/2	10YR3/3	10YR4/2	10YR4/3	10YR6/4
76-90	A	5/10	5/10	4/10	4/10	8/10	7/10
	B	10YR3/4	10YR3/4	10YR3/4	10YR4/3	10YR3/4	10YR3/3
91-105	A	5/10	5/10	4/10	4/10	8/10	7/10
	B	10YR3/4	10YR3/4	10YR3/2	10YR4/2	10YR3/2	10YR5/4
106-120	A	3/10	3/10	4/10	4/10	8/10	8/10
	B	10YR5/1	10YR1/2	10YR3/2	10YR4/3	10YR3/2	10YR5/3
121-135	A	Fine sandy		4/10	4/10	8/10	8/10
	B	clay bottom		10YR3/2	10YR4/3	10YR3/2	10YR4/3
136-150	A			4/10	4/10	8/10	8/10
	B			10YR3/4	10YR4/2	10YR2/2	10YR3/4
151-165	A			4/10	4/10	8/10	7/10
	B			10YR3/4	10YR4/2	10YR2/2	10YR5/3
166-180	A			3/10	2/10	7/10	7/10
	B			10YR4/1	10YR4/1	10YR2/2	10YR4/3
181-195	A			1/10	<1/10	6/10	6/10
	B			10YR5/1	10YR5/1	10YR3/1	10YR4/2
196-210	A			Water ↓		6/10	6/10
	B					10YR2/1	10YR3/4
211-225	A			Silty clay bottom		6/10	6/10
	B					10YR2/1	10YR3/4
226-240	A					6/10	5/10
	B					10YR3/1	10YR3/4
241-255	A					5/10	5/10
	B					10YR3/1	10YR3/4
256-270	A					3/10	3/10
	B					10YR5/2	10YR5/2
271-285	A					3/10	3/10
	B					10YR6/1	10YR6/1
286-300	A					4/10	4/10
	B					10YR6/1	10YR6/1
301-315	A					1/10	<1/10
	B					10YR5/1	10YR5/1
316-330						Clay bottom	