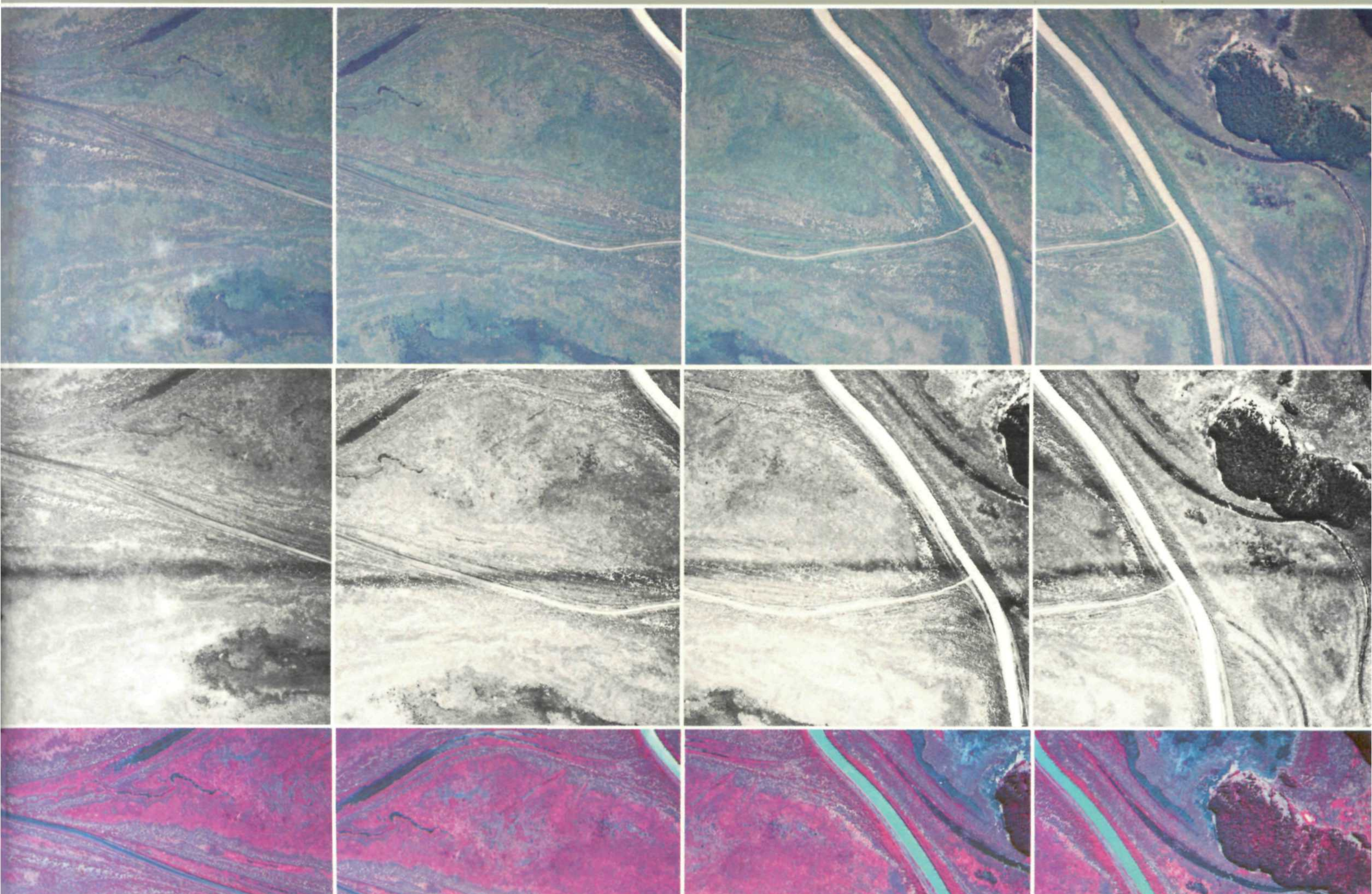
by Herman J. Dirschl,
Don L. Dabbs
and Garry C. Gentle

Landscape classification and plant successional trends: Peace-Athabasca Delta



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Cover: Example of three-film simultaneous 70 mm strip aerial photography taken in the Peace–Athabasca Delta, July 1972.
Contact scale: 1:30,000.
Top strip: true colour; Ektachrome Aero film; haze filter
Middle strip: black and white; Double-X Aerographic film; haze filter
Bottom strip: infrared colour; Ektachrome Infrared Aero film (emulsion no. 2443); Wratten 12 filter

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Pilot J. Olson and D. Dabbs preparing for a reconnaissance flight in a Piper Apache.

The authors

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Acknowledgements

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Perspective

The construction of large hydroelectric projects brings about significant ecological changes in the river systems in which they are located. To date, these often massive environmental side effects have usually been ignored in the cost-benefit analysis and planning phases of the projects. The giant W. A. C. Bennett Dam on the upper Peace River which was completed in 1967 has greatly altered the downstream river regime and has induced major changes in the 1,700 sq.-mile Peace–Athabasca Delta in northeastern Alberta. The delta is largely contained within Wood Buffalo National Park and is important as bison habitat and as a waterfowl breeding, moulting and fall staging area. Muskrat trapping and fishing in the delta have been traditional sources of income for the 1,500 Cree, Chipewyan and Métis residents of Fort Chipewyan.

The Canadian Wildlife Service anticipated that the altered flow regime of the Peace River would bring about changes in the vegetation and wildlife habitats, and therefore in 1968 initiated a 4-year ecological study to evaluate the short and long-term environmental effects that would ensue. This study has illustrated that the greatly reduced water levels in the delta from 1968 through 1970 have begun a sequence of vegetation adjustments that are rapidly reducing the extent of the widespread shallow-marsh and wet-meadow communities and replacing them with drier grass and shrub vegetation. If these low water levels were to persist indefinitely, the vegetational diversity of the delta would be much reduced. Consequently, the wildlife productivity, which depends on the previously existing diversity of vegetation types, would also be significantly reduced unless appropriate measures are implemented to more or less restore the previous water regime in the delta.

These findings have re-emphasized the need to consider all potential environmental impacts in the assessment and planning of proposed projects that alter natural flow regimes of river systems.

Abstract

The dynamics of the formation of the Peace–Athabasca Delta are discussed. Viewed as a single, large ecosystem, the vegetative–landform components of the delta are defined and mapped with the aid of conventional and large-scale colour aerial photography. At a scale of 1:37,000, eight terrestrial community types and seven water body types are defined. Within the framework of this small-scale classification, six deltaic land facets are described at a scale of 1:10,000. The dominant plants and their autecological relationships on each of these land facets are discussed.

An agglomerative, multivariate classification proved fairly successful in identifying major permutations of land facets and vegetation types.

Plant successional trends are discussed within two time scales; the short-term adjustment of the near-shore vegetation to a rapid decrease in water levels and the long-term successional trends related to the processes of delta development and maturation.

Résumé

Les auteurs traitent de la dynamique de formation du delta Paix–Athabasca. Considérées comme un seul et vaste écosystème, les composantes du relief végétatif du delta sont définies et mises sur carte à l'aide de photographies aériennes ordinaires ou en couleur et à grande échelle. À l'échelle du 1:37,000ᵉ, huit types de collectivités terrestres et sept types de cours d'eau sont définis. A l'intérieur de la structure de cette classification à petite échelle, six facettes de terrain deltaïque sont décrites à l'échelle du 1:10,000ᵉ. On traite aussi des plantes dominantes et de leurs rapports *autécologiques avec chacune de ces facettes* de terrain.

Une classification agglomérante et multivariante a été passablement réussie quant à l'identification des principales permutations des facettes du terrain et des types de végétation.

Les tendances successives des plantes sont étudiées par rapport à deux échelles de temps: l'adaptation à court terme de la végétation située près des rives à la baisse rapide du niveau de l'eau et les tendances successives à long terme liées aux procédés de formation et de développement du delta.

Абстракт

В статье обсуждается динамика формирования дельты Пис–Атабаски. Дельта рассматривается как отдельная крупная экологическая система, ее растительно-топографические особенности охарактеризованы и нанесены на карту при использовании общепринятых методов, а также крупно-масштабной цветной воздушной фотосъемки. В масштабе 1:37.000 описано восемь семейств территориальных формаций и семь типов водных образований. На фоне такой мелкомасштабной классификации дается описание шести дельтовых земляных ответвлений с использованием масштаба 1:10.000. Обсуждаются преобладающие виды растительного покрова и взаимодействие с окружающей средой на каждом из этих земляных ответвлений.

Совокупный, многовариантный метод классификации оправдался как вполне пригодный для определения крупных пермутаций земляных ответвлений и типов растительности.

Направления перемещения растительности рассматриваются с точки зрения двух разных отрезков времени; кратковременное приспособление прибрежной растительности к резкому спаду уровня воды и долговременные потомственные изменения, причастные к процессам развития и процессам созревания дельты.

Introduction

Concern about the potential environmental impact on the Peace–Athabasca Delta of alterations to the flow of the Peace River, following completion of the W. A. C. Bennett Dam, led the Canadian Wildlife Service in 1968 to initiate an ecological study of the delta. The annual rise in the level of the Peace River to an elevation equal to or higher than Lake Athabasca has been significant in determining the ecological character of the delta, for the spring floods have acted as a hydrological dam that stopped, and even reversed, outflow from Lake Athabasca and the contiguous delta lakes. As the flora and fauna of the region are adapted to the annual flooding, any change in the water regime was expected to result in new and possibly unfavourable adjustments within the ecosystem.

The objectives of the study were

a. To determine the relationships between vegetational patterns and physical environmental features, particularly the water regime, and to develop a landform–vegetation classification of the delta's landscape;

b. To determine the prevailing, long-term successional trends in the delta; and

c. To monitor and assess the ecological adjustments initiated by the altered water regime.

Research on these aspects of the study was carried out between May and September of 1968 to 1971 and preliminary results have been reported in the following publications: Dirschl (1970a, 1970b, 1971, 1972a), Dirschl and Dabbs (1972), and Dabbs (1971b).

A subsidiary objective of the study was to determine how waterfowl use the various deltaic habitats for breeding, nesting, brood rearing, moulting, and spring and fall staging. These were studied in 1969 and 1970 and the results reported by Nieman (1971) and Nieman and Dirschl (1973).

This study provided important background data for formulating the wider objectives of the Peace–Athabasca Delta Project initiated by the governments of Canada, Alberta and Saskatchewan in December 1970.

This report describes the landscape classification which was developed for the delta, and presents our findings in respect to vegetation–environmental relationships and ongoing plant successional trends.

Dynamic processes in river deltas

A river delta is formed where a sediment-carrying river begins to empty into a lake or sea. As the stream gradient lessens, the suspended sediments are deposited on the river bed. Gradually, point bars and islands emerge within the stream bed, and the river branches into a series of channels that meander across the forming delta plain. Local differences in erosion and deposition result in the cutting-off and ponding of channels (oxbows) and in the formation of numerous shallow depressions (perched basins). As the delta continues to advance into the lake, channels deepen in the upper reaches. In this manner, a delta matures upstream as it grows downstream.

Parallel with the evolution of the physical landscape occurs a replacement of the biological ecosystem components. Plant species capable of establishing in the aquatic and nutrient-rich environment of young sites gradually become unable to persist as these sites mature, and are replaced by species adapted to drier and nutrient-poorer conditions. Thus the vegetation occupying a given location changes, in time, from aquatic to meadow, to wooded communities. Animal populations exhibit a similar change as their habitat is altered by these delta-forming processes.

The evolution of the physical landscape is the main driving force of this ecological succession (allogenic succession). Plant communities, however, can play a modifying role in this process. By locally reducing flow rates and entrapping silt or by accumulating organic matter, the vegetation can control moisture, nutrient, and soil temperature conditions, and enables species adapted to this modified environment to invade (autogenic succession).

Plant succession normally proceeds too slowly to permit direct observation of the time-sequence through which communities change in a given location. It is observable only by viewing the spatial distribution of landform and vegetation types within the delta as a whole.

However, some natural events such as droughts, floods, and lightning fires produce abrupt changes in local environments, initiating rapid adjustments in plant cover with consequent changes in wildlife populations. Interest tends to focus on these short-term interactions between the environment and the plant and animal communities rather than on the long-term successional trends. However, as both processes occur simultaneously, it is clearly impossible to study one without reference to the other.

So far, the discussion has been confined to natural processes in the delta. Man-made environmental alterations likewise produce ecological changes within a delta. Reduction in river flow through upstream diversion or impoundment results in the expansion of terrestrial communities and concurrent reduction in aquatic and marsh habitats and thus increases the rate of aging of the delta. Conversely, raised water levels resulting from increased river flow or from downstream impoundment enlarge the area occupied by aquatic and marsh habitats at the expense of terrestrial communities and thus set back succession to an earlier seral stage.

1. Deltaic processes in the Peace–Athabasca Delta

The Peace–Athabasca Delta is a complex of the deltas of the Peace, the Athabasca and the Birch rivers which, since deglaciation, have emptied into the lowlands at the western extremity of Lake Athabasca (Bayrock and Root, 1971). The ecological character of the Peace–Athabasca Delta has evolved through a unique hydrological system formed by the interaction of these rivers and Lake Athabasca and its outflow channels.

Under natural conditions, the Peace River experienced a spring flood of variable height which acted as a hydrological dam, stopping and, to some extent, reversing the outflow from Lake Athabasca and the contiguous delta lakes. Consequently the rising level of Lake Athabasca, and simultaneously occurring freshets on the Athabasca and Birch rivers, flooded most of the delta, recharged lakes and the numerous perched basins with nutrient-rich waters, deposited silt and plant seeds, and flushed out or buried plant debris. This flood, occurring in the spring of most years, slowed the normal longterm development of the delta and held much of the area at early successional stages (Fuller and LaRoi, 1971). During the remainder of the year, outflow and evapo-transpiration gradually lowered the water levels. The vegetation patterns and animal life which now characterize the delta have developed in response to this fluctuating water level and are thus adapted to it. Any change in the hydrological regime, therefore, initiates ecological adjustments within the delta (Dirschl, 1972a).

Filling of Lake Williston, the reservoir behind W.A.C. Bennett Dam, began in December 1967 and the annual high stage on the Peace River has been much reduced. Hydrological studies have shown that this altered water regime would remain in force and the observed drying trend would continue (Bennett, 1971; Kellerhals, 1971).

Background studies

Previous ecological studies in the Peace–Athabasca Delta are few. Fauna and flora were described, in varying detail, by the early explorers and fur traders (e.g. Mackenzie, 1801). Fuller and LaRoi (1971) have recently compiled a review of the delta's exploration history.

During the summers of 1926 to 1930, Raup made a botanical and ecological survey of the delta and the Lake Athabasca and Great Slave Lake lowlands (Raup, 1930; 1933; 1935; 1936; 1946). His papers form the most significant background for an understanding of vegetation patterns and landscape evolution in the area.

Fuller (1951), who carried out studies of muskrat populations in the delta from 1947 to 1949, found that sloughs that had presumably dried out during the low water years of 1944 to 1946, had become invaded by willow and balsam poplar seedlings.

Novakowski (1967) described the geomorphology of the delta, stressed the importance of seasonal flooding to vegetation pattern and wildlife habitat conditions and warned of the ecological consequences of the water regime changes in the delta expected to follow the completion of Bennett Dam.

Ecological studies in other deltas and large marsh areas provide interesting comparisons. Dirschl (1970c) and Dirschl and Coupland (1972) studied the ecology of the Saskatchewan River Delta in east-central Saskatchewan. This delta differs from the Peace–Athabasca Delta in having evolved under less drastic fluctuations in water levels, at least during the past several thousand years. The result has been the development of extensive floating sedge mat shorelines and of floating islands of phragmites and sedge. Areas of closed drainage have developed into sphagnum moss–black spruce bogs. Such types are only minor constituents of the Peace–Athabasca Delta where seasonal rise and fall of water levels and annual deposition of calcareous sediments prevented their development.

The zones described by Walker (1959, 1965) in the marshes adjacent to the south shore of Lake Manitoba resemble the colonization observed on emerging mudflats in the Peace–Athabasca Delta. Gill (1971) has shown that, in the Mackenzie Delta, deltaic processes and landscape evolution are considerably affected by permafrost conditions.

Many other ecological studies in marsh and wetland areas (e.g., Sjörs, 1948; Kulczynski, 1949; Kadlec, 1962; Harris and Marshall, 1963; Gorham, 1967; Walker and Coupland, 1968; 1970) are pertinent to the present study. In general, these authors have illustrated the ecological significance of water circulation, seasonal inundation, length of drawdown period, silt deposition, flushing out of decomposition products, and nutrient availability, all of which interact in controlling types and distribution of biota.

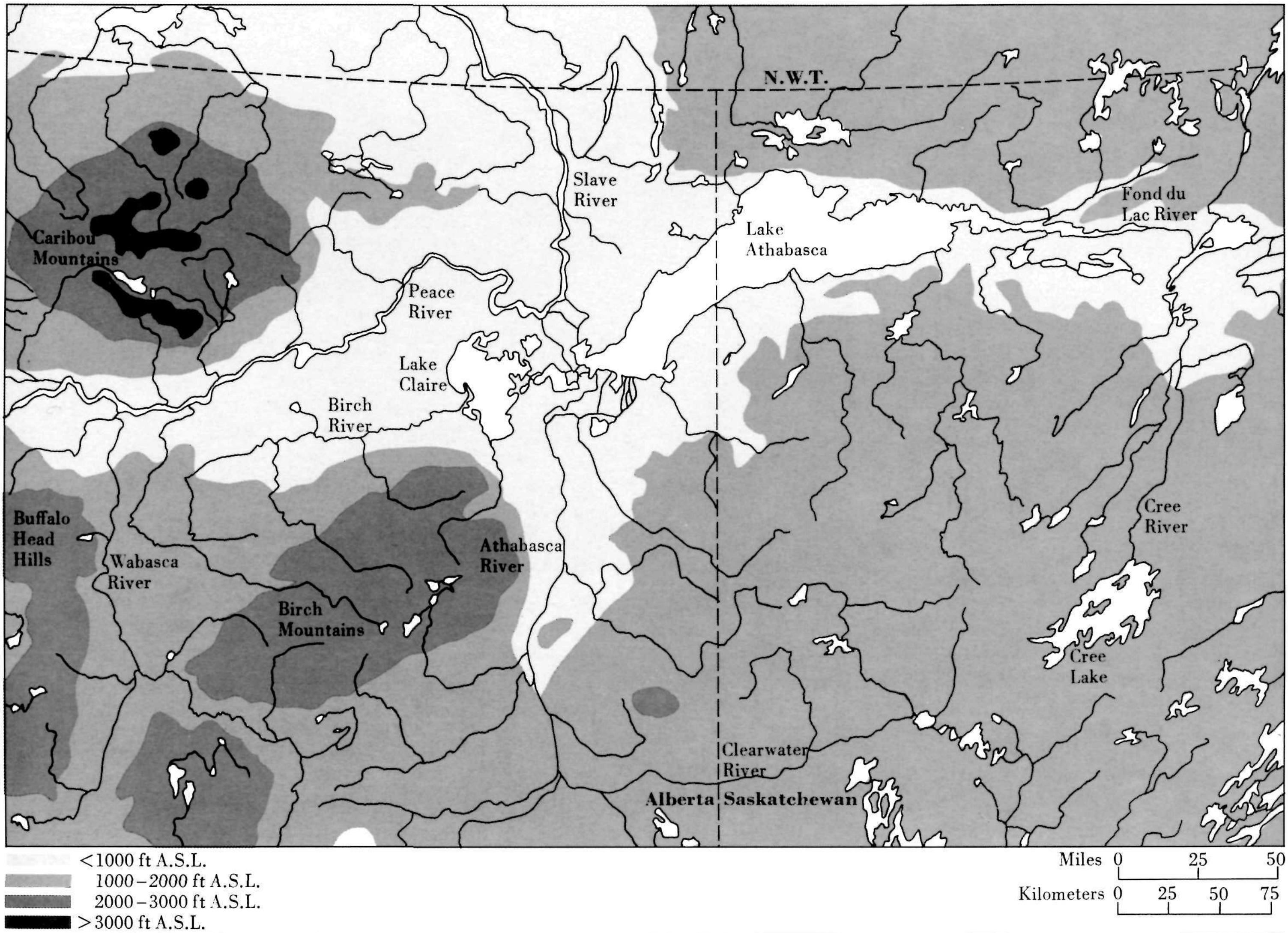
The area

Figure 1. Location of the Peace–Athabasca Delta in western Canada showing the major river systems influencing the delta.

Figure 1

Figure 2. Topography and drainage of the Peace–Athabasca Delta.

Figure 2



1. Geographic location

The Peace–Athabasca Delta is adjacent to the western extremity of Lake Athabasca in northeastern Alberta (Fig. 1) and covers an area of about 1,700 sq. mi. (4,400 km^2). A detailed description of the area may be found elsewhere (Dirschl, 1972a).

2. Glacial history and surface geology

Approximately 31,000 years ago, the Keewatin sheet of the Wisconsin glacier covered the Peace–Athabasca Delta (Bayrock, 1962). Large ice-marginal lakes formed as the ice sheet retreated gradually. Glacial Lake Tyrrell covered the Peace River lowlands south and west of the present town of Peace River, extended up the Athabasca River basin to Lac La Biche, and included all of Lake Athabasca and its surrounding lowlands (Taylor, 1958). The ice retreated completely approximately 10,500 years ago.

After deglaciation, the level of Lake Athabasca was probably about 100 ft (ca. 30 m) higher than it is now (Bayrock, 1962). Since the Peace and Athabasca rivers deposited extensive areas of coarse

Figure 3. Precambrian outcrop surrounded by flat delta plain.

sands and gravels, the rivers probably had a steeper gradient than they do now. The subsequent lowering of Lake Athabasca reduced the base level of the two major rivers and deposited silt and clay on top of the older, coarser materials (Bayrock, 1962). Closed depressions have gradually filled with flood-deposited silt and clay and with muck and fibrous organic matter. Regional bedrock ranges from Precambrian granites and gneisses to unconsolidated, Cretaceous sandstones and shales (Bayrock, 1961).

3. Topography and drainage

The delta lies in the Peace River lowlands at the confluence of the Athabasca, Peace and Slave river drainage basins (Fig. 2). It is bounded by the Birch and Caribou mountains on the southwest and northwest and the edge of the Precambrian Shield on the northeast.

Lake Athabasca measures 3,085 sq. mi. (7,990 km^2) but, because it controls water levels in the contiguous delta, its effective surface area exceeds 4,500 sq. mi. (11,755km^2) (Bennett, 1970). Two major rivers enter the lake: the Athabasca River from the south originates in the Rocky Mountains and has the low winter and high summer flow characteristic of mountain-fed rivers; the Fond-du-Lac River from the east drains Precambrian Shield country and flows more evenly throughout the year. The Peace River springs from the mountains of northern British Columbia, bypasses the Peace–Athabasca Delta on the north and, with the outflow channels of Lake Athabasca, forms the Slave River which in turn drains northward into Great Slave Lake.

4. Climate

The study area lies in the subarctic zone (Dfc) of the Köppen classification and is characterized by short, cool summers and long, cold winters. The mean wind direction in the delta is from the northwest (Odynsky, 1958).

The mean monthly temperatures are 28 to 30°F (−2.2 to −1.2°C) in April, 60 to 62°F (15.6 to 16.7°C) in July, 34 to 36°F (1.1 to 2.2°C) in October, and −10 to 12°F (−23.3 to −24.4°C) in January (Longley, 1968). The moderating influence of the large water bodies extends the frost-free period to 100 days, 20 days longer than in the surrounding uplands. The last spring frost normally occurs June 1–15; the first fall frost September 1–15.

Mean annual precipitation is 16 in. (406 mm) of which 9–10 in. (229–254 mm) falls between April 1 and September 30.

5. The present landscape

The following brief description of present landform and vegetation patterns is abstracted from the detailed account by Raup (1935). The lacustrine-alluvial plain is broken to the east (Fig. 3) by rounded, almost barren hills, outliers of the Precambrian rocks. The lakes, although of large area, average only 4–5 ft (1.2–1.5 m) in depth. Their shores are very marshy, but where exposed to the action of waves, they are cut back and comparatively dry (Fig. 4). Abandoned stream channels and ponds formed by the cutting-off of sections of the lakes are in all stages of filling, in general being drier toward the outer margins of the delta plain.

Although the differences in the elevation of the plain above the water table are slight, they are enough to determine the arrangement of the plant cover. Lands subject to floods have a herbaceous vegetation ranging from semifloating aquatic plants to sedges and grasses. Large areas are covered by almost pure stands of awned sedge (*Carex atherodes*) or reed grass (*Calamagrostis* spp.). On the slightly elevated margins of stream channels, abandoned or otherwise, are long lines of willows (*Salix* spp.) (Fig. 5). Shrub and tree growth increases toward the margins of the plain, so that the upper (and older) part of the delta and the banks of the larger channels support a forest of white spruce (*Picea glauca*) and balsam poplar (*Populus balsamifera*). The granite hills have a scrubby timber of white spruce, jackpine (*Pinus banksiana*) and white birch (*Betula papyrifera* var. *neoalaskana*) (Fig. 3).

Figure 4. The south shoreline of Mamawi Lake showing an intermittent creek and perched basins.

Figure 5. Tall willows along the margins of slightly elevated stream levees.

Methods and procedures

We chose our methods with the following considerations and assumptions in mind:

a. Since the soil content throughout the Peace–Athabasca Delta is uniform, we assumed that moisture differences are the principal factors determining vegetation zones in the area.

b. Because of the delta's low relief, very slight differences in the topography are reflected in the vegetation pattern.

c. Since the filling of the reservoir was underway when we began to collect field data, we expected rapid vegetational changes in those portions of the delta directly affected by the falling water levels. To assess these ongoing vegetational changes, it was essential to obtain efficient and accurate means of monitoring them.

d. Short-term vegetational adjustments and long-term developmental processes would have to be studied simultaneously.

Therefore, we adopted a system of aerial photographic sampling which permitted rapid recording of vegetation patterns and changes, and ready storage of sets of information for subsequent comparison and analysis. Traditional methods of ground sampling would not have allowed us to recognize and evaluate vegetational changes in such a large and complex area.

1. Reconnaissance classification and mapping

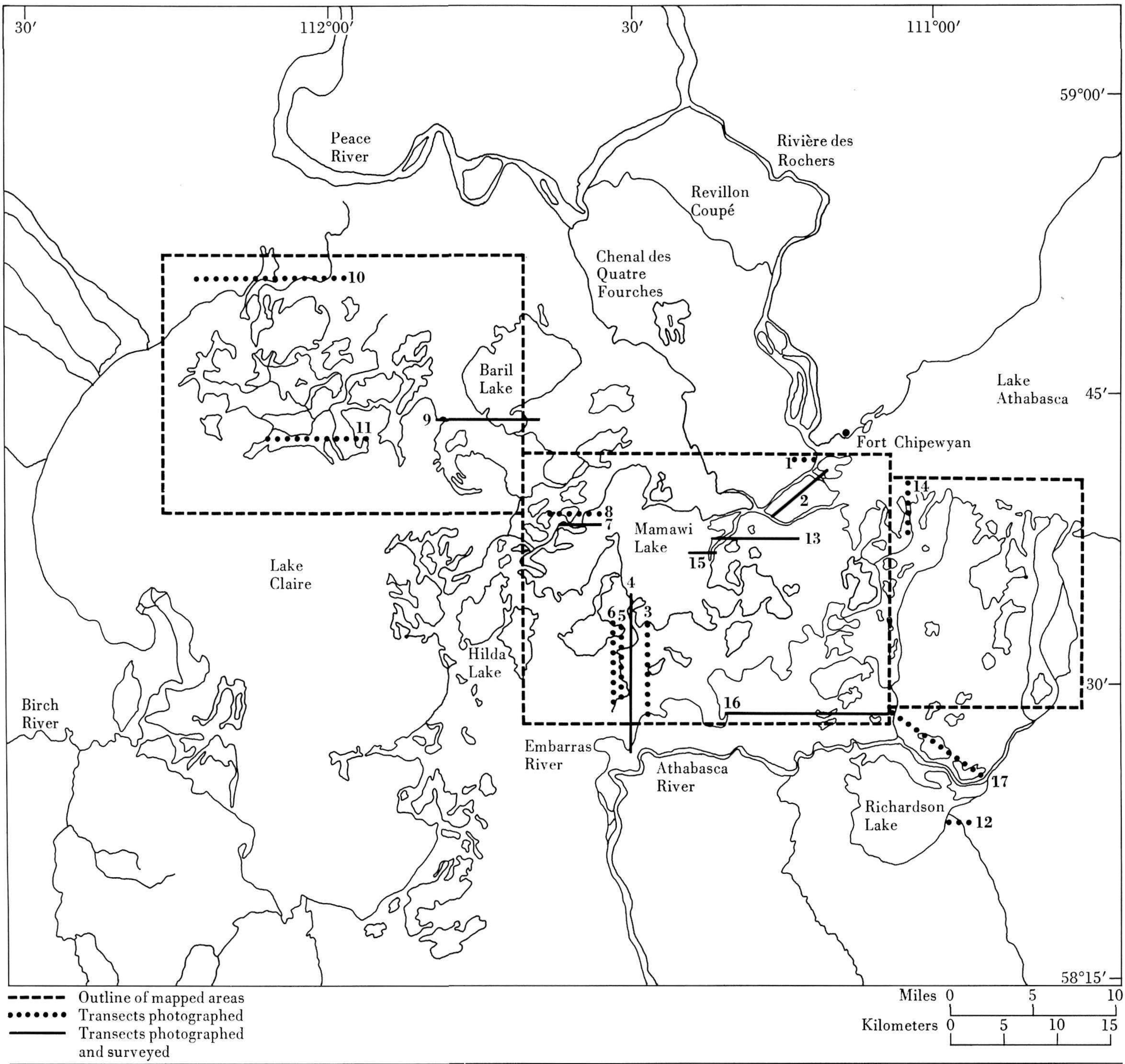
1.1 Prior to 1969

Three maps were prepared, each of a different section of delta (Fig. 6), using air photos taken in 1955 and 1956 and uncontrolled mosaics (1:37,000). A simple breakdown of the landscape into a general classification system of landform, water types, and vegetation types was used: A, open water; B, emergent aquatic vegetation; C, mudflat; D, fen; E, tall shrub; F, forest on levee; G, forest on bedrock.

Using these three maps, 16 representative transects were selected, marked with markers visible from the air, and all further ground and air study was confined to these transects.

Figure 6. Outline of mapped areas showing transects surveyed and photographed.

Figure 6



1.2 After 1970

A map (Map 1) was prepared of the Mamawi Lake study area (one of the three mentioned above) using air photos taken in 1955 and 1956 and uncontrolled mosaic (1:37,000). A very detailed and complete landscape classification, based on information on plant species collected in 1969 and 1970, was used to prepare this map.

2. Aerial photographic techniques

Strip photographs of the marked transects were taken to obtain detailed information on vegetation – land surface – water relationships in the delta, and to measure the vegetational responses to falling water levels.

Hasselblad 500 EL camera equipment mounted in a Piper Apache twin-engined aircraft was used in this study. Dabbs (1971b) has provided a detailed description of the value of 70 mm photography and several types of film for landscape–ecological study.

Photographs were taken with 80 mm lenses at scales of 1:6,000 (1,500 ft (457 m) above average terrain) and 1:30,000 (7,900 ft (2,408 m) above average terrain). Three films were used: Double-X Aerographic black and white film, Ektachrome Aero true colour film and Ektachrome Infrared Aero false colour film. During the field seasons of 1969 and 1970, three-film coverage of the transect lines was obtained by consecutive photography with a single camera. In 1971, three cameras, each loaded with one of the three films, were simultaneously exposed using a Hasselblad command unit.

During the course of the 1969 and 1970 growing seasons, we made two coverages of each transect — a few weeks after growth had begun (June 16–22) and at the height of the growing season (July 22–30) — to evaluate the seasonal and annual differences in the existing plant communities and to monitor the colonization of newly exposed silt surfaces. In 1969, a third coverage was obtained at the end of the growing season (September 17–19). In 1971, we carried out two coverages — at the beginning of July and at the end of July. Most of the films were developed by project staff at the Canadian Wildlife Service field station in Fort Chipewyan, Alberta; some were sent to the Air Photo Unit of the National Air Photo Library in Ottawa for processing.

Table 1
Classification for mapping study area at the scale of 1:37,000

Landscape type	Class	
	Terrestrial community-types:	
Delta	Coniferous forest	D1
	Deciduous forest	D2
	Tall shrub: 3–6 m	D3
	Low shrub: <3 m	D4
	Fen: predominantly graminoids, may contain a few scattered low shrubs	D5
	Immature fen: scattered low plants on newly colonized mudflats	D6
Precambrian outcrop	Forest	P1
	Grassland	P2
	Water body types:	
Water channel	Flowing stream and river	C1
	Intermittent stream	C2
	Abandoned stream bed and meander scroll	C3
Standing water	Freely drained: deep and open	S1
	Freely drained: shallow open with emergent vegetation	S2
	Restricted drainage: open with emergent vegetation	S3
	Severely restricted drainage: open with emergent vegetation	S4

3. Analysis of 70 mm large-scale photos

Strip mosaics of the transects were prepared by feather-cutting black and white 70 mm photographs, printed to a scale of 1:10,000, on double weight, high-contrast paper.

Whereas the classification (Table 1) used to map the study area at 1:37,000 showed only broad "land systems", the classification used to map the transects at a scale of 1:10,000 was one of land facet–vegetation units (Table 2). No comparable breakdown of the classification of water systems was attempted.

4. Mapping techniques

The maps were prepared in the following manner. The central portion of a photograph, printed to the appropriate scale, was feather-cut and arranged to blend with the image of the next photo. These prints formed the mosaic which was glued to a sheet of masonite and a mylar overlay applied overall.

The mapping of prominent features in the landscape such as streams, rivers, trees and shrubs was accomplished by simply viewing the black and white photos in stereo and outlining these units on the overlay, as recommended by Küchler (1967, p. 94). Differences between the plant species components of the fen and lakeshore areas, low herbaceous vegetation types, were difficult and often impossible to see in black and white photographs but showed up clearly on colour infrared photos. The 70 mm colour infrared positives were enlarged and projected onto the mylar overlying the mosaic which ensured that the orientation and placement of the projected image was absolutely correct. The fen communities were then marked out on the overlay.

Because vegetation shows up on colour infrared photographs in shades grading from pink to dark magenta, it is often difficult to identify the plant species of each map component. It was necessary in many cases to examine the true colour Ektachrome film in order to make accurate identifications. The working combination of the two colour films proved extremely effective in mapping the low herbaceous vegetation.

5. Vegetation sampling

Plots 0.3–0.6 ha (0.75–1.50 acres) in area were selected within visually homogeneous vegetation types to sample important vegetational and physiographic condi-

Table 2
Land facet–vegetation type classification for mapping of field transects at the scale of 1:10,000 in the Peace–Athabasca Delta

Active delta (I)			Inactive delta (III)		
Point bar and levee (IA)	Lakeshore and delta plain (IB)	Semiactive delta (II) (perched basin and backslope of levee)	Backswamp (wet depression) (IIIA)	Meander scroll (dry channel) (IIIB)	Precambrian outcrop (IV)
Equisetum	*Potamogeton*	*Potamogeton–Nuphar*	*Potamogeton–Nuphar–Myriophyllum*	*Carex*	*Populus–Picea*
Eleocharis–Glyceria	Sparsely vegetated mudflat	*Typha–Scirpus*	*Scirpus–Typha*	*Calamagrostis*	*Juniperus*
Salix interior	*Senecio*	*Senecio*	*Phragmites*	*Salix*	*Stipa–Artemisia*
Salix–Alnus	*Scirpus*	*Equisetum*	*Equisetum–Acorus*	*Betula*	
Betula	*Eleocharis–Carex*	*Scolochloa*	*Carex–Potentilla* (floating mat)		
Populus	*Beckmannia–Scolochloa–Carex*	*Eleocharis–Carex*	*Salix–Menyanthes* (floating mat)		
Picea	*Carex*	*Carex*			
	Salix–Carex	*Calamagrostis*			
	Calamagrostis	*Salix*			
	Phragmites				

tions revealed on the large-scale 70 mm air photos. Initial emphasis was on sampling mudflat areas peripheral to the major lakes in the study area. Marked plots were studied for 3–4 consecutive years at approximately the same time of the season for data on the successional sequence initiated by the falling water levels. Part of the stands were distributed along the near-shore parts of the marked field transects.

In a second phase of sampling, data on existing vegetation types were collected along the field transects, taking care that a number of stands from each of the mapping categories of the reconnaissance map were included.

In order to obtain data on both stand composition and structure which could be related to the detail observable on large-scale air photos, we chose to obtain quantitative estimates of vegetative cover of three subjectively delineated strata.

For each stratum, we estimated vegetative cover according to these six classes:

Cover class	Range of cover, %	Mid-point, %
1	1–5	2.5
2	6–25	15.0
3	26–50	37.5
4	51–75	62.5
5	76–100	87.5
+	Present but rare	0.25

We sampled both the herbaceous and the low shrub strata in systematically placed quadrats, 1 × 0.5 m (3.28 × 1.64 ft). Either 20 or 40 quadrats were studied depending on the degree of heterogeneity of the vegetation in the stand.

We obtained cover estimates of the tall shrub and tree canopy by pointing the Hasselblad camera vertically upward and viewing the image on the ground glass screen through the 80 mm lens. We then averaged 20 systematically distributed visual estimates from each stand. To be able to verify the visual estimates later, black and white photographs were also taken at each sampling point. A total of 89 stand samples were obtained in this manner.

When analyzing the vegetation data, the mid-point value of each cover class was used as an estimate of the percentage of the ground covered by each species in that quadrat. Mid-point values for each species were totalled and divided by the number of quadrats sampled to generate a value for the percentage of the ground covered by that species in the stand.

These vegetation data provided the basis for the interpretation of the 70 mm strip photography and input for subsequent multivariate analysis of vegetation–environmental interrelations and successional trends.

6. Environmental measurements

To obtain exact detail on the distribution of vegetation types in relation to microtopography and water levels, 7 of the 16 transects were surveyed with standard differential level surveying techniques. Elevational profiles were then drawn to the same scale as the strip mosaics to facilitate evaluation (Maps 2 and 3).

Depositional history was studied by means of a series of soil pits dug along several transects. The various horizons were described and photographed, and samples of major strata were collected for subsequent laboratory analysis. Compound soil samples were also obtained from the upper 30 cm (12 in.) in most of the vegetation stands sampled. Particle size distribution, organic matter content and pH were later determined. Chemical analyses of ground, lake and stream water samples were also carried out.

7. Transformation of vegetation data and multivariate analysis

Agglomerative classification was used to reduce the total vegetational variation contained in the sampling data to reasonably homogeneous groups of stands, which could be associated with major environmental features and positions in the landscape. This numerical technique, described in detail by Orloci (1967), was helpful in view of the multivariate nature of the data. The particular program used, written in Fortran IV for an IBM 360 computer, was obtained from Dr. J. W. Sheard, University of Saskatchewan. The essence of the technique is that a hierarchical classification of individuals (stands) is constructed on the basis of their attributes (species presence and absence, or quantitative measurements). The system treats all attributes as being independent of each other and compares individuals according to standardized distance between them so that both qualitative and quantitative data can be used (Morral *et al.*, 1972). In the present case, data consisted of per cent ground cover of the species present in each stand.

The hierarchy produced by agglomerative classification is represented by a dendrogram which arranges the stands in groups along the horizontal axis. The vertical axis indicates the mean squares within groups expressed as a percentage of the whole sample mean square.

Classification and mapping of the landscape

Figure 7. White spruce and balsam poplar on levee of the Embarras River.

The complex mosaic of vegetation and landforms which makes up a large wilderness area such as the Peace–Athabasca Delta presents the investigator with the problems of reducing the landscape to basic, understandable units.

We adopted a "divisive" approach to mapping and classifying of the landscape, i.e., by proceeding from the large to the small units. In this method there is less chance of inadvertently neglecting important components of the landscape, as might occur if a classification were to be "agglomerative", starting from the detailed units and working up to the broader units.

Our approach agrees with Küchler (1951) who states that "mapping is a method of portraying nature, and the classification must permit the mapper to approximate the true conditions as closely as possible" (p. 282). He also suggests that vegetation mapping should come first and classifying second, which has been the philosophy of this study. The classification grew out of ground studies and air photo interpretation.

1. Classification and map at the scale 1:37,000

Map 1 illustrates the small-scale breakdown of the delta landscape and Table 1 outlines the classification used. We recognized eight terrestrial and seven aquatic types.

1.1. Terrestrial community-types

The forest types of the delta are found on the higher, well-drained levees of streams and rivers (Fig. 7). The coniferous forest (D1) is made up primarily of white spruce (*Picea glauca*) accompanied by balsam fir (*Abies balsamea*) on some sites. The deciduous forest (D2), mostly balsam poplar (*Populus balsamifera*), is found in slightly lower positions than the coniferous forest. It is not extensive, but forms the transition from coniferous forest to the tall willows. Paper birch (*Betula papyrifera*) is codominant in many stands and dominant in a few locations along the Embarras River.

Shrub communities are the most extensive woody vegetation types of the delta.

Except for the occurrence of alder (*Alnus tenuifolia*) on some levees, willows are the most important species. They have been divided into two classes: tall shrub (3–6 m (9.6–19.2 ft) tall) and low shrub (less than 3 m (9.6 ft) high).

The tall shrub type (D3) is dominated by *Salix bebbiana* and *S. discolor*. This class is positioned slightly lower in the landscape than the deciduous forest type and is found on the backslope of the levees of larger rivers. It also dominates the lower levees of streams throughout the delta. The low shrub type (D4), slightly lower in the landscape than the tall shrubs, is common where the backslope of the stream levee grades into perched basin areas. This type is frequently an admixture of *Salix planifolia*, *S. petiolaris* and *S. serissima*. *Salix interior* is usually the dominant species on the lower levees and sandbars of actively flowing streams and rivers.

Fen (D5) refers to communities of sedges and grasses on wet organic soil through which basic mineral sediments are usually mixed. Major species in this type are: *Carex atherodes*, *C. aquatilis*, *Calamagrostis canadensis*, and *Scolochloa festucacea*. This type is rich with many other species of flora, as described later.

Class D6, immature fen or marsh, refers to the near lakeshore areas of recently exposed mudflats which support a variety of low plants such as *Scirpus validus*, *Typha latifolia*, *Carex aquatilis*, *Eleocharis palustris*, and *Beckmannia syzigachne*. In the first season that these areas are exposed, the above species are seedlings and generally less than 10 per cent of the ground is covered by plants. If, however, these areas are not reflooded for two or three seasons, they develop into fen (D5) type.

A prominent feature in the very flat delta landscape is the outcroppings of "islands" of granitic bedrock between Mamawi Lake and Lake Athabasca. They form a relatively small part of the total landscape and are not affected directly by changing water levels of the delta. Precipitation is the only source of moisture. Two broad divisions of vegetation are recognized: the forest (P1) which covers most of the areas and is dominantly white spruce (*Picea glauca*) with balsam poplar (*Populus balsamifera*) and paper birch (*Betula papyrifera*), and grassland (P2) found in small patches of xeric southwest slopes. Two prominent species in the grasslands are *Stipa spartea* and *Artemisia frigida*, with *Symphoricarpos occidentalis* and *Shepherdia canadensis* occupying the region between the open and forested areas. *Juniperus communis* is found in scattered locations on the open slopes and ledges.

1.2. Aquatic community-types

We recognized three important categories of water channels according to water movement and stage of development due to sedimentation. The first (C1 in Table 1) comprises streams and rivers flowing throughout the year, or at least throughout the unfrozen season of the year. Intermittent streams (C2) usually flow only during spring runoff and at flood time. As the upstream part of the delta has matured, these streams have been cut off and are no longer part of the main drainage network of the delta. The best example is Mamawi Creek which flows only when flood waters spill over from the Embarras River (Fig. 5). The third category, abandoned stream beds and meander scrolls (C3) are those channels that, through the maturing of the delta, no longer actively transport water during any season of the year. Usually they are replenished during spring runoff, and hold standing water for part or all of the season.

At the small scale, C1 and C2 types can be mapped as open water, but it is not practical to map the very small, sinuous C3 types. They have been indicated therefore by broken lines which serve also to indicate the genesis of the associated landforms. For example, the old streams that flowed through the meander areas built low levees and ridges that now appear as meander scrolls, marked by typical willow vegetation.

Standing water, lakes and ponds, are divided into four types according to basin shape and especially drainage, for the latter indicates the permanency of the water body during years of drawdown.

The first category is that of freely drained, deep and open lakes (S1). These water bodies are at least 2 m (6.5 ft) deep at some point and thus capable of tolerating severe reductions in water levels without drying up completely. Lake Athabasca falls into this type.

Freely drained, but shallow ponds and lakes (S2) are those with less than 2 m (6.5 ft) of water at their deepest point. These water bodies are connected by channels to the main drainage or flow system of the delta and therefore are subject to rapid drawdown at times of low water levels and rapid rise at times of high water levels. Consequently, they tend to be unstable and the vegetation in and around them is maintained in an early successional stage. The S2 class of lakes and ponds, the most extensive on Map 1, is further broken into areas of open water and areas with emergent vegetation.

Water bodies included in the restricted drainage (S3) class (perched basins) are those which are not connected to the main drainage system by surface channels. Their water loss is due mainly to evaporation and subsurface seepage. Such perched basins generally hold water long after freely drained water bodies have dried up during a period of low water levels. Because of their relative stability they often support emergent aquatic vegetation intolerant of drastically fluctuating water levels, such as *Scirpus acutus* (Dabbs, 1971b). Shoreline vegetation around S3 ponds is generally in a more advanced stage of succession than around freely drained lakes. Dense stands of *Carex atherodes* fringe these ponds, backed by *Calamagrostis canadensis* meadows and encroaching willows. This class is also divided into two subclasses: open water and areas with emergent vegetation.

The fourth category includes ponds with severely restricted drainage (S4). These areas are usually small in size, but unique in position and vegetation. They are either completely surrounded by high confining levees, e.g. oxbow lakes (Fig. 8), or by the banks of old meander scrolls. These ponds are recharged likely only when such rivers as the Embarras are in a high flood stage. These permanent water bodies have been negligibly affected by generally low water levels in the remainder of the delta over the 3-year period of observation. During a prolonged drought, these ponds would be the last to dry up.

The vegetation which characterizes S4 areas is quite different from the rest of the delta. Marginal floating mats have developed, made up of various sedges, such as *Carex aquatilis* and *C. rostrata; Calla palustris* and *Menyanthes trifoliata* are also important. Scattered low willows (*Salix pedicellaris*) occur. *Phragmites communis* and *Typha latifolia* frequently fringe the water edge, while willow and alder form a zone on the landward edge. The sequence is very similar to the distribution in such habitats in the Saskatchewan River Delta (Dirschl and Dabbs, 1969; Dirschl, 1972b).

Water lilies (*Nuphar variegatum*) usually make up the emergent aquatic vegetation in S4 ponds. Beyond the edge of the floating mat the water is generally too deep (>1 m (3 ft)) for other rooted aquatics to grow.

2. Land facet–vegetation classification at the scale of 1:10,000

Within the framework of the small-scale classification discussed above, each class was further broken down into land facet categories by interpretation of 1:6,000 and 1:30,000 air photos in black and white, true colour and infrared colour,[1] and mapped at the larger scale of 1:10,000. The land facet is comparable to the land type described by Lacate (1969) and the land unit of the Australian C.S.I.R.O. land inventory (Christian, 1952); viz., an area of land on a particular parent material having a fairly homogeneous soil. Land facet–vegetation units can be delineated at this scale as relatively homogeneous components of the landscape. Because of the extremely low relief of river deltas, vegetation–topographic relationships are sometimes not easily detected. However, visual changes in vegetation patterns were found to reflect small changes in topography, providing the clues for large-scale mapping and classification.

[1]Characteristics of the three films in respect to landform and vegetation interpretation are discussed by Dabbs (1971a).

The form and materials of the land facets control the types of vegetation which grow on them, primarily as a result of the associated drainage. As plants become established and develop, secondary factors come into play which in turn influence vegetation growth on the various sites. For example, accumulation of organic matter affects water retention and the formation of ground ice, which in turn affects drainage, soil temperature and biota.

The large-scale classification is summarized in Table 2. Five land facets are recognized as significant subdivisions of the deltaic ecosystem. A sixth land facet is the Precambrian rock outcroppings which occur as outliers of the Precambrian Shield within the delta.

2.1. The land facets

The following is a description of each of the six land facets mapped (Table 2).

2.1.1. Active delta (I)

Point bar and levee (IA)

Point bars are small deposits on the convex side of river or stream curves, the "slip off" slope left behind as the meanders migrate. They are an unstable habitat of actively flowing rivers, but are soon colonized by upland species when streams cease to flow.

Levees are the "raised berm or crest" (Leopold *et al.*, 1964, p. 317) adjacent to channels built up during years of flooding. They are made up of alluvium, which is relatively uniform in composition within the same region of the delta, and are generally well drained. Levee foreslopes are narrow and drop fairly steeply to the water's edge whereas the backslopes grade gently downward and merge into the delta plain or,

Figure 8. Oxbow lakes confined on all sides by high levees near the Embarras River.

Figure 9. Exposed lake bottom at the east side of Mamawi Lake.

more steeply, into perched basin and backswamp locations.

Lakeshore and delta plain (IB)

This facet consists of the nearly level shores of the open basin lakes, and former, exposed lake bottoms (Fig. 9). In appearance the lakeshore areas are extremely uniform and have developed by gradual settling in the basin of the silt load suspended in the lake water. This very extensive area of the delta is directly affected by the seasonal and annual fluctuation in the water levels of Lake Athabasca and the contiguous, open basin lakes.

2.1.2. Semiactive delta (perched basin and levee backslope) (II)

We have defined perched basins as those depressions, formed by low levees of old channels, which are not directly connected with the delta's main water system but which have been recharged, in most years, by the spring flood. Physiographically these basins are backswamps. However, owing to the frequent spill-in of flood waters, they are distinct from characteristic backswamps, being wetter and richer in nutrients and possessing different plant communities.

The backslopes of the encircling levees gradually slope toward the floor of the depressions and have, therefore, been included in this facet.

2.1.3. Inactive delta (III)

Backswamp (wet depression) (IIIA)

In this classification, we have confined the term backswamp to those basins which are in higher (and older) positions in the delta landscape than the perched basins, and thus are rarely inundated by flood waters (Fig. 10). Backswamps are nutritionally deficient, gradually filling with muck and peat from incomplete plant decomposition and developing into bogs or muskegs.

Meander scrolls (dry channel) (IIIB)

Meander scrolls are dried up channels which support fen and upland vegetation.

Figure 10. A typical backswamp depression nearly covered over by a floating sedge mat.

They result when meander loops are cut off, forming oxbow lakes, which, in turn, dry out through evaporation or fill in through peat accumulation leaving a sinuous depression, the meander scroll or scar.

2.1.4. Precambrian outcrop (IV)

Existing outcroppings of granite bedrock are treated as a facet, although not strictly part of the deltaic landscape. They originally were islands in postglacial Lake Athabasca around which the delta filled in by alluvial deposition (Fig. 3).

2.2. Dominant plants and autecological relations

This section describes the vegetation types (named after dominant species) on each of the six land facets, with notes on autecological and successional relationships. The data were collected from numerous sites. These vegetation types, as interpreted from 1:6,000 and 1:30,000 imagery formed the units used to map the field transects (see Maps 2 and 3).

2.2.1. Point bar and levee (IA)

Equisetum. Dominant species: *Equisetum fluviatile*. *Equisetum* exists in monodominant stands on the point bars of such rivers as the Chenal des Quatre Fourches and outlet channels from Mamawi Lake.

Eleocharis–Glyceria. Dominant species: *Eleocharis palustris* and *Glyceria grandis*. This class is found on more stable sites, on point bars of intermittent streams where erosion and development occur for only short periods during spring floods or runoff.

Salix interior. On older point bars and on levees subject to frequent flooding along flowing rivers, *Salix interior* is usually dominant, though scattered *S. rigida* may also be present. Due to a lack of organic litter to hold moisture, these positions are very dry during periods of low water levels.

Salix–Alnus. Dominant species: *Salix bebbiana*, *S. discolor* and *Alnus tenuifolia*. On levees rarely subject to flooding, these tall shrub communities are common.

Betula. Dominant species: *Betula papyrifera*. Scattered individuals or small clumps are found with tall willows and alders along high stream levees. However, this species is usually found mixed with other forest plants on the river levees and is monodominant in only a few stands along the Embarras River.

Populus. Dominant species: *Populus balsamifera*. High, well-drained levees of rivers and major channels are dominated by this species. This type forms the transition from the *Salix–Alnus* shrub to the white spruce forest in the highest position in the landscape.

Picea. Dominant species: *Picea glauca*. Within the delta, white spruce is found only on the highest river levees, the best drained positions in the landscape. They may reach up to 35 m (115 ft) tall and 2 m (6.5 ft) d.b.h. Balsam fir (*Abies balsamea*) is a common associate.

2.2.2. Lakeshore and delta plain (IB)

Potamogeton. Various pondweeds (*Potamogeton* spp.) are abundant near lakeshores where the water exceeds 1 m (3 ft) in depth.

Sparsely vegetated mudflat. These are areas which havê very recently been exposed and support only scattered seedlings. There was no definite indication as to what species will eventually dominate.

Senecio. Dominant species: *Senecio congestus*. This type, found in very shallow water on gradually sloping bottoms, grows rapidly, blooms in mid July and by mid August of the same season may be invaded by *Scirpus* and *Typha*. The type rarely persists beyond 1 or 2 years.

Scirpus. The dominant species, *Scirpus validus*, is usually considered emergent; however we found it growing vigorously on recently exposed lake bottoms. *Typha latifolia* also occurs. Evidently these species are adapted to germination under wet mud conditions (see Harris and Marshall, 1963).

Eleocharis–Carex. Dominant species: *Eleocharis palustris* and *Carex aquatilis*. As lake water levels continue to drop and areas which were previously lakeshores dry up, *Eleocharis* tends to succeed *Scirpus*. Though the surface may be dry, the water table, at 50 cm (20 in.) in mid July 1970, is still high under this vegetation type.

Beckmannia–Scolochloa–Carex. Dominant species: *Beckmannia syzigachne*, *Scolochloa festucacea* and *Carex* spp. This heterogeneous type often is found on mudflats that had been exposed for at least 1 year. Species composition seems to depend on viable seeds present in the moist silt. The type has been observed to rapidly develop into a *Carex* fen.

Carex. Dominant species: *Carex atherodes* and *Carex aquatilis*. This is also an early seral stage which may persist for 1 or 2 years in slightly drier conditions than *Eleocharis*. Where there is annual spring flooding, with a slow drawdown, the *Carex atherodes* may persist (Dirschl and Coupland, 1972). However, as water levels have remained low since 1968, with only brief spring flooding, *Salix* spp. are invading these areas.

Salix–Carex. Dominant species: *Carex atherodes*, *Salix planifolia* and *S. rigida*. This type covers much of the recently exposed lake bottom areas. Here the willows have rapidly overtopped the sedges of the field layer. Mature areas of this type are extensive farther away from the lakes.

Calamagrostis. Dominant species: *Calamagrostis inexpansa*. The present distribution of this type is not related to the recent low water levels. *Calamagrostis inexpansa* forms dense, monodominant stands where the substrate is moist to wet but not submerged for much of the growing season. It thus occupies a slightly higher and drier position in the landscape than the *Carex* type.

Phragmites. Dominant species: *Phragmites communis*. Clonal groupings of *Phragmites* are found in several areas which evidently were the shorelines of lakes under the former water regime. Aerial photographs show that the clones have persisted in their present locations for many years. The monodominant nature of these stands indicates that their growth habit and the microclimate which they create excludes other fen species. Seedlings and runners of *Phragmites communis* are now expanding these dense stands and may, if present conditions persist, close the openings between the clones. The vigorous expansion of the stands indicates that the low moisture conditions are not detrimental and may actually be favourable to the species.

2.2.3. Perched basin and levee backslope (II)

Potamogeton–Nuphar. Dominant species: *Potamogeton* spp. and *Nuphar variegatum*. Pondweeds and water lilies are abundant in relatively deep perched basins, whereas *Myriophyllum exalbescens* and *Ranunculus* spp. are frequent in slightly shallower waters.

Scirpus–Typha. Dominant species: *Scirpus validus* and *Typha latifolia*. These species form bands at the edge of deeper basins or may cover the entire surface of shallow (<60 cm (24 in.)) basins.

Senecio. The dominant species, *Senecio congestus*, initially covered large areas as the lakes declined. This type now occurs only in perched basins which have almost dried out.

Equisetum. Dominant species: *Equisetum fluviatile*. This is not a widespread dominant type. It is found on the backslopes of the lower levees along Mamawi Channel, spreading out to what were, under former water levels, shoreline vegetation zones on the east side of Mamawi Lake. Soil profiles indicate that *Equisetum* has persisted in these positions for a very long time, as stalks were found at a depth of 1 m (39 in.). Willow seedlings are now beginning to invade these stands.

Scolochloa. Dominant species: *Scolochloa festucacea*. This species is found in the wettest depressed meadows which held shallow water for most of the season under the former water regime of the delta. Under the present drying regime there is very little surface water, but the subsoil is saturated.

Eleocharis–Carex. Dominant species: *Eleocharis palustris* and *Carex rostrata*. This type is common on drying basin bottoms and tends to succeed *Scirpus validus* and *Typha latifolia* under these conditions.

Carex. Dominant species: *Carex atherodes* and *C. rostrata*. Areas around the edge of perched basins, generally flooded during the early part of the growing season but exposed later on, are often dominated by *Carex atherodes* and *C. rostrata*. Persistent surface water leads to the gradual replacement of *C. atherodes* by species such as *Scolochloa festucacea*. Prolonged drier conditions decrease vigour noticeably.

Calamagrostis. Dominant species: *Calamagrostis canadensis*. *Calamagrostis* is positioned between the marshy species and the upland woody species. On the moderately high levees it is positioned on the backslope, with willows dominating the better drained crest of the levee.

The high insulating effect of the sod formed by this species results in the retention of ground ice at a depth of 50 cm (19.7 in.) until mid July (Dabbs, 1971b). It may be that *Calamagrostis* in this position creates a physical environment which excludes invading species until either the form of the land is changed sufficiently by sedimentation or the general ground water level is lowered.

Salix. Dominant species: *Salix planifolia* and *S. bebbiana*. Low willows (*S. planifolia*) are the first to replace *Calamagrostis* on the backslope of levees. As the delta ages, perched basins are filled, drainage conditions improve, and larger willows invade. Tall willows (*S. bebbiana*) eventually dominate on the backslopes of the highest levees in the old portions of the delta.

2.2.4. Backswamp (wet depression) (IIIA)

Potamogeton–Nuphar–Myriophyllum. Dominant species: *Potamogeton* spp., *Nuphar variegatum*, and *Myriophyllum exalbescens*. Submerged and floating-leaf aquatic species occur in all backswamps; they contribute organic plant matter to the gradual filling of the basin.

Scirpus–Typha. Dominant species: *Scirpus validus* and *Typha latifolia*. These emergents occur in shallow waters of most backswamps.

Phragmites. Phragmites communis forms dense, monodominant stands along the margins of backswamp lakes and ponds. Frequently, portions of the buoyant root mat break off and become floating islands.

Equisetum–Acorus. Dominant species: *Equisetum fluviatile* and *Acorus calamus.* This type forms dense stands on wet silt surfaces adjacent to backswamp lakes and ponds.

Carex–Potentilla. Dominant species: *Carex rostrata*, *C. aquatilis*, and *Potentilla palustris.* This type occurs in the form of floating mats of fibrous plant debris within backswamp lakes in the highest (and oldest) delta locations.

Salix–Menyanthes. Dominant species: *Salix pedicellaris* and *Menyanthes trifoliata.* *Carex rostrata* and *Calla palustris* are also common. This type occurs in the same landscape position as the previous type. It appears that *S. pedicellaris* and *Menyanthes* establish themselves on the floating mat previously formed by the *Carex–Potentilla* type.

2.2.5. Meander scroll (dry channel) (IIIB)

Carex. Dominant species: *Carex atherodes.* This type is found in meander scrolls which may be flooded temporarily each spring.

Calamagrostis. Dominant species: *Calamagrostis canadensis.* Meander scroll channels which are not subject to frequent or persistent flooding often support *Calamagrostis.*

Salix. Dominant species: *Salix bebbiana.* The levee of the Embarras River is frequently dissected by meander scrolls which are well drained at the periphery and support tall willows.

Betula. Dominant species: *Betula papyrifera.* In the meander scrolls in the larger river levees, white birch frequently dominates the better drained positions. Birch stands are often side by side with stands of white spruce.

2.2.6. Precambrian outcrop (IV)

Populus–Picea. Dominant species: *Populus balsamifera* and *Picea glauca.* On some sites, however, *Betula papyrifera* is the dominant species. These trees are rooted in a very shallow layer (10–30 cm) (4–12 in.) of mineral and organic matter over bedrock. Their only source of moisture is rainfall.

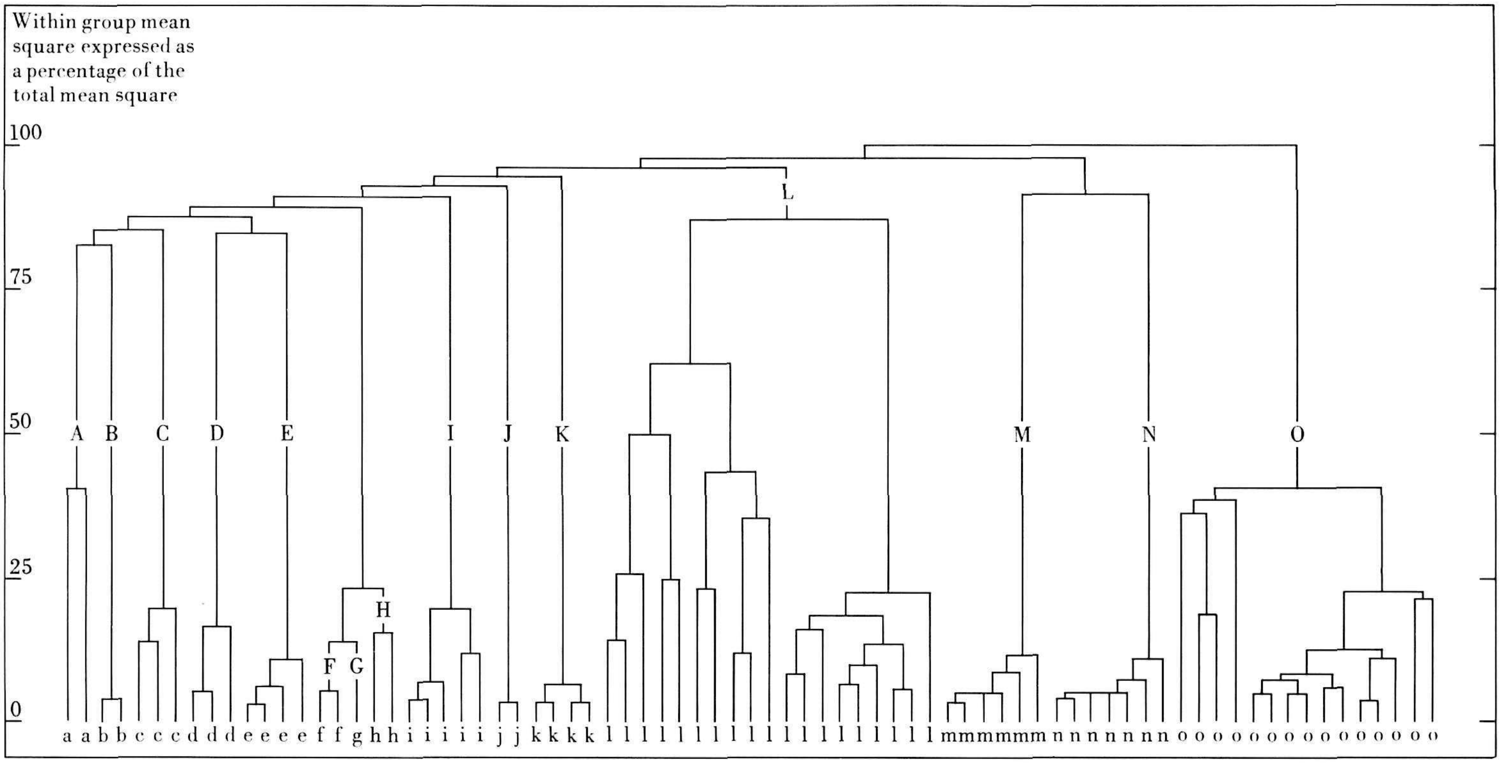
Juniperus. Juniperus communis often forms a narrow strip around the edges of the *Populus–Picea* type.

Stipa–Artemisia. Dominant species: *Stipa spartea* and *Artemisia frigida.* These "grassland" species grow on well-drained, southwest slopes which have a very shallow layer of accumulated organic material over the bedrock. *Juniperus horizontalis* is a common associate in this type.

Vegetation–environmental relationships

Figure 11. Association analysis hierarchy showing the grouping of major vegetation groups.

Figure 11



1. Multivariate classification

Examination of the fusion-dendrogram, resulting from the agglomerative classification program, revealed that the total vegetational variation in the 89 stand samples could be grouped into 15 ecologically significant final groups (Fig. 11). For each final group, the prevalent ground stratum species, i.e., those occurring in a majority of the stands, were determined (Table 3). Average organic matter content and mineral soil texture were computed. Land facets and vegetation types — according to the large-scale classification — into which the stands in each final group fell, were also identified.

The agglomerative classification program proved fairly successful in identifying major permutations of land facets and vegetation types occurring in the delta, thus lending support to the value of the air photo-based classification as an ecological tool.

Following is a brief description of the final groups and their vegetation–environmental relationships. In order to facilitate reference to the land facet–vegetation types of the large-scale classification (see Table 2), the description follows the same sequence.

Group F. Stands in this group are associated with *Equisetum* fen on point bars. The substrate consists of recent, fine-textured alluvium; soil organic matter is almost absent. *Equisetum fluviatile* is the dominant species; *Salix interior* and *E. pratense* are common associates.

Group M. Stands in this group are associated with more stabilized point bars. They tend to be more complex in species composition than those in Group F.

Group E. This group consists of *Eleocharis–Glyceria* vegetation on point bars and lakeshores. The species composition is characteristic of short-lived pioneer communities on newly exposed wet mudflats. The substrate is fine-textured and organic matter content is very low. Prevalent species are *Eleocharis acicularis*, *Scirpus validus* and *Glyceria* spp.

Group H. Stands falling into this final group are typically associated with *Salix–Alnus* shrub on low, frequently flooded levees. The substrate is fairly sandy and contains an average of 18% organic matter. *Equisetum pratense* is the dominant ground stratum species; *Rubus idaeus* var. *strigosus*, *Rosa woodsii*, *Cornus stolonifera* and *Viburnum trilobum* are common low shrubs in this community type.

Group G. This group consists of *Populus balsamifera* communities on stream levees which are rarely flooded. The substrate is not as sandy as the previous type but organic matter averages 30%, indicating that these are older sites than those of Group H. *Equisetum pratense* is still the

Table 3
Prevalent ground stratum species and mean soil parameters for the final groups of the agglomerative vegetation classification. Correspondence of the groups with land facets and vegetation types of the large-scale air photo classification (see Table 2) are also given

Final group	Prevalent ground stratum species	Organic content, %, in upper 30 cm	Particle size distribution, %, in mineral soil fraction			Soil pH	Land facet	Vegetation type
			Sand	Silt	Clay			
A	*Carex rostrata* *Lysimachia thyrsiflora* *Potentilla palustris*	>80				6.4	Backswamp (IIIA)	*Carex–Potentilla* and *Salix–Menyanthes*
B	*Calamagrostis canadensis* *Polygonum amphibium*	49				5.2	Perched basin (II)	*Calamagrostis*
C	*Phragmites communis* *Carex atherodes* *Salix planifolia* *Rorippa islandica* *Puccinellia nuttalliana*	3	7	66	27	6.9	Lakeshore (IB)	*Phragmites*
D	*Cornus canadensis* *Mitella nuda* *Viburnum edule* *Rubus pubescens* *Hylocomium splendens*	35	15	67	18	6.2	High levee (IA)	*Picea*
E	*Eleocharis acicularis* *Scirpus validus* *Glyceria borealis* *Glyceria grandis*	5	3	59	38	6.9	Point bar (IA) and lakeshore (IB)	*Eleocharis–Glyceria*
F	*Equisetum fluviatile* *Equisetum pratense* *Salix interior*	4	0	56	44	6.9	Point bar (IA)	*Equisetum*
G	*Equisetum pratense* *Rubus pubescens* *Maianthemum canadense* *Rubus idaeus* var. *strigosus* *Rosa woodsii*	30	8	49	43	6.4	Intermediate levee (IA)	*Populus*
H	*Equisetum pratense* *Rubus idaeus* var. *strigosus* *Rosa woodsii* *Cornus stolonifera* *Viburnum trilobum*	18	24	49	27	6.5	Low levee (IA)	*Salix–Alnus*
I	*Typha latifolia* *Scirpus validus* *Carex atherodes* *Carex aquatilis* *Glyceria borealis* *Eleocharis palustris*	3	1	66	33	7.1	Perched basin (II) and lakeshore (IB)	*Typha–Scirpus*
J	*Calamagrostis inexpansa* *Galium trifidum* *Polygonum amphibium* *Carex atherodes*	17	3	43	54	5.8	Delta plain (IB)	*Calamagrostis*

cont'd. on page 26

dominant field-layer species, but the prevalence of *Maianthemum canadense* and *Rubus pubescens* indicates drier and more mature site conditions than Group H.

Group D. This group contains *Picea glauca*-dominated stands in high, dry levee positions. The high organic matter content of the upper soil stratum and the dense carpet of feather moss (*Hylocomium splendens*) suggest that these are very mature sites almost totally out of reach of floods.

Group L. This very large group of stands is made up of early successional communities on emerging silt surfaces of lakeshores and delta plains. These communities grow on recent, fine-textured alluvium, low in organic matter. Total species composition is quite varied and probably depends mainly on the accidental presence of viable seeds within the wet silt, following drawdowns. Prevalent species are *Scirpus validus*, *Eleocharis palustris*, *Salix interior*, *Carex atherodes*, *Beckmannia syzigachne* and *Rorippa islandica*.

More discriminatory analyses would be required to sort out fine environmental and successional differences among the stands in this group.

Group O. This large group of stands is associated with *Carex* fens on lakeshores and delta plains. It appears that these communities are successional to the *Eleocharis–Carex* type of Group L and are on slightly higher and thus drier sites. *Carex aquatilis* and *C. atherodes* are dominant; *Beckmannia syzigachne* and *Eleocharis palustris* are common associates. *Phragmites communis* and *Salix interior* seedlings are more scattered.

Group C. Phragmites communis–dominated stands on the shore of delta lakes make up this group. The sites appear to be identical to those in Group O.

Group J. In this group, *Calamagrostis inexpansa* stands occur at slightly higher elevations of the delta plain. The substrate is fairly rich in organic matter, indicating that these are relatively mature and successionally advanced communities.

Group I. Stands in this group predominantly occur at lower elevations in the

Table 3, cont'd.

Final group	Prevalent ground stratum species	Organic content, %, in upper 30 cm	Particle size, distribution, %, in mineral soil fraction Sand	Silt	Clay	Soil pH	Land facet	Vegetation type
K	*Scolochloa festucacea* *Carex atherodes* *Eleocharis palustris* *Rorippa islandica* *Salix interior*	23	5	49	46	6.0	Perched basin (II)	*Scolochloa*
L	*Scirpus validus* *Eleocharis palustris* *Salix interior* *Carex atherodes* *Beckmannia syzigachne* *Rorippa islandica*	4	8	54	38	6.9	Lakeshore (IB)	*Eleocharis–Carex*
M	*Equisetum fluviatile* *Carex atherodes* *Epilobium glandulosum* *Carex rostrata* *Epilobium angustifolium*	3	0	64	36	6.8	Point bar (IA)	*Equisetum*
N	*Carex atherodes* *Calamagrostis inexpansa*	11	4	49	47	6.9	Perched basin (II)	*Carex*
O	*Carex aquatilis* *Beckmannia syzigachne* *Carex atherodes* *Salix interior* *Eleocharis palustris* *Phragmites communis*	5	2	62	36	7.1	Lakeshore and delta plain (IB)	*Carex*

shallow water of perched basins. The substrate consists mainly of flood-deposited silt. *Typha latifolia*, *Scirpus validus*, *Carex* spp., *Glyceria borealis* and *Eleocharis palustris* are the prevalent species.

Group K. Scolochloa-stands make up this group and occur at slightly higher sites within perched basins. The alluvial substrate has an average organic content of 23%, indicating that vegetative growth has continued for quite some time.

Group N. Carex atherodes meadows, situated near the outside edge of perched basins, are found in this group. In addition to the dense growth of *Carex atherodes*, *Calamagrostis inexpansa* is the only other species consistently present. These stands are thought to be flooded in most years during the early part of the growing season but above water during the remainder of the growing season.

Group B. This group is associated with the outside edge of the perched basins, i.e., sites that are only briefly flooded in most years. *Calamagrostis canadensis* forms almost pure stands in this position over a substrate very rich in accumulated organic matter. These communities appear to be very persistent in this location.

Group A. This final group occurs on floating mats of backswamps rarely in contact with flood waters, and consists almost entirely of poorly decomposed organic matter. *Carex rostrata*, *Lysimachia thyrsiflora*, *Menyanthes trifoliata*, and *Potentilla palustris* are prevalent herbaceous species; *Salix pedicellaris* is a common low shrub.

2. Species distribution in relation to moisture gradient

The agglomerative classification produced clusters according to species presence or abundance in the individual stands. It was then found possible to associate distinct positions in the landscape with these groups (see previous section).

As exact topographic data for a number of the field transects had been obtained, the converse approach, viz., to determine species occurrence in stands ordered along an environmental gradient could also be tested. Specifically, 39 stands sampled in 1970 in active delta locations (lakeshores, delta plains, levees) were ordered according to their elevation above Lake Athabasca and Mamawi Lake whose levels have controlled the relative wetness of these sites. Ranking of the stands according to elevation represents a gradient of relative moisture status (Table 4).

The species align themselves in a predictable manner, ranging from the emergent aquatics of shallow water and immediate lakeshores through fen species to those typical of tall shrub and forested communities on high levees. Table 4 also indicates that many species are abundant only within a short width of the moisture gradient, while others (e.g., *Carex atherodes*, *C. aquatilis*, *Equisetum fluviatile*) have very wide amplitudes in respect to the moisture gradient. The latter are species typical of the extensive areas of the delta directly influenced by the natural seasonal and annual fluctuations of lake water levels.

Table 4
Matrix relating major species occurrence to a gradient of relative site moisture as indicated by elevations above lake level. Only species cover values of 5 per cent or greater are included

Stand	27	11	22	13	12	21	28	6	16	3	2	1a	1b	35	26	4	14	17	43	42	36	30	25	29	20	9	37	8	24	44	41	18	19	31	40	38	34	32	33
Species	Wet ———																																						——> Dry
Senecio congestus	33																																						
Scirpus validus	6																																						
Typha latifolia																15																							
Eleocharis palustris	24	21	8		6	24	20	35				5	6	21							15																		
Beckmannia syzigachne		9						7			6																			27									
Salix interior			11	6	11	7																																	
Carex atherodes						8		21							22	10	27			84	22	21	11	46		9							66						
Chenopodium glaucum			7																																				
Salix planifolia				10		6			11				9			8																27							
Sium suave							6			14																													
Juncus nodosus								6																															
Rorippa islandica									9																														
Phragmites communis									16										73											5									
Chenopodium album									6																														
Puccinella nuttaliana									9																														
Carex aquatilis										17	21	27	11													43		37											
Deschampsia caespitosa										6																													
Juncus brevicaudatus											9																												
Salix rigida													8													7						12							
Glyceria grandis														23							5																		
Eleocharis acicularis														9																									
Equisetum scirpoides																14																							
Scolochloa festucacea															51			53				64																	
Equisetum fluviatile																			7						76						51	47							
Calamagrostis inexpansa																					11					7	88		80				86						
Galium trifidum																							33																
Calamagrostis canadensis																																			45				
Rosa woodsii																																			3	13			
Equisetum pratense																																			23	19		9	
Maianthemum canadense																																			12				
Salix discolor																																			17	10			
Salix bebbiana																																				57			
Populus balsamifera																																					34		
Betula papyrifera																																					7	12	
Rubus pubescens																																						8	
Cornus canadensis																																						17	
Picea glauca																																						64	58
Abies balsamea																																							7
Mitella nuda																																							6
Hylocomium splendens																																							81

Plant successional trends

Figure 12. Mudflat with scattered sedge seedlings in 1968.

Figure 13. Dominant *Carex atherodes* on the same site in 1970.

1. Short-term adjustments to falling water levels

From 1968 to 1971, the level of Lake Athabasca has remained several feet below the previous long-term average (Bennett, 1971). Water levels of the delta lakes connected with Lake Athabasca have experienced a similar decline. Owing to the slight relief in the delta, the falling water levels have led to gross reductions in open water areas. By the summer of 1970, the total area of the nine largest water bodies had decreased by 28% (Dirschl, 1972a). The numerous perched basins dotting the delta plain had, in the absence of the annual spring flood, progressively dried up through evaporation and transpiration at the approximate rate of 13% per year (G. H. Townsend, pers. comm.).

The extensive silt flats, emerging from the shrinking lakes and ponds, have experienced extremely rapid colonization by germinating seeds present within the silt or distributed by wind. This colonization proceeded from an open mudflat (Fig. 12) with scattered seedlings of emergent aquatics, sedges and grasses during 1968 to an immature fen, consisting of a variety of herbaceous plants in 1969. By summer 1970, dense sedge meadows, dominated by *Carex atherodes* had developed (Fig. 13). On the silt flats surrounding Mamawi Lake, numerous willow seedlings began to germinate in 1969; by 1971 they had reached a height of 5–6 ft and had become visually dominant (Fig. 14). Elsewhere, particularly in perched basins, willow seedlings were less abundant but the development of herbaceous cover proceeded at a similar rate.

Study plots and repeated aerial photography have also shown that sedge (*Carex*) meadows, which existed prior to 1968, are beginning to change toward *Calamagrostis canadensis* meadows, reflecting drier soil conditions. Previously existing, small *Phragmites communis* clumps have also begun to spread over wider adjacent areas of previous lakeshore.

Water levels as low as those experienced during 1968–71 have occurred natur-

Figure 14. Willows were visually dominant on the site in 1971.

ally from time to time, e.g., during 1944–46 (Fuller, 1951; Bennett, 1971). Consequently, the currently observed plant colonization of lake bottoms must also have occurred during previous dry periods but subsequently ceased with the returning floods. A number of the soil pits dug in this study have revealed thin layers of fen vegetation and charcoal seams buried beneath flood-deposited silt (Dirschl, 1972a).

It is quite clear that the described colonization of newly emerged silt sites that has occurred in response to the falling lake levels or the drying up of perched basins, represents a stage in the long-term successional trends operating in the delta. These long-term events will be discussed in the following section.

2. Long-term successional trends

Raup (1935, p. 88) produced an outline of plant succession in the Athabasca, Peace and Slave River lowlands, based on his field research in the years 1926–30. Our studies have led us to modify Raup's successional sequences to portray accurately the long-term successional processes that we consider to operate in the Peace–Athabasca Delta (Fig. 15).

Within the total delta complex, Fig. 15 distinguishes three broad categories according to the prevailing physical deltaic processes: (1) active delta, (2) semiactive delta, and (3) inactive delta.

As described earlier, the *active delta* consists of those locations directly affected by the hydrological interactions of the major rivers and Lake Athabasca. *Semiactive delta* includes locations which are not connected with the major hydrological system but are recharged by the spring flood in most years. The *inactive delta* category is affected by the spring flood only rarely during extremely high water years. Therefore, in broad terms, nutrient availability decreases from left to right.

The various plant communities recognized in the replacement series have been grouped into five community-types as follows: (1) aquatic communities; (2) shore communities; (3) meadow communities; (4) shrub communities; and (5) forest communities.

In this sequence within active and semiactive delta locations, aquatic and emergent communities are replaced by various shoreline pioneers on emerging mudflats which develop into fen meadows. These meadows then change into willow shrub communities and eventually into terminal forest communities. It is obvious from Fig. 15 that succession in the delta does not follow a single pathway, but takes the form of a branching network in which various species or species-groups may dominate in different locations during the same seral stage and fuse during a succeeding stage. The variety of alternate dominance-types is particularly great among shoreline and meadow communities.

It is not always clear why sites which appear to be identical are occupied by different species groups. The following factors, however, are involved in producing this diversity:

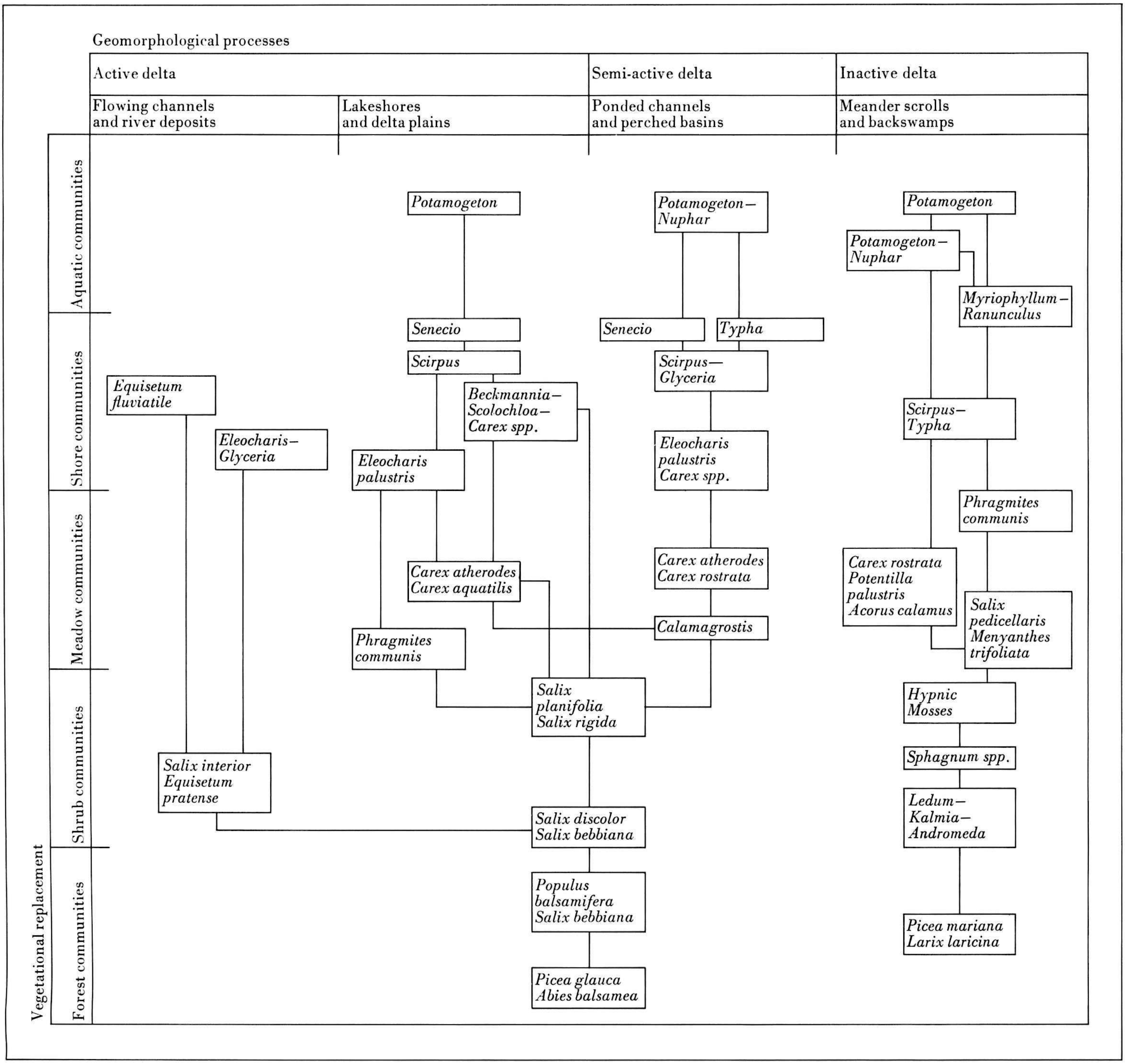
a. The availability of plant seeds at the time when conditions are favourable for germination and

b. minute local differences in moisture and nutrient status.

While the vegetative replacement series in active and semiactive delta environments is mainly driven by allogenic forces, succession in the inactive delta locations is controlled predominantly by autogenic processes. Here the lack of a source of nutrient-rich waters results in a gradual

Figure 15. Outline of plant successional trends in the Peace–Athabasca Delta.

Figure 15



fixing of the available nutrients in undecomposed vegetative matter, in the growth of floating sedge mats over the basin, and finally the filling of the entire basin with muck and peat.

In this process, the peat surface eventually grows completely out of reach of the mineral water table, is invaded by *Sphagnum* mosses, and develops into an ombrotrophic bog or muskeg. Because of the previous frequency of high floods, inactive delta is largely confined to the upper portion of the Athabasca Delta and even there has not evolved beyond the floating mat stage. Permanent elimination of the spring flood, however, would speed the development toward ombrotrophic bog in backswamp locations. For example, in the Saskatchewan River Delta, where major floods have in the past been less frequent, extensive bogs are found (Dirschl and Coupland, 1972).

The time frame, within which long-term succession proceeds, is not well understood. We know that the entire vegetational development in the Peace–Athabasca Delta took place during the past 10,000 years. But it is difficult to determine the average rate by which seral stages replace each other. The narratives of the early explorers and fur traders who passed through the delta suggest that the delta's overall appearance has not changed in 300 years (see Fuller and LaRoi, 1971).

Locally, however, some successional changes can be verified. For example, Raup mapped an area south of Mamawi Lake in 1930 (Raup, 1935). This area (Transect 4) was remapped during the present study from air photos taken in 1970 (Dabbs, 1971b). Comparison of the two maps shows that the younger low-lying positions close to the lake have all changed to some extent. Most of these locations in 1930 consisted of meadows dominated by *Carex atherodes*. Forty years later, in many of these low-lying areas *Calamagrostis* meadows had replaced the *Carex* stage and, in some areas, low willow shrub had become established.

From our study of the colonization of mudflats following the closure of Bennett Dam, we know that early successional changes from bare silt surface to immature fen to meadows and low willow shrub can occur within a few years under conditions of continually low water levels.

From the data on hand, it is apparent that:

a. successional events in the delta are mainly controlled by the water regime;

b. vegetative replacement under falling or persistently low water levels, as caused by the regulation of the Peace River, does proceed very rapidly in the initial stages but more and more slowly through the shrub and forest types; and

c. in the course of the natural hydrological cycle, years of below average water levels are followed by years of above average levels. Under these conditions, sites directly influenced by this fluctuating water regime are held at early successional stages until ongoing deltaic processes such as channel shifting or levee building drastically alter the local water regime.

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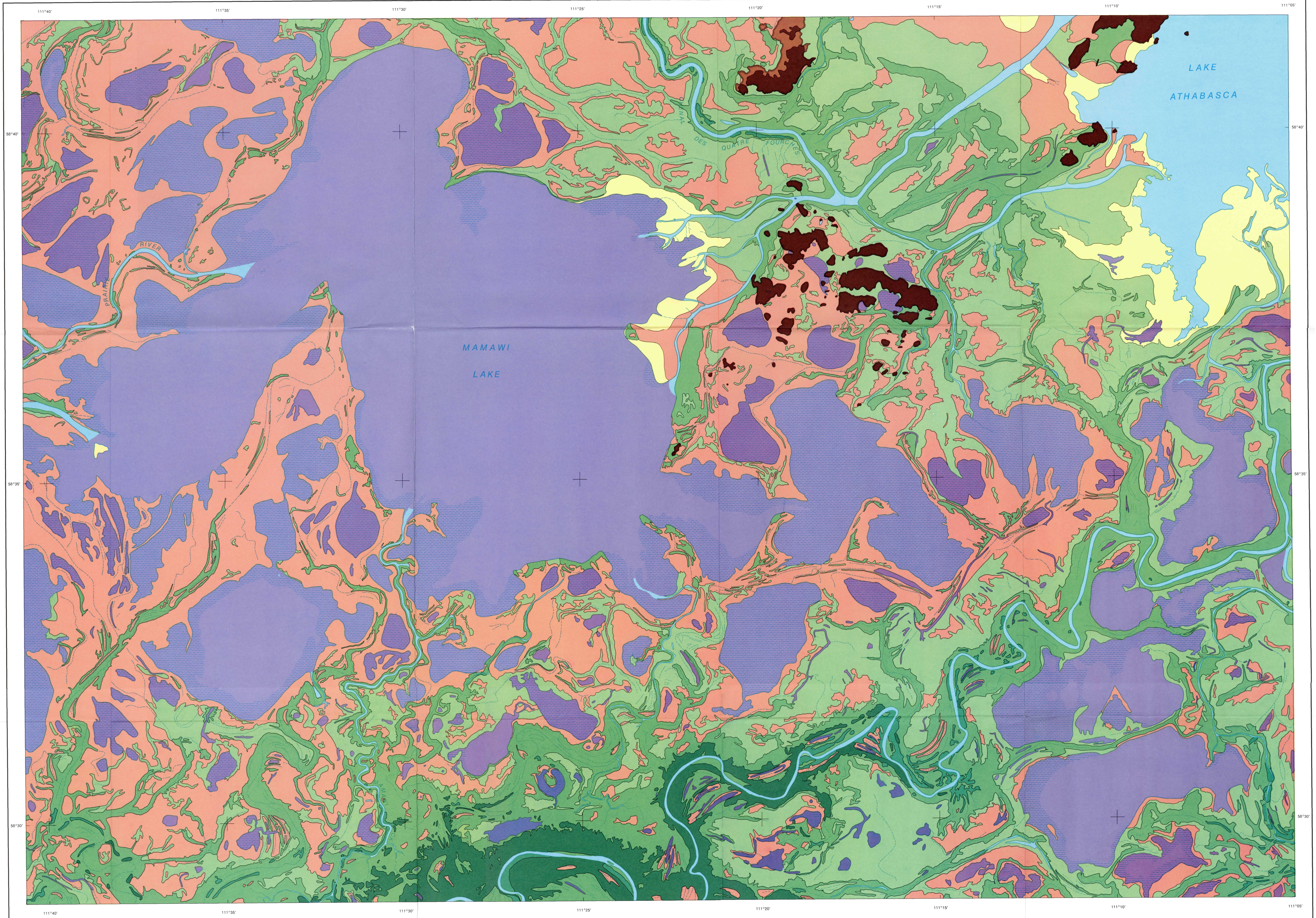

Map 1. Vegetation of the Mamawi Lake study area

Report Series: Landscape classification and plant successional trends in the Peace – Athabasca Delta

Scale 1 : 37,000

Miles 1 0 1 2 3 Miles

Kilometres 1 0 1 2 3 4 Kilometres

Delta

Vegetation

- Coniferous Forest
- Deciduous Forest
- Tall Shrub
- Low Shrub
- Fen
- Immature Fen

Precambrian Rock

Vegetation

- Forest
- Grass

Water Channels

- Flowing streams and rivers
- Intermittent streams
- Abandoned stream beds and meander scrolls

Standing Water

Freely drained — deep and open

Freely drained — shallow
- — open
- — with emergent vegetation

Restricted drainage
- — open
- — with emergent vegetation

Severely restricted drainage
- — open
- — with emergent vegetation

Map prepared by Cartographic Section, Graphic Services Division, 1973.

From 1955–56 aerial photography.

Map 1. Vegetation of the Mamawi Lake study area

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Map 2. Land facet-vegetation breakdown of field transect 4 including elevational profiles

Report Series: Landscape classification and plant successional trends in the Peace – Athabasca Delta

Map prepared by Cartographic Section, Graphic Services Division, 1973.

Active delta (I)

Point bar and levee (IA)

— Eleocharis-Glyceria
— Salix interior
— Salix-Alnus
— Populus
— Picea

Lakeshore and delta plain (IB)

— Scirpus
— Eleocharis-Carex
— Carex

Semiactive delta (II)

(perched basin and backslope of levee)

— Potamogeton-Nuphar
— Typha-Scirpus
— Scolochloa
— Eleocharis-Carex
— Carex
— Calamagrostis
— Salix

Inactive delta (III)

Back swamp (wet depression) (IIIA)

— Potamogeton-Nuphar - Ranunculus
— Phragmites

Meander scroll (dry channel) (IIIB)

— Carex
— Salix

Water channels

— Flowing streams and rivers
— Intermittent streams

Standing water

— Freely drained A
— Restricted drainage

Soil type

— Organic soil
— Mineral soil

Location of stands sampled 27

Actual survey line

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Map prepared by Cartographic Section, Graphic Services Division, 1973.

Map 3. Land facet-vegetation breakdown of field transect 16 including elevational profiles

Report Series: Landscape classification and plant successional trends in the Peace – Athabasca Delta

Active delta (I)
Point bar and levee (IA)

— Salix-Alnus
— Populus
— Picea

Semiactive delta (II)
(perched basin and backslope of levee)

— Carex
— Salix

Inactive delta (III)
Backswamp (wet depression) (IIIA)

— Potamogeton-Nuphar-Ranunculus
— Scirpus-Typha
— Equisetum-Acorus
— Carex-Potentilla (floating mat)
— Salix-Menyanthes (floating mat)

Water channels

— Flowing streams and rivers
— Intermittent streams
— Abandoned stream beds

Open water

— Restricted drainage

Actual survey line