Floristics of a plant succession sequence in the Mackenzie Delta, Northwest Territories

By Don Gill *

Abstract: The most dynamic plant succession in the Mackenzie Delta occurs along convex bends of actively shifting distributaries. In such locations 5 plant communities commonly make up the seral sequence. Succession is initiated on the newly deposited sediment of prograding slipoff slopes, and the subsequent physical (allogenic) influences of flooding and sedimentation severely restrict the number of species in the first 2 seres. The third sere originates above normal flood level so that a more diverse flora is able to develop. Retrogression of the sequence occurs in the fourth sere where ponding of water in meander scroll depressions causes the successional trend to again be dominated by physical influences. In the fifth sere, flooding and sedimentation are again minimal, and the climax community attains a relatively rich flora. This study analyzes the successional status of each species making up this sequence, and outlines how flooding and sedimentation influences the successional direction.

Zusammenfassung: Die dynamischste Pflanzensukzession im Mackenzie Delta findet sich auf Gleithängen pendelnder Flußarme. An solchen Standorten bilden zumeist 5 Gesellschaften eine Serienfolge. Die Sukzession beginnt auf den frischen Sedimenten vorrückender Gleithänge. Äußere Einflüsse wie Überflutung und Sedimentation beschränken die Artenzahl in den ersten beiden Serien. Die dritte Serie beginnt über dem normalen Überflutungsniveau, so daß sich eine artenreiche Flora entwickeln kann. Rückentwicklungen erfolgen in der vierten Serie, wenn durch stehendes Wasser in den Mäanderarmen die physikalischen Einflüsse erneut vorherrschen. In der fünften Serie sind die Einflüsse von Überflutung und Sedimentation derart gering, daß sich ein relativ reiches Klimaxstadium entwickeln kann. In der Untersuchung werden die Stellung jeder einzelnen Art innerhalb der Serie sowie der Einfluß von Überflutung und Ablagerung auf die Entwicklung der Sukzession beschrieben.

Introduction

There are few regions in Northern Canada that have been as intensively investigated as the Mackenzie Delta area, and few northern localities have received the scrutiny of such a great variety of scientific disciplines. There is, however, little published information on the vegetation of the modern Mackenzie Delta (Fig. 1).

A number of individuals have collected plant specimens from this area, such as Porsild (1943) who made extensive collections in the Mackenzie Delta region between 1927 and 1935, and noted their occurrence. Cody (1965) collected specimens in 1953 and 1957, and published a checklist annotating the plants of the Delta and adjacent reindeer grazing preserve. However, aside from Mackay (1963) who gives a concise regional description of vegetation types, and Gill (1972), who analyzes the point bar *Populus* association, little other work is available concerning the Delta vegetation; in particular, no information has been published on primary plant succession within the Mackenzie River Delta.

Owing to the greatly increasing developmental pressure in the Mackenzie Delta, there is applied as well as scientific interest in the ecology of this area. Mackay (1963:1) indicated a decade ago that the Mackenzie Delta area "is the centrum of population, economic activity, and transportation facilities in extreme northwestern Canada". Accelerated activities associated with oil and natural gas exploration since that time add impact to this statement.

Purpose

The most dynamic sequence of primary plant succession in the Mackenzie Delta occurs along the convex bends of actively shifting channels (Fig. 2). Succession begins with the pioneer *Equisetum* community and extends through the *Salix-Equisetum, Populus,* and Decadent *Populus* communities, to culminate in a climax *Picea* ecosystem. The purpose of this paper is to examine the successional status of each plant species that takes part in this seral sequence.

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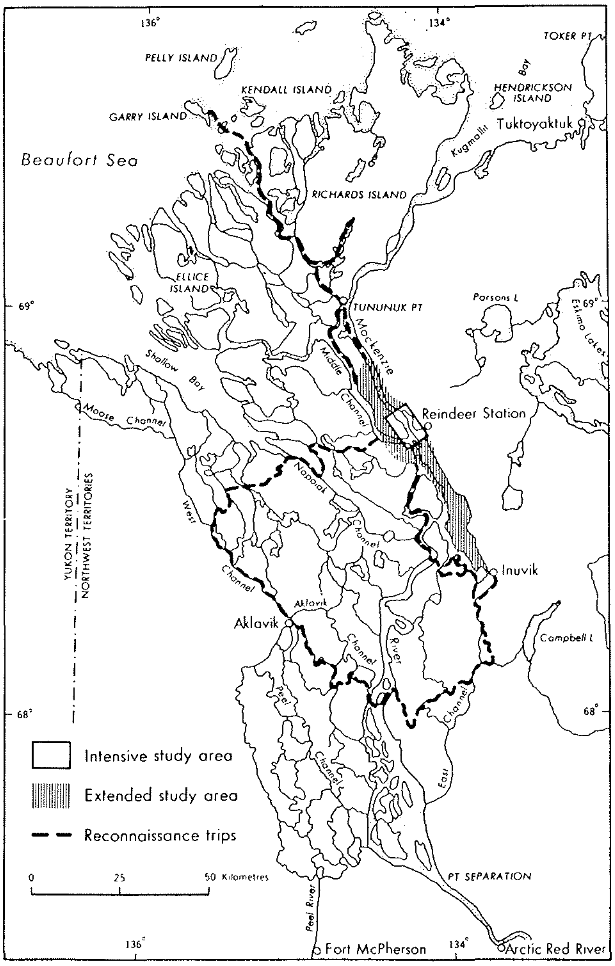


Fig. 1: The modern Mackenzie River Delta. This study took place in the "Intensive study area" shown by box.

Abb. 1: Das moderne Mackenzie Delta. Die Untersuchung wurde durchgeführt in dem als „Intensive study area" gekennzeichneten Gebiet (Kasten).

Study location

The northeast sector of the Mackenzie Delta (Fig. 1) was chosen as the area of study for the following reasons: The southern half of the Delta is comprised of older and higher floodplains which have poorly developed levees that flood only infrequently (Mackay, 1963). Plant succession here is less dynamic than succession in the northern half of the Delta (Gill, 1971). In the northern sector, levee form provides relatively abrupt changes in micro-relief, a feature which contributes to rapid vegetational changes over short distances (Fig. 3) and over a short period of time.

Field work

Field work was carried out during the 1966 and 1967 field seasons. Supplemental field observations were made during the summers of 1971 and 1972.

Methods

The most practical method that can be applied to a successional study which is based upon a few field seasons is the time-proven qualitative procedure of inference (Clements,

Fig. 2: Low oblique air photo of the modern Mackenzie River Delta. The most dynamic sequence of plant succession takes place along convex bends of actively shifting channels (arrow shows typical location). August 1972.

Abb. 2: Schrägaufnahme des gegenwärtigen Mackenzie Deltas aus geringer Flughöhe. Die dynamischste Pflanzensukzession findet entlang der Gleithänge mäandrierender Wasserläufe statt. (Der Pfeil weist auf eine solche Stelle.) August 1972.

1928), where successional trends are predicted from the plant communities occupying a location. According to Odum (1969) ecological succession is an orderly process of community development that is reasonably directional and, therefore, predictable. Plant succession in the Mackenzie Delta is particularly directional and clearly predictable.

The transect method has been used in most investigations of northern streamside succession (Drury, 1956; Johnson and Vogel, 1966; Viereck, 1966); this method as used here is simply an elongated sample plot in which plant communities are analyzed in order of their appearance along the transect. The locations and apparent causes of boundaries between communities were studied to determine the pattern of plant dissemination with increasing distance from an actively shifting channel. Topography along these transects was surveyed to correlate the distribution of successional communities with changes in micro-relief, flooding, and sediment deposition (see Fig. 3). Plant succession was intensively examined along 14 transects and further compared on 40 additional transects. Sample plots were established in the pioneer community near channel margins followed by locating plots in succeeding zones. The transects terminated in the climax *Picea* stands which are established on older levee surfaces.

Plant succession

Fig. 4 summarizes the successional trend that develops along actively prograding channels. Species taking part in this sequence and their degree of cover-abundance in successive communities are shown. The successional status of each species is discussed in the order in which it appears in the figure.

It is visually evident from Fig. 4 that *Equisetum fluviatile* L. not only dominates the pioneer community, but the plant also demonstrates great fidelity to this site. *Equisetum fluviatile* is thus a major indicator species, being the one plant in the Delta that is well adapted to the exposure, prolonged periods of flooding, and high rates of sedimentation (Fig. 5) that characterize the lower margins of prograding slipoff slopes.

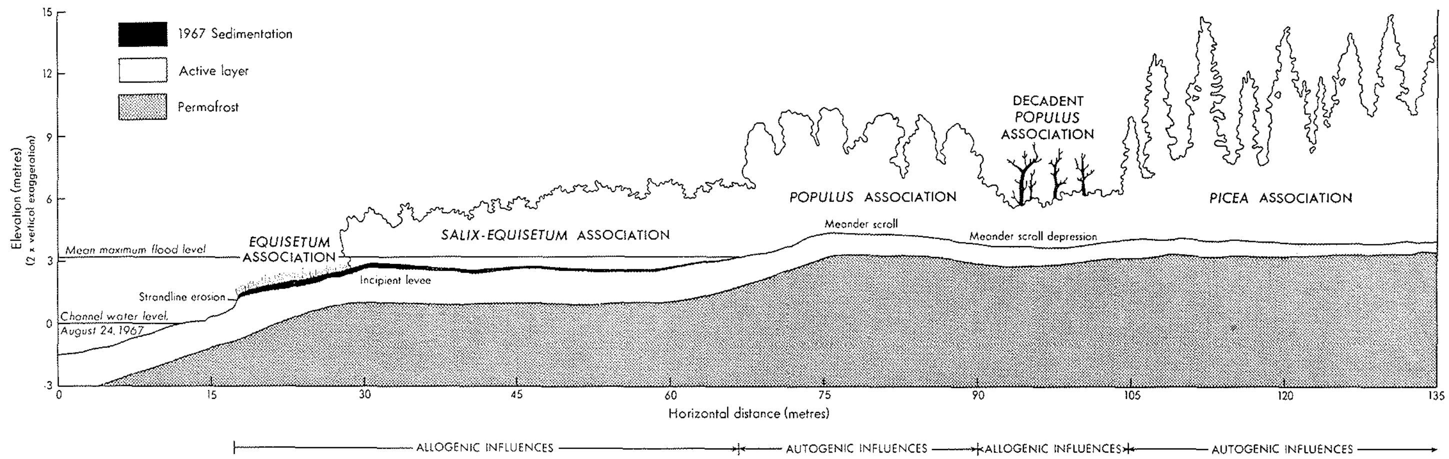


Fig. 3: Successional communities and environmental conditions along a dynamic plant succession sequence in the Mackenzie River Delta. Slipoff slope is prograding to the left as channel shifts.

Abb. 3: Sukzessionsgesellschaft und Standortsbedingungen in einer dynamischen Sukzessionsserie im Mackenzie Delta. Der „Spülsaum" wandert mit der Verlagerung des Wasserlaufes nach links.

Leptobryum pyriforme (Hedw.) Lind. is the only bryophyte that was found to occupy *Equisetum* sites; it forms a thin carpet on newly deposited sediment underneath *Equisetum* but never completes its life cycle here. This moss has a rather wide range of tolerances, and continues to grow in two of the following successional communities.

Equisetum arvense L. adds some coverage to the pioneer community, then because of its shade tolerance, it completely replaces the shade intolerant *Equisetum fluviatile* in the herb layer of the second sere (Fig. 4). It loses much of its significance in the drier *Populus* community, but again dominates the herb layer in the hygric Decadent *Populus* sites. Once the climax *Picea* community succeeds, this plant remains, although it is reduced to minor significance; it thus exhibits high frequency but low fidelity values, the reverse of *Equisetum fluviatile.*

Salix alaxensis (Anderss.) Cov. appears occasionally in the pioneer community but creates little cover (Fig. 4). However, after it succeeds on the *Equisetum* site it completely dominates the second sere, largely because of its shade intolerance and its ability to withstand sedimentation through adventitious rooting (Fig. 5). Similar to *Equisetum arvense,* it loses dominance in the drier *Populus* successional community, but regains it somewhat in the wetter Decadent *Populus* site. (The vigour of *Salix alaxensis* is low in the latter community, however, and the coverage it adds is made up of old-growth individuals.) This willow is nearly excluded from the *Picea* community, primarily because of its low shade tolerance. Like *Equisetum arvense,* it too exhibits high frequency and low fidelity values.

A grass, *Arctagrostis latifolia* (R. Br.) Griseb., is initiated in the *Equisetum* community and slowly gains significance in the seral sequence until the Decadent *Populus* community is reached (Fig. 4). It is not found in the climax community.

The sedge *Carex aquatilis* Wahl. is found in the first 2 communities, but is completely succeeded in the *Populus* sere by species adapted to the drier conditions of this site. Its significance is greatest in the wetter locations within Decadent *Populus* communities; it does not occur in the climax community because soil conditions are too dry. Another sedge, *Carex physocarpa* Presl, occurs as an accidental in some *Equisetum* stands but does not become important in the seral sequence until the hygric conditions of the Decadent *Populus* site, which enables it to attain considerable significance there (Fig. 4).

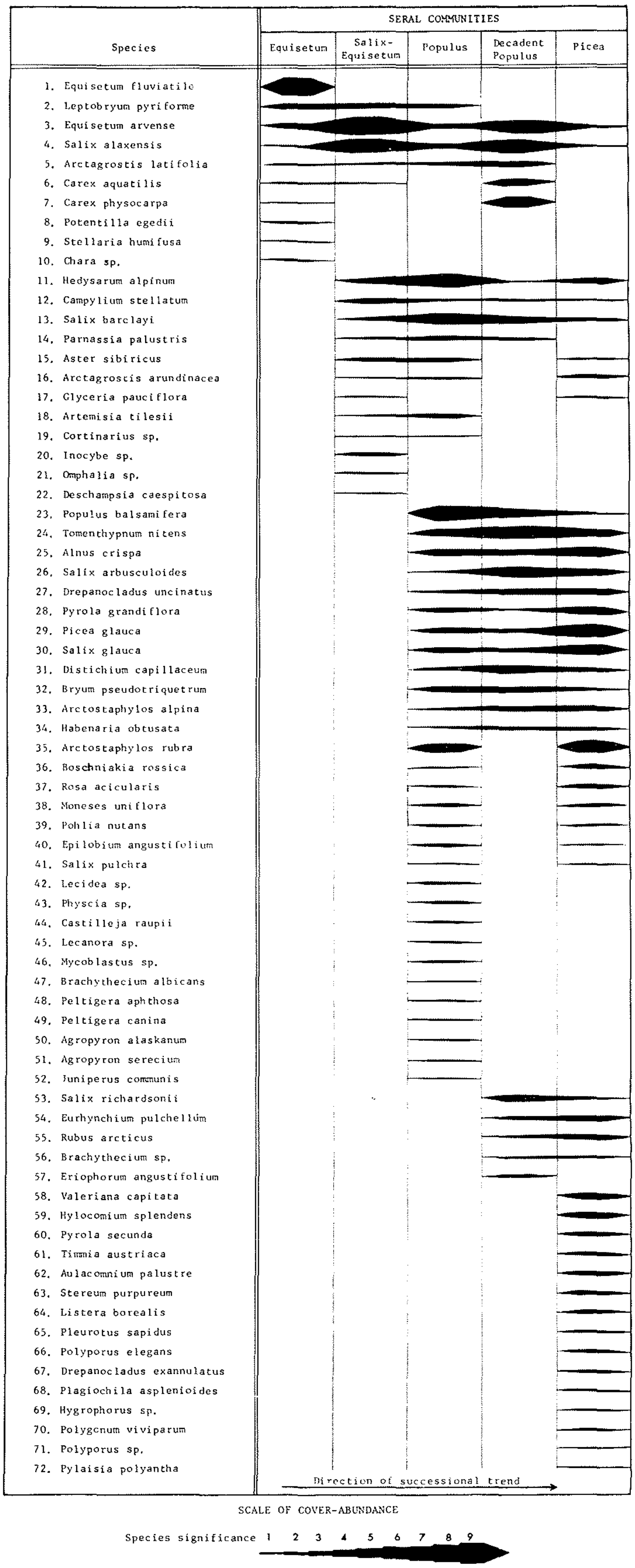
Species 8—10 in Fig. 4 usually occur as mere accidentals on *Equisetum* sites and contribute very little to the total flora of the community. Since they were found in no other community, however, they have some value as indicator species.

Hedysarum alpinum L. is most characteristic of the *Populus* community, but it also invades the landward portion of preceding *Salix-Equisetum* communities. As the *Populus* site degenerates into a Decadent *Populus* community, *Hedysarum* remains only on the higher microtopographic features. It also contributes to a small degree to the flora of the *Picea* community (Fig. 4).

Campylium stellatum (Hedw.) L. & Jens., a bryophyte, enters the successional sequence in the *Salix-Equisetum* community, attains a low cover-abundance, and maintains it through the seral stages to the climax community (Fig. 4).

The willow *Salix barclayi* Anderss. enters the second sere (*Salix-Equisetum* community) to a minor degree, but occurs only along the periphery of the third sere poplar stands. It attains considerable signifance in the *Populus* community, then declines in importance as the next two seres succeed (Fig. 4). This willow is most successful on drier sites; for example, where it grows in the Decadent *Populus* stands it remains viable only on the highest protrusions.

Parnassia palustris L. also enters the second sere, and maintains rather sparse populations until the *Picea* community succeeds (Fig.). It is non-tolerant of the conditions in either the pioneer or climax communities. *Aster sibiricus* L. and *Arctagrostis arundinacea*



The development of each species in the successional sequence is shown as a black line to correspond with its average significance in each community.

Fig. 5: Lower margin of prograding slipoff slope in the Mackenzie River Delta shortly after floodstage (June 22, 1968). Note recent deposit of sediment, 12—15 cm thick, exposed by wave action. Erosion has also exposed roots of *Equisetum fluviatile*, the plant most adapted to the exposure, flooding, and high sedimentation that characterizes such locations. To the left is *Salix alaxensis*, the dominant species of the second sere, similarly well adapted to lower slipoff slopes.

Abb. 5: Der untere Rand eines vorrückenden Spülsaumes im Mackenzie Delta kurz nach einer Überflutung (22. Juni 1968). Zu beachten ist die 12—15 cm mächtige Sedimentschicht, die durch den Wellenschlag bloßgelegt worden ist. Auch die Wurzeln von *Equisetum fluviatile*, jener der Exposition, der Überflutung und der starken Sedimentation am besten angepaßten Pflanze, sind von der Erosion freigelegt worden. Weiter nach links findet sich *Salix alaxensis*, die im zweiten Sukzessionsstadium vorherrschende Art, welche den Standortsverhältnissen des unteren Spülsaumes ähnlich gut angepaßt ist.

(Trin.) Beal on the other hand do not tolerate the hygric conditions of the Decadent *Populus* sites but inhabit the climax *Picea* community to a limited extent (Fig. 4).

Artemisia tilesii Ledeb., although appearing to a minor degree in the *Salix-Equisetum* sere, grows only where a poplar stand abuts this community. It is thus not truly fidel to the *Populus* community although it is one of the most characteristic plants of poplar stands; it is found only in this community and in portions of *Salix-Equisetum* communities that border on a *Populus* stand. The fungus *Cortinarius* was also found to occur only in these two seres but does not characterize the flora of either community as does *Artemisia*. Two additional agarics (species of *Inocybe* and *Omphalina)* are fidel to the *Salix-Equisetum* community (Fig. 4).

The plant having least cover-abundance in the *Salix-Equisetum* sere is *Deschampsia caespitosa* (L.) Beauv., which is found in virtually no other location (Fig. 4). This grass

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Fig. 4: Dynamic plant succession sequence: species development from pioneer *Equisetum* community to climax *Picea* community. This diagram typifies the successional sequence shown in Figure 3.
Species significance index (cover-abundance):

1. Occurring seldom, cover negligible
2. Rare, covering up to 5% of the plot
3. Common, covering 6—10% of the plot
4. Occurring often, covering 11—20% of the plot
5. Occurring very often, covering 21—35% of the plot
6. Abundant, covering 36—50% of the plot
7. Abundant, covering 51—75% of the plot
8. Very abundant, covering 76—95% of the plot
9. Very abundant, covering 96—100% of the plot

Abb. 4: Dynamische Pflanzensukzession: Artenentwicklung vom Pionierstadium (*Equisetum*-Gesellschaft) zum Klimaxstadium (*Picea*-Gesellschaft). Das Diagramm stellt die in Abbildung 3 aufgezeigte Sukzession dar. Abundanz und Deckungsgrad der Arten:

1. Sehr spärlich vorhanden, Deckungsgrad minimal
2. Spärlich vorhanden, bis zu 5% deckend
3. Verbreitet vorhanden, 6—10% deckend
4. Häufig, 11—20% deckend
5. Sehr häufig, 21—35% deckend
6. Zahlreich, 36—50% deckend
7. Zahlreich, 51—75% deckend
8. Sehr zahlreich, 76—95% deckend
9. Sehr zahlreich, 96—100% deckend

appears primarily as an accidental, and contributes little to the successional ecology of this community.

Once a *Salix-Equisetum* stand is sufficiently aggraded above flood-level, *Populus balsamifera* L. and associated species rapidly succeed the site. Fig. 4 well indicates the significance of this species to this community, and further shows its diminishing significance as the site succeeds to the climax stage. Poplar in its initial sere is vigorous (surprisingly so for such a northerly location), but as the site deteriorates into the Decadent *Populus* stage trough the ponding of local runoff water (Fig. 3), they die. All poplar trees that occupy such sites are dead or dying. Some remnant individuals are scattered in parts of the *Picea* community, but they are usually in poor vigour and represent the last stage in the succession from *Populus* to the climax community.

Tomenthypnum nitens (Hedw.) Loeske, a sediment-intolerant bryophyte, enters the succession sequence in the seldom alluviated *Populus* community where it forms dense carpets in moist sections of the stand. This moss reaches its greatest amplitude in the Decandent *Populus* community but also continues to be prominent in the climax sere (Fig. 4).

Alder (*Alnus crispa* [Ait.] Pursh) also becomes significant in the *Populus* community (Fig. 4). It especially contributes to the flora along the wetter inland edges of poplar stands where they merge with Decadent *Populus* sites. *Alnus crispa* extends along the increasing moisture gradient into the Decadent *Populus* community until excessive soil moisture causes it to cease growth. (It grows throughout this community but only on micro-features of maximum relief.) Alder is not an active successor in these areas; it merely tolerates the subhygric conditions of such sites. It does, however, succeed to the climax stage, and there adds considerably to the autogenic forces of succession, particularly nitrification of the soil (Krajina, 1966 — Personal Communication).

Although taxa 26—34 enter the seral sequence in the *Populus* community (and continue to participate to a greater or lesser degree to the climax stage) none has its greatest amplitude in that community. Two, *Salix arbusculoides* Anderss. and *Distichium capillaceum* (Hedw.) B.S.G., have their highest cover-abundance in the subhygric Decadent *Populus* sites (Fig. 4), and thus profit from the retrogressive ponding at these locations. Conversely, *Pyrola grandiflora* Radius, a predominantly mesic species, declines greatly in the Decadent *Populus* sites but regains much of its previous significance in the *Picea* community. *Picea glauca* (Moench) Voss and *Salix glauca* L. both enter the successional stage at this point; they are mesic species and have similar amplitudes in the three seres (Fig. 4).

The next 7 species in Fig. 4 (taxa 35—41) have an interrupted distribution along this successional sequence. All are initiated in the *Populus* community but none are able to withstand the hygric conditions of the Decadent *Populus* sere, thus are absent from this community. They once again occur (usually with a greater cover-abundance) in the drier *Picea* community. Of this group, *Arctostaphylos rubra* (Rehd. and Wils.) Fern. is most responsive to mesic and submesic conditions, thus is especially suited to enter the seral stage in the *Populus* community.

Species 42—52 (Fig. 4) are characteristic of the study area's *Populus* communities. No single plant is abundant and even in combination the 11 species do not provide a significant amount of coverage, yet they contribute greatly to the floral distinctiveness of the *Populus* association. Corticolous lichens of the *Lecidea, Physcia, Lecanora,* and *Mycoblastus* genera are very representative of this association, since they are epiphytic only on the calcium-rich bark of *Populus balsamifera.* Two additional lichens, numbers 48 and 49, were found only in the *Populus* community. These *Peltigera* species are epiphytic directly on the humus layer. Lichens have a well-earned reputation as pioneer species, but along this successional transect they enter the successional stage only in the third and most xeric sere. Lichen succession is largely directional (Hale, 1967) thus changes in the environment determine the ultimate fate of lichen populations. Since the *Populus* community is greatly modified by allogenic influences (which largely determine the environment of the following sere) the inclusion of most lichens in this sequence is short-lived, and restricted to the one community.

The last 4 species characteristic of the *Populus* community are also restricted to these sites because of their preference for drier, well-drained situations. *Castilleja raupii* Pennell, *Agropyron alaskanum* Scribn. & Merr., *A. sericeum* Hitch., and *Juniperus communis* L. all prefer sandy, somewhat xeric conditions (Polunin, 1959).

To conclude discussion of the species occurring in the *Populus* community, it should be observed that many of the plants in this sere (especially the characteristic species) do not greatly affect the successional direction. Succession along this transect is largely allogenically controlled, thus if certain environmental factors combine in one location to create a condition which deviates from the norm, the flora will reflect this deviation. The environment of a *Populus* site, because of its relatively coarse soil and its position above mean flood level (Fig. 3), is the most xeric community in the study area (Gill, 1972), thus it can be expected to host a number of specialized taxa which might not otherwise germinate in the Delta environment. The autogenic influence of these species upon the trend of succession is thus limited.

Four species along this sequence (taxa 53—56, Fig. 4) are initiated in the Decadent *Populus* community and succeed to the climax stage. *Salix richardsonii* Hook. characteristically occurs on wet tundra (Polunin, 1959) but also grows well in the wet environment of this community. As the site becomes drier through organic accumulation and the buildup of sediments, it succeeds to the climax *Picea stage* but the vigour and cover-abundance of this willow decreases. The bryophytes *Eurhynchium pulchellum* (Hedw). Jenn. and *Brachythecium* sp. initiate on the higher protrusions of organic material and dead wood in portions of this community and they continue to maintain populations as the site succeeds to a *Picea* community (Fig. 4); the former moss increases somewhat in significance while the latter's coverage remains approximately the same. *Rubus arcticus* L. occurs sparsely and in poor vigour in the moist Decadent *Populus* localities, but increases in coverage and vigour in the climax sere. The Decadent *Populus* community contains only one characteristic species — *Eriophorum angustifolium* Honckn. The cotton-grass is a common inhabitant of wet bogs and marshes, and is thus one of the best indicator species of this community; its participation in the seral stage is limited to the production of organic material which assists in the accretion necessary for the succeeding community.

Species 58—60 are found only in the *Picea* communities of this successional sequence (Fig. 4), although they are present in the *Salix-Alnus* community of a different seral sequence which is reported elsewhere (Gill, 1971).

A final 12 taxa germinate within the climax community — characteristic species that appear in no other community of the study area (Fig. 4). Five of these plants are mosses (numbers 61, 62, 67, 68 and 72), 2 of which (*Drepanocladus exannulatus* (B.S.G.) Warnst. and *Pylaisia polyantha* B.S.G.) are corticolous, growing only on substrates of trunks or decaying wood. Five others (numbers 63, 65, 66, 69 and 71) are fungi which are saprophytic on organic material within the herb stratum or on decaying wood. The remaining 2 species are vasculars, *Listera borealis* Morong and *Polygonum viviparum* L. While the 12 final species are exclusive to the climax community, only numbers 61—66 were present in 4 or more of the 7 *Picea* study plots. Only 6 species may thus be confidently used as floristic criteria for outlining the limits of the climax ecosystem. Species 67—68 (*Drepanocladus exannulatus* and *Plagiochila asplenioides* [L.] Dum.) have a sufficient presence-value (3 out of 7 plots) that some measure of characterization may be attached to them. The remaining species (numbers 69—72) have such a low constancy that they cannot be used as indicators.

The time factor in Mackenzie Delta plant succession

The Mackenzie River Delta provides an ideal location for the study of compressed successional processes in a northern alluvial environment. A climax ecosystem can evolve on an originally unvegetated surface within 2 centuries (Gill, 1971). Plant succession is primarily allogenic (Fig. 3), thus it closely reflects the rate of physiographic development by alluvial accretion. The physical environment of any sere is highly time-dependent; contrasts between sites result almost exclusively from differences in age.

Environmental time-dependency is paralleled by temporal variations in the floristic development of each community. The majority of species in each sere are at much the same stage of succession at the same time, reflecting uniformity in the physical and temporal attributes of the environment. Time as a variable thus largely accounts for both the allogenic and floral individuality of a given site.

Allogenic and Autogenic Forces of Succession

Odum (1969) argues that ecological succession results from modification of the physical environment by the organisms present; that succession is community-controlled (although he acknowledges that the physical environment does determine the pattern, the rate of change, and may limit how far development can go). It is true that the community controls the successional orientation of many terrestrial ecosystems, but this does not necessarily hold for the early seres of floodplain successions and is especially not true of the early seres of the Mackenzie Delta successional sequence.

Daubenmire (1968) contends that the forces which initiate a sere may be either purely autogenic or purely allogenic, and information gained during the present study bears this out. Terrestrial seres in the Mackenzie Delta are initiated by the creation of a bare area and the subsequent allogenic changes in environment (caused especially by sedimentation and flooding) force the successional direction. This is similar to the findings of Bliss and Cantlon (1957) along the Colville River.

Once a prisere is initiated on *terra nova* in the Mackenzie Delta, plants do cause changes in their immediate environment which directly or indirectly favor the next sere. Autogenic forces slowly increase until the climax *Picea* community is attained, at which stage they dominate over allogenic influences (Fig. 3).

Acknowledgements

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