Papers

Ecological Modifications Caused by the Removal of Tree and Shrub Canopies in the Mackenzie Delta

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ABSTRACT. Environmental and floristic evidence is presented to show that after removal of the white spruce (*Picea glauca*) and willow-alder (*Salix* spp.-*Alnus crispa*) canopies from exposed sites in the Mackenzie River Delta, Northwest Territories, environmental degradation is such that secondary succession of low-arctic tundra heath, moss and lichen species takes place. The extreme exposure of cleared sites enables a hardy group of tundra plants to compete with the local flora and invade the previously forested location. Site degeneration is further evidenced by turf hummocks and a characteristic "hummock-type" active layer configuration that developed within only 20 years after clear-cutting.

RÉSUMÉ: *Modifications écologiques causées par l'enlèvement des couvertures arborescente et broussailleuse dans le delta du Mackenzie.* L'auteur présente des exemples écologiques et floristiques qui démontrent qu'après l'enlèvement du couvert d'épinette blanche *(Picea glauca)* et de la saulaie-aulnaie *(Salix* spp.-*Alnus crispa)* de sites exposés dans le delta du Mackenzie, Territoires du Nord-Ouest, la dégradation du milieu est telle qu'une succession secondaire d'espèces toundriques basses: bruyères, mousses et lichens, s'installe. L'extrême exposition de ces sites découverts permet à un robuste groupe de plantes de la toundra de concurrencer la flore locale et d'envahir l'ancien site forestier. La formation de thufurs et une configuration caractéristique du gélisol en buttes qui se développe dans les vingt ans qui suivent la coupe à blanc, marquent encore plus la dégénérescence du site.

РЕЗЮМЕ. *Экологические изменения, вызванные снятием древесных и кустарниковых пологов в дельте реки Макензи.* На основе исследования окружающей среды и растительного покрова показано, что после снятия пологов ели сизой (Picea glauca) и ивы-ольхи (Salix-Alnus crispa) из открытых мест в дельте реки Макензи (Северо-Западные Территории) происходит деградация окружающей среды, сопровождающаяся появлением вторичной последовательности низкоарктического тундрового вереска, мха и лишайников. При продолжительном выдерживании очищенных участков создаются условия для конкуренции выносливых групп тундровых растений с местной флорой и вторжения их в ранее залесённый район. Вырождение участков подтверждается далее образованием торфяных кочек и характерной «кочкарной» конфигурации активного слоя, развившихся всего лишь за 20 лет после расчистки участков.

INTRODUCTION

Secondary plant succession may develop on a given site after the climax community is disrupted by any disturbance that destroys the principal species. In temperate climates, the later stages of secondary succession are normally similar to the original vegetation. This is especially true when the derangement is not extreme, such as that caused by wind-throw or logging. In disturbances such as these, many of the products of community reaction remain, succession is rapid, and the climax community is normally replaced. Many of the principles concerning plant succession have emerged from work carried out in temperate regions,

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however, and secondary succession in areas underlain by permafrost may thus be quite different, particularly if environmental stress in addition to that of permafrost is present.

The Mackenzie River Delta supports a northern extension of the boreal forest (Gill 1971), and along the Delta's upper levees there are a number of small clearings where secondary plant succession is occurring, usually resulting from the clear-cutting of white spruce by natives for building material and fuel. These locations are normally adjacent to long-occupied cabins, where Eskimos cut the smaller spruce, willow and alder for fuel. The upper and lower canopies are often completely removed in this process.

A number of such sites were examined during the 1966-67 and 1971 field seasons (the general study area is shown in Fig. 1), and one was examined in detail, after which it was concluded that secondary succession was not following

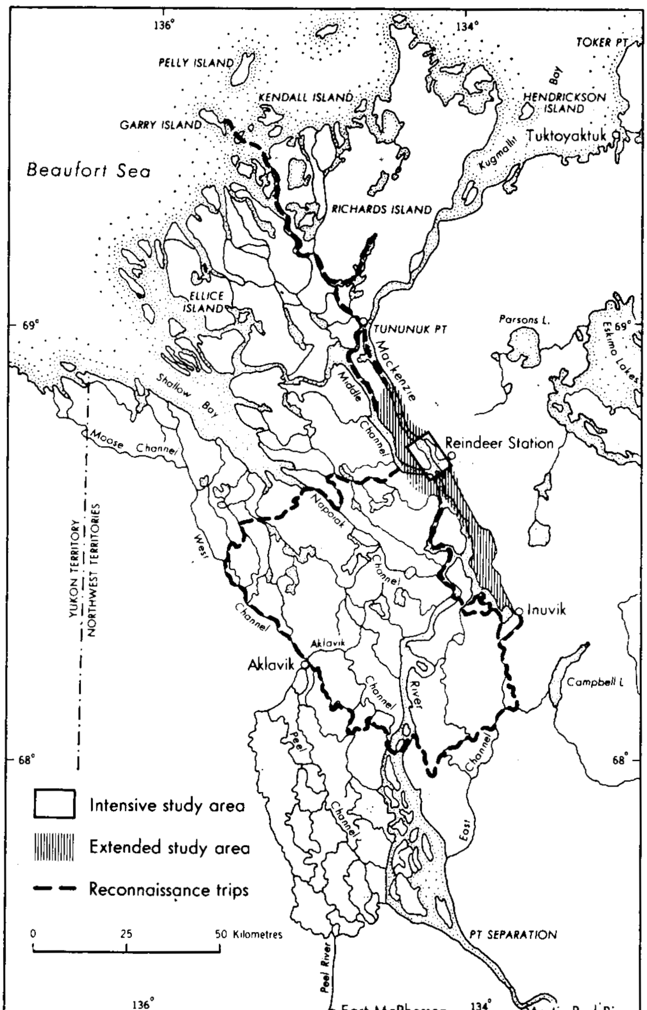

FIG. 1. Study area within the Mackenzie River Delta, Northwest Territories.

the usual trend of plant succession that culminates in a re-establishment of the original plant cover. Instead, a heath association has succeeded (called here the "tundra" association) which is similar in species composition to the low-arctic shrub tundra adjacent to the Mackenzie River Delta. The vegetation of the climax spruce community which originally occupied the "tundra" site developed through an active channel successional sequence (Gill 1971). A brief discussion of the dominant members in this sequence will be given so that a comparison can be made between normal plant succession and the secondary succession of the "tundra" site.

PRIMARY PLANT SUCCESSION IN THE MACKENZIE RIVER DELTA

The most dynamic and rapidly changing sequence of plant succession in the Mackenzie Delta begins along point bars and adjacent (down-channel) slipoff slopes of actively shifting channels. Vegetation differences here reflect the irregularities of alluvial landform construction; moving transversely from a shifting channel to the older portions of the floodplain, five discrete vegetation zones are crossed (Fig. 2). This successional sequence begins with the pioneer *Equisetum* association.

Equisetum Association

Equisetum fluviatile is the single most important pioneer species in the Mackenzie Delta. It is shade intolerant and withstands flooding and high rates of sedimentation, thus is well suited to the exposed lower slipoff slopes where it forms nearly pure communities (Fig. 2).

Salix-Equisetum Association

This association is restricted to the upper surfaces of young levees (Fig. 2) where it succeeds the *Equisetum* sere. The dominant and often sole shrub is the feltleaf willow (*Salix alaxensis*). It is particularly capable of developing adventitious roots, which enables it to colonize sites that build up rapidly through alluviation. The herb layer is also dominated by one plant, *Equisetum arvense*, a species capable of withstanding extended flood periods and high rates of sedimentation.

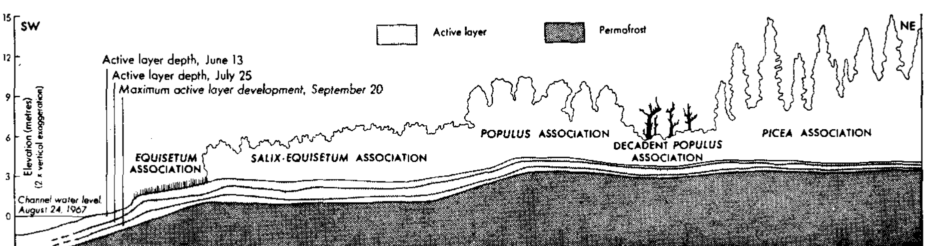

FIG. 2. Successional associations along an actively shifting channel in the Mackenzie Delta. The ground surface configuration and depths-to-frost (measured during 1967) are representative for most of the Delta.

Populus Association

After the *Salix-Equisetum* site builds up to a maximum height through alluviation, the third or *Populus* sere begins to succeed (Fig. 2) (Gill 1972a). The site is now above normal flood level, thus the constraints of flooding and sedimentation are reduced, and the flora is more diverse than in the previous two seres. Balsam poplar (*Populus balsamifera*) is normally the sole dominant in the tree stratum, but the shrub layer is diversified. In order of descending significance the important components are *Salix alaxensis, S. glauca, S. pulchra, S. arbusculoides,* and *Alnus crispa.* A few spruce seedlings are also present, heralding the climax association. The herb layer is made up of an increasing number of vascular plants, most cover being provided by *Hedysarum alpinum, Arctostaphylos rubra, Artemisia tilesii,* and *Equisetum arvense.*

Decadent Populus Association

Immediately inland from most *Populus* communities are low areas, or meander scroll depressions (Fig. 2). In the process of colonizing the upper point bar and levee surfaces, balsam poplar extends down the front of the levee toward the channel (note the channelward distribution of poplar in Fig. 2). Channel shifting normally occurs at an irregular pace, causing levee and point bar construction to build unevenly. When poplar trees extend down the face of a levee, their ultimate site is therefore a poorly-drained depression when accelerated deposition constructs another meander scroll of higher elevation in front of it (Gill 1972b). Accumulation of water in the depressions causes much floristic alteration, beginning with the killing of poplar trees, and permits willow species to gain ascendency. *Salix alaxensis* and *S. arbusculoides* co-dominate in this association, with lesser representation of *S. richardsonii, S. glauca,* and *S. barclayi. Alnus crispa* and *Picea glauca* are also present on the higher and drier microtopography. The herb layer is dominated by *Carex physocarpa, C. aquatilis, Equisetum arvense* and *Eriophorum angustifolium.* A thin moss stratum, made up of *Tomenthypnum nitens, Drepanocladus uncinatus,* and *Distichium capillaceum,* has been able to develop because sediment deposition is reduced here.

The Climax Picea Association

The white spruce climax association in the Mackenzie Delta almost invariably occupies the uppermost levee surfaces which only rarely experience flooding and sedimentation (Fig. 2). In the study area, spruce occupy a vertical zone some 3.3 m. to 4.5 m. above mean summer channel levels. This narrow vertical distribution characterizes the strict limits that are imposed by flooding and sedimentation.

White spruce is usually the sole dominant of the tree stratum in the climax association (Table 1). Considerably more species diversity is evident in the upper and lower shrub layers, however (Table 1). A thick canopy is formed by *Alnus crispa, Salix glauca, S. arbusculoides, S. pulchra, S. alaxensis, S. richardsonii,* and *S. barclayi.*

The number of species in the herb stratum is greater than in the preceding seres. *Arctostaphylos rubra* is ubiquitous, as is *Pyrola grandiflora.* Also present in less significance are *Hedysarum alpinum*, *Valeriana capitata*, *Arctostaphylos alpina*, *Rosa acicularis*, and *Moneses uniflora*. Another dozen less significant species comprise the herb stratum (Table 1).

Most spruce stands are carpeted by a thin layer of mosses. *Tomenthypnum nitens* is the most important, followed in significance by *Hylocomium splendens*, *Drepanocladus uncinatus*, and *Distichium capillaceum*. Seven additional mosses are found (Table 1) but contribute little to the coverage.

The climax spruce association in the Mackenzie Delta is at least relatively stable, and can be said to be in equilibrium with the deltaic environment. *Picea glauca*, which attains considerable longevity in the Delta, forms unevenly-aged stands, within which are senile members as well as occasional dead individuals. It is generally thought that the climax is reached when this state exists — where the lifespan of the dominant species is shorter than the age of the stand itself (Clements 1928; Polunin 1960). A problem exists, however, in this view of the time span of the "climax" association; the continued destruction of levees by erosion may be instrumental in maintaining white spruce as the dominant species. It is probable that if an upper levee section remained intact for a sufficient period, autogenic processes would result in an increasingly thick organic layer, acidification of the soil, lowered soil temperatures, and a decrease in the thickness of the active layer. Under such circumstances, white spruce could be gradually replaced by acidic- and moisture-tolerant shrub tundra heath species which are now adjacent to but seldom occur in the Delta. The time necessary to establish such conditions is probably greater than the present age of most segments of Delta surface owing to the continued replacement of mature levees by *terra nova* through distributary shifting. The process of erosion may thus be interrupting a more extended successional sequence than is now measurable in most parts of the Mackenzie Delta (Gill 1972c).

THE "TUNDRA" SITE — ENVIRONMENT

As indicated by Beschel (1963, p. 51), in the complicated interaction of vegetation and frozen ground phenomena the time scale of changes is rarely known. Surface forms may change rapidly within a few years or may persist virtually unchanged for centuries. The Mackenzie Delta study site provides a rare opportunity to obtain data on the time scale of changes in the formation of turf hummocks, one of the more common results of interaction between vegetation and permafrost.

There are two major types of hummocks in the Mackenzie Delta area, differentiated by being composed of organic or mineral material. Only the former, or turf hummocks, are present in the study area, and they are found exclusively in the "tundra" site. Incipient turf hummocks have formed on most of the cutover area, and the characteristic configuration of the frost table, which closely mirrors surface micro-relief, is present (see Mackay 1958, pp. 14-15). Fig. 3 is a cross-section which illustrates the alterations in micro-relief and active layer depths that have developed under the dominance of a heath-tundra type of vegetation. When this is compared with the normal configuration of deltaic surface and frost-

TABLE 1. The climax *Picea* association.

Stratum	Species	Averages of 7 Sample Plots Species Significance	Sociability	Vigour	Percent Total Coverage
Tree Layer A (Above 5.5 m.)	*Picea glauca*	6.3	1	4.0	52
Shrub Layer B1 (Below 5.5 m.)	*Alnus crispa*	4.9	2	3.3	59
	Salix glauca	4.1	2	3.0	
	Salix arbusculoides	3.6	2	3.0	
	Salix pulchra	0.6	2	2.7	
	Salix alaxensis	0.4	1	2.3	
	Salix richardsonii	0.3	2	2.0	
	Picea glauca	0.1	1	0.0	
	Populus balsamifera	0.1	1	2.0	
Shrub Layer B2 (Below 1.5 m.)	*Alnus crispa*	4.3	2	3.0	37
	Salix arbusculoides	2.3	2	3.0	
	Salix glauca	1.9	2	3.0	
	Salix barclayi	0.7	2	3.0	
	Salix richardsonii	0.4	2	3.0	
	Picea glauca	0.3	1	2.0	
	Salix alaxensis	0.3	2	2.5	
Herb Layer C	*Arctostaphylos rubra*	5.0	4	2.7	76
	Pyrola grandiflora	3.7	2	3.0	
	Hedysarum alpinum	1.9	2	2.8	
	Valeriana capitata	1.6	3	3.0	
	Arctostaphylos alpina	1.3	2	2.2	
	Rosa acicularis	1.3	2	2.6	
	Moneses uniflora	1.1	2	2.7	
	Listera borealis	0.9	1	2.8	
	Rubus arcticus	0.9	1	2.6	
	Boschniakia rossica	0.7	2	3.0	
	Equisetum arvense	0.7	2	1.8	
	Pyrola secunda	0.7	2	2.8	
	Habenaria obtusata	0.7	2	3.0	
	Arctagrostis arundinacea	0.6	2	2.8	
	Aster sibiricus	0.3	1	2.0	
	Hygrophorus sp.	0.3	2	3.0	
	Polygonum viviparum	0.3	1	3.0	
	Epilobium angustifolium	0.1	1	2.0	
	Glyceria pauciflora	0.1	1	2.0	
Moss Layer D (On humus and sediment)	*Tomenthypnum nitens*	4.0	4	3.0	54
	Hylocomium splendens	2.6	3	2.8	
	Drepanocladus uncinatus	2.4	3	2.9	
	Distichium capillaceum	2.1	3	3.0	
	Campylium stellatum	1.4	3	3.0	
	Timmia austriaca	1.1	3	3.0	
	Aulacomnium palustre	1.0	3	3.0	
	Eurhynchium pulchellum	0.9	3	3.0	
	Bryum pseudotriquetrum	0.7	3	3.0	
	Plagiochila asplenioides	0.4	3	3.0	
	Brachythecium sp.	0.4	3	3.0	
Moss Layer D (On decaying wood)	*Drepanocladus uncinatus*	2.4	3	3.0	6
	Pohlia nutans	1.1	2	3.0	
	Drepanocladus exannulatus	0.4	3	3.0	
	Distichium capillaceum	0.3	3	3.0	
	Pylaisia polyantha	0.1	2	2.0	
Epiphytic Layer (On dead *Salix* and *Alnus*)	*Stereum purpureum*	1.0	2	2.6	1
	Pleurotus sapidus	0.7	2	2.6	
	Polyporus elegans	0.6	2	3.0	
	Polyporus sp.	0.1	2	2.0	

TABLE 2. The "tundra" association.

Stratum	Species	Averages of 2 Sample Plots Species Significance	Sociability	Vigour	Percent Total Coverage
Shrub Layer (Below 1.5 m.)	*Alnus crispa*	3.5	2	2.5	23
	Salix glauca	2.5	2	3.0	
	Picea glauca	1.5	1	2.0	
	*Salix niphoclada**	1.5	2	3.0	
	Salix richardsonii	1.0	2	3.0	
	Salix arbusculoides	0.5	1	3.0	
Herb Layer	*Vaccinium uliginosum**	5.5	2	4.0	85
	*Empetrum hermaphroditum**	4.5	1	3.0	
	*Vaccinium vitis-idaea**	4.0	2	3.0	
	*Ledum palustre**	2.0	1	3.0	
	*Senecio fuscatus**	2.0	1	3.0	
	Arctostaphylos alpina	1.5	1	2.0	
	*Petasites frigidus**	1.5	1	1.5	
	*Stellaria ciliatosepala**	1.5	1	3.0	
	Arctagrostis latifolia	1.0	1	3.0	
	*Carex lugens**	1.0	2	3.0	
	*Carex vaginata**	1.0	1	3.0	
	Equisetum arvense	1.0	1	2.0	
	Pyrola secunda	1.0	1	3.0	
	Boschniakia rossica	0.5	2	2.0	
	Pyrola grandiflora	0.5	1	2.0	
	Rosa acicularis	0.5	1	2.0	
Moss and Lichen Layer (On humus)	*Cladonia arbuscula**	6.0	4	3.0	100
	*Cladonia amaurocraea**	3.5	3	3.0	
	Aulacomnium palustre	3.0	3	3.0	
	*Dicranum elongatum**	2.0	3	2.0	
	Hylocomium splendens	2.0	3	2.0	
	Peltigera aphthosa	2.0	3	2.0	
	*Barbilophozia barbata**	1.0	3	3.0	
	*Cladonia gracilis**	1.0	3	3.0	
	*Lophozia alpestris**	1.0	2	3.0	
	*Sphenolobus minutus**	1.0	3	3.0	
	*Cetraria islandica**	0.5	3	3.0	
	*Stereocaulon tomentosum**	0.5	3	3.0	
	*Cetraria nivalis**	0.5	3	3.0	
	*Cladonia rangiferina**	0.5	3	3.0	
	*Ptilidium ciliare**	0.5	3	2.0	

*Species common to the low-arctic shrub tundra communities adjacent to the Mackenzie Delta, but not found in the study area (Fig. 1) except in the "tundra" association.

Explanation of Indexes, Tables 1 and 2.

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.

Sociability Index
1) Growing singly; 2) Grouped or tufted; 3) Growing in small patches or cushions; 4) Growing in small colonies, extensive patches, or forming carpets; 5) Forming pure populations.

Vigour Index
0) Dead; 1) Dying; 2) Poor vigour, barely successful in setting seed; 3) Good vigour, successful, abundant seed; 4) Excellent vigour, most successful in community, much seed.

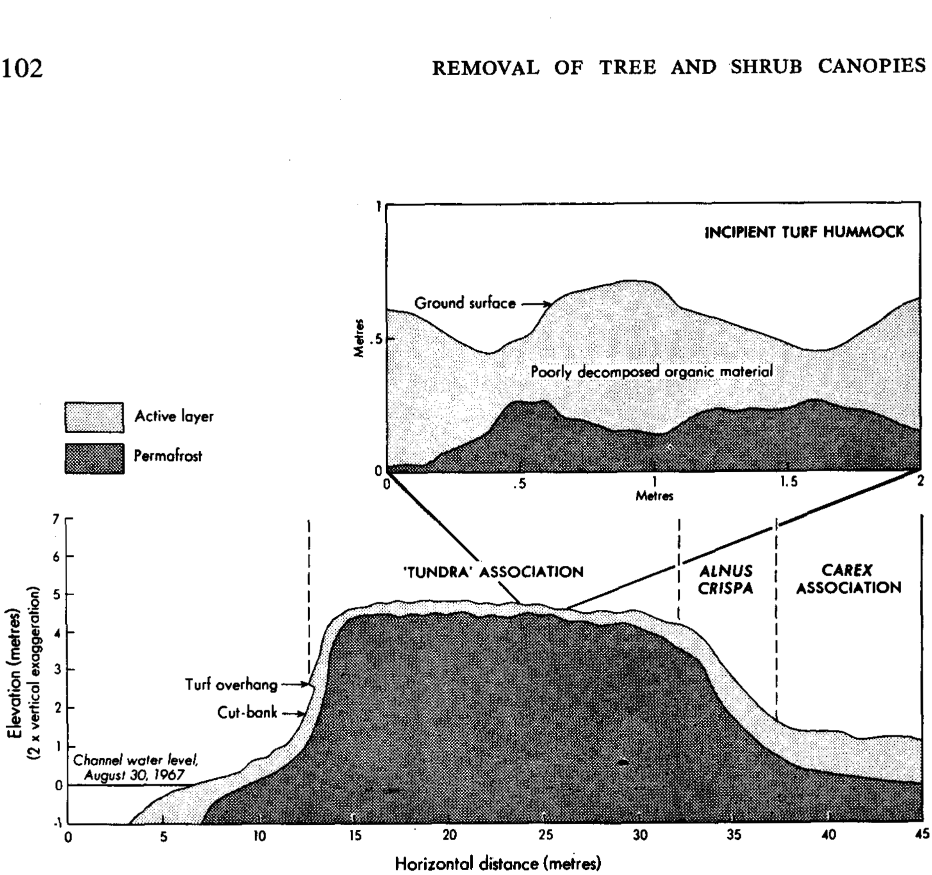

FIG. 3. Incipient hummock development in the "tundra" association of the study area.

table relief as shown in Fig. 2 it is seen that there is a significant difference between typical deltaic morphology and the form of the modified site.

For hummocks to develop on an active delta surface, certain conditions must be present; most importantly, there must be a reduction in flooding and sedimentation, a requirement met only by higher levees that are above normal flood level. Since turf hummocks are composed of organic material, it follows that where the ground surface frequently has alluvium deposited upon it, the growth of ground vegetation will be diminished and the mass of organic material necessary for hummock genesis will not be produced. Secondly, for hummocks to develop in the modern Mackenzie Delta, the closed canopy formed by spruce, willow, and alder must be removed. Its removal creates a severe environment at the ground surface so that the existing relatively low-biomass shade-tolerant plants cannot compete with the hardy higher-biomass shade-intolerant heath, moss and lichen species. Fig. 4 is a soil profile which illustrates that a rapid buildup of organic material apparently did occur after the study site was logged. Also shown is a temperature profile taken 11 August 1967 that indicates a low temperature within the active layer. The thick (21 cm.) poorly decomposed organic material was nearly saturated at the time of measurement, accounting in part for the high frost table and the low temperature of the active layer.

The foregoing conditions have combined at the study site to enable a very rapid development of turf hummocks. By interviewing local natives, it was determined that the site was clear-cut in 1946, thus relatively well-structured organic hummocks and a characteristic "hummock type" active layer (Fig. 3) developed in a

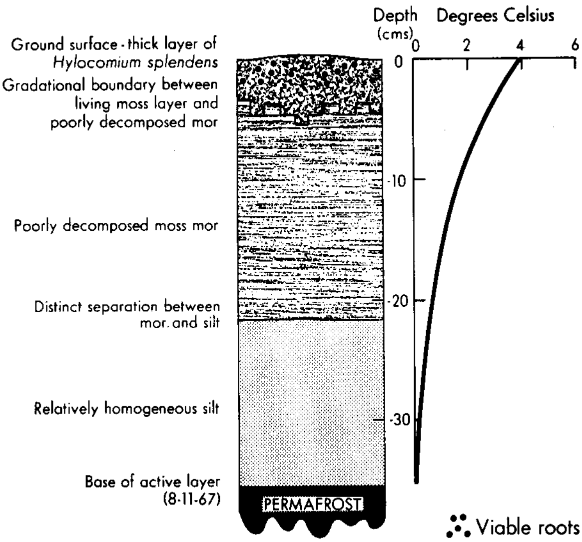

FIG. 4. "Tundra" association soil and temperature profile.

mere 20 years. This may be an even more rapid process of hummock development than reported for the Mesters Vig district of Greenland. Raup (1966) found that turf hummocks developed (by accumulations of organic material similar to the present study) and were destroyed by desiccation and erosion within 60 years.

During the period since clear-cutting, soil acidity appears to have increased. The mean pH value measured in 90 locations within all the plant communities of the study area was 7.38 (standard deviation 0.29). Average soil acidity in the "tundra" site on the other hand measured 6.20. The lowering of pH values is probably a combination of non-replacement of hydrogen ions due to the relative lack of flooding, and more importantly, by the large accumulation of organic matter which upon slow decomposition yields acid products. A pH of 6.2 is not botanically significant, however, since most boreal and tundra species tolerate a rather wide range of soil acidity. This figure is stated only to supplement the observations on site degradation which has apparently taken place.

THE "TUNDRA" SITE — FLORISTICS

The only shrubs of the "tundra" site that are remnant from the previous white spruce community are low growths of *Alnus crispa*, *Salix glauca*, *S. richardsonii*, and *S. arbusculoides* (Fig. 5; Table 2). Several remnant spruce saplings, 20 to 30 years old, are also present but they are stunted and in very poor vigour, indicating that spruce is not in the process of re-colonizing the site. The most dominant of the shrubs is *Alnus crispa*, although it covered no more than 15 per cent of one study plot.

The shrub which best heralds the secondary succession is *Salix niphoclada* (*Salix lingulata* of some authors — Polunin 1959). Although Argus (1965, p. 125) cites one specimen of this willow collected in the Mackenzie Delta (which he considers to be a subspecies of *Salix brachycarpa*), I found it in no other location within the study area except on similarly cutover sites. V. J. Krajina (per-

FIG. 5. The "tundra" association: note stumps of spruce cut in 1946 behind figure. The low shrubs (*Alnus crispa*, *Salix glauca*, *S. richardsonii*, and *S. arbusculoides*) are remnant from the *Picea* association which previously occupied the site. Note light patches of lichens. 11 August 1967.

sonal communication 1966) observed that this species is frequent in the subalpine zone of the Richardson Mountains and in the low arctic tundra on Richards Island (Fig. 1). Cody (1965, p. 27) found *S. niphoclada* along the arctic coast, but does not include it with the Salicaceae of the Delta. Porsild (1951, p. 142) observed *S. niphoclada* in the Yukon as an alpine species; Raup (1959, p. 59) is not clear as to the habitat of this willow but also states that it is occasionally found in alpine tundra. He does not include it as an understory of spruce or other woodlands, nor is it included by Jeffrey (1959), Ritchie (1959) or LaRoi (1967) as a component of the boreal forest. Argus (1965, p. 124) states that it occurs in a variety of usually (but not always) arctic or alpine habitats. It is thus evident that *Salix niphoclada* is not a common species of the boreal forest or the Mackenzie Delta, but is representative of an arctic-alpine tundra environment. Furthermore, 6 specimens of *S. niphoclada* from the "tundra" community ranged in age between 9 and 14 years, illustrating that they became established after the site was clear-cut.

The herb-low shrub layer gives much greater evidence of floristic change since the initiation of secondary succession. Of the 16 species included in this stratum (Table 2), more than half of the plants were absent from the other 62 study plots in the Mackenzie Delta. Even more importantly, the 5 species that have the greatest significance (and thus create the great majority of cover in this stratum) are typically low-arctic shrub-tundra species normally not found within the Delta. Of these species, arctic blueberry (*Vaccinium uliginosum*) has the greatest cover-abundance. Northeast of the Mackenzie Delta this plant is common on hummocky tundra and lichen-heath tundra (Cody 1965, p. 46); I noted that it was common on the shrub tundra east of Reindeer Station and in the subalpine zone of the Richardson Mountains. Lambert (1968) also states that *V. uliginosum* occurs frequently in the Richardson Mountains. Since this plant was observed nowhere in the Delta except as a member of the "tundra" secondary succession, it is clear that this species typifies Mackenzie tundra vegetation and is not representative of the Delta flora. (It should be noted however that this species occurs sporadically in white and black spruce forests of the Canadian Northwest, but it does not commonly grow in the Mackenzie Delta, presumably because it does not tolerate an actively alluviating environment.)

Nearly as significant to this community is *Empetrum hermaphroditum* (the *E. nigrum* of many authors — Porsild 1951; Anderson 1959; Moss 1959; Polunin 1959). The widespread crowberry occurs almost throughout the low- and middle-arctic (Polunin 1959, p. 309); in the Mackenzie region it is very common on upland tundra and lichen-heath tundra. It is also present (though less commonly) in *Salix*, *Alnus*, *Betula glandulosa*, and *Picea* understories (Cody 1965; Lambert 1968). The significant occurrence of this species in the "tundra" association may help to impede the regeneration of white spruce. *Empetrum hermaphroditum* harbours a rust (*Chrysomyxa empetri*) that alternates to *Picea* and may almost wholly defoliate seedlings. This rust seldom kills seedlings, but it creates a serious drain on the vitality of young spruce so that they are easily killed by environmental stress or are crowded out by other plants (Savile 1963).

The mountain cranberry (*Vaccinium vitis-idaea*) is also prevalent in the "tundra" community. Cody (1965, p. 46) states that this low shrub is a very common part of the moist to dry tundra and lichen-heath tundra vegetation of the Mackenzie area, but does not list it as occurring in the Delta; Lambert (1968) lists it as a species common to the Richardson Mountains. This plant in the Mackenzie Delta is thus more representative of tundra than taiga vegetation although (similar to *V. uliginosum*) it does occur in non-alluvial forest environments.

Labrador tea (*Ledum palustre*) constitutes approximately 5 per cent of the cover in the herb-low shrub layer of this community. This shrub does not represent tundra communities as well as the previously discussed species; while it is a dominant plant on moist tundra (Cody 1965; Lambert 1968), it also occurs in open woods in the Mackenzie region. In the western portion of the Delta, V. J. Krajina (personal communication 1966) found *L. palustre* growing in spruce stands near Aklavik. In the study area, however, I found it only in the community under discussion. Similar to *Empetrum hermaphroditum*, it too harbours rusts that alternate to white spruce and reduce the vigour of seedlings (Savile 1963).

The fifth most dominant member of this stratum is *Senecio fuscatus*. This composite reaches the Arctic in Eurasia and along the Bering Sea and arctic Coast of Alaska (Anderson 1959, p. 498), but it had not been previously reported for the Mackenzie Delta region until Lambert (1968) listed it in his study of the Richardson Mountains. According to Polunin (1959, p. 459) and Hultén (1968) it is not typical of either tundra or taiga vegetation, and is found in rather poorly-vegetated, stony areas and on dry hill sides and in alpine situations. Krajina (personal communication 1966) on the other hand maintains that it is a very frequent component of subalpine tundra communities in the Richardson Mountains. This plant thus also has value in indicating the retrogression of the "tundra" site.

Several other species in the community are worth discussing. The following plants contribute little cover to the "tundra" association, but were not found to occur anywhere else in the Delta; they thus help to indicate the changing environmental conditions that accompany this type of secondary succession. In order of descending cover-abundance, they are *Petasites frigidus*, *Stellaria ciliatosepala*, *Carex lugens*, and *C. vaginata*. Combined they create less than 5 per cent cover, although most were in good vigour (Table 2) and appeared to be relatively successful in the community.

Petasites frigidus is noted by Cody (1965, p. 53) and Lambert (1968) as being frequent on moist tundra in the Mackenzie region, although it occurs on silt in the Delta as well. *Stellaria ciliatosepala* on the other hand grows only in open peaty situations (Cody 1965, p. 30) — conditions that are ubiquitous over much of the Mackenzie region except in the Delta. *Carex lugens* commonly grows in sedgy-grassy areas of tundra (Polunin 1959, p. 103) and is a "very common species of mature tundra formations" (Cody 1965, p. 24) in the Mackenzie District. Lambert (1968) also found this plant to be common to the Richardson Mountains. The second sedge (*Carex vaginata*) also occurs in the subalpine zone of the Richardson Mountains (Lambert 1968), and is a constituent of wet mossy and hummocky tundra vegetation in the Eskimo Lake Basin to the east of the Delta (Cody 1965, p. 23). Neither of these sedges has previously been reported from the Delta proper.

Some 7 additional species make up the herb-low shrub layer of the "tundra" association (Table 2), all of which are more or less common to the Delta, and all but one of which are components of the previously dominant *Picea* association (Table 1). It was interesting to observe that these species, which normally enjoy excellent vigour in the *Picea* association (Table 1), were generally growing less successfully in the cleared area. *Pyrola grandiflora* for example is one of the dominant shrubs in spruce stands but occurs only as a sparse, non-vigorous growth in the "tundra" community. A factor restricting its growth on the latter site seems to be the reduced amount of shading; as Cody (1965, p. 45) similarly found, this plant usually occurs in shaded locations in the Mackenzie area.

The moss and lichen stratum (Fig. 6) provides additional floristic evidence of the environmental changes that take place on such sites when the canopy is removed: 15 species assemble to create this stratum, only 3 of which are normally found in other communities of the Delta study area (Table 2). Except for one study (Lambert 1968), little comparative information is available concerning the distribution of bryophytes and lichens in the Mackenzie region. Cody's (1965) work does not include these species nor do Anderson's (1959), Polunin's (1959) or Hultén's (1968) treatments of arctic flora.

According to Lambert (1968) the following bryophytes are present to the east

FIG. 6. The herb-low shrub and moss-lichen stratum in the "tundra" association. The major lichen is *Stereocaulon tomentosum*. *Cladonia arbuscula*, *Cetraria islandica*, and *C. nivalis* are also present. Note also *Ledum palustre* (upper left), *Empetrum hermaphroditum* (lower center), and *Vaccinium uliginosum* (upper center). These plants are common members of upland shrub tundra communities east of the Caribou Hills and in the Richardson Mountains. 11 August 1967.

of the Mackenzie Delta in the low arctic subalpine zone of the Richardson Mountains: *Dicranum elongatum*, *Barbilophozia barbata*, *Lophozia alpestris*, *Sphenolubus minutus*, and *Ptilidium ciliare*. These mosses are also found in the "tundra" association but are not otherwise present in the study area. The following lichens are also common to the Richardson Mountains (Lambert 1968) and to the "tundra" association but are not otherwise located in this portion of the Mackenzie Delta: *Cladonia amaurocraea*, *C. gracilis*, *C. rangiferina*, *Cetraria islandica*, *C. nivalis*, and *Stereocaulon tomentosum*. One species of lichen, *Cladonia arbuscula*, was found in the "tundra" association which was not listed in Lambert's study; however, I collected this lichen in the shrub tundra to the east of the Mackenzie Delta.

The probable seed source of species now growing in the study location is the low arctic shrub tundra which occupies uplands 3 km. to the east. The Caribou Hills parallel the east side of the Delta, and local pressure gradients here cause strong northeast winds periodically to sweep down the hill slopes and onto the Delta surface. This enables air-borne seed to be readily transported into the Delta.

CONCLUSIONS

The Mackenzie River Delta contains one of the northernmost extensions of boreal forest in North America, and the environmental balance here may be sufficiently critical that certain of man's activities could alter the vegetation from a coniferous forest to a tundra cover. It seems evident that the occupation by common tundra species of a previously forested deltaic site demonstrates that the ecologic changes caused by clear-cutting are sufficient to tilt the environmental balance from one major biome type to another. Environmental modification caused by the removal of tree and shrub canopies has either initiated a new stage in the pattern of plant succession or it has greatly accelerated a slow natural process (see Strang 1973) that would ultimately replace a spruce stand on any segment of delta surface that stayed intact for a sufficient length of time.

An objection to this conclusion might easily be the question: if clear-cutting initiates a tundra type of vegetation, why is the Delta not now tundra rather than being covered by Boreal-Arctic Transition vegetation? The following reasons may help to account for this:

1) It is known that spruce colonized the Mackenzie Delta region some 8000 years B.P. (Mackay and Terasmae 1963, p. 233) and this tree appears to have reached its maximum northward extension during the period of postglacial warming some 6000 years ago. Porsild (1938, p. 57) located well-preserved spruce stumps *in situ* under 1 m. of peat along the northeast edge of the Mackenzie Delta; this is 100 to 120 km. north of today's treeline, thus evidence exists for a degeneration of growing conditions since the time when these spruce became established. Any climatic retrogression that occurred has not extended to the present, for indications are that yet another climatic amelioration began at the early part of this century and is still proceeding (Bird 1967, p. 32). Today's climate is more severe than that of the hypsithermal period however. If spruce became established in the Mackenzie Delta during a period of climatic amelioration, it could continue to exist within the Delta during a period of deteriorating temperatures (if not too great) since it is well known that forest stands improve the microclimate under which they grow (see especially Geiger 1965, and Shaw 1967). Conversely, it has been observed in forest-tundra regions that destruction of the woody vegetation leads to a lowering of soil and permafrost temperatures (Tyrtikov 1959). Thus today if an area occupied by spruce is clear-cut (especially a site such as the upper levee shown in Fig. 3 which is greatly exposed) the environmental conditions of the site may become too severe for the regeneration of spruce, and a more hardy tundra vegetation would succeed.

2) A second possible reason for the establishment of a tundra type of vegetation on such sites is that in regions of severe environmental stress, the climax association develops best if there is an orderly, uninterrupted sequence of seres. Vegetation in each community interacts together and with elements of the environment (autogenic succession) to create a condition whereby the next sere may succeed. The climax *Picea* association in the Mackenzie Delta thus evolves only where certain demands are met by the environment: the site must be above mean flood level — it must be protected by an overstory of *Salix* spp., *Alnus crispa*, *Populus balsamifera*, or some combination of these species — the ground vegetation cannot be too dense or thick for the spruce germinule to become rooted — the mor layer cannot retain a high moisture content to cause waterlogging of the seed bed. Conditions necessary for the ecesis of spruce are optimally present in the communities that immediately precede the spruce sere, but once a spruce

stand and its upper shrub canopy have been removed, the low shrub, herb, and moss layers that remain cannot sufficiently ameliorate the environment for spruce to regenerate. (Furthermore, it has been shown in many areas that a moss layer makes it difficult for white spruce to germinate.) Conversely, disseminules that are more adapted to the now-severe site conditions may invade and successfully initiate a secondary succession.

Too little time has elapsed since the "tundra" secondary succession became initiated to draw final conclusions about the potential climax vegetation of these locations, but available evidence indicates that spruce will not re-establish under the exposed conditions of clear-cut areas. It is possible, of course, that spruce could eventually regenerate if an alder and willow canopy becomes re-established which then ameliorates the ground surface environment and reduces the cover (especially ericaceous shrubs) through shading.

Since clear-cutting may result in site degradation, it is of considerable interest that in 1967 the Mackenzie Forest Service instituted a study of spruce growth rates in the Delta to determine the feasibility of using this resource for commercial purposes (Wellstead 1967). Commercial cutting of white spruce in fact began on the east side of the Delta during the 1971-72 winter season. If the forestry resource of the Mackenzie River Delta is to be maintained through the process of natural regeneration, then a program of selective cutting should be considered. If a good portion of the spruce and willow-alder canopy is left intact, environmental conditions at the forest floor should continue to be adequate for normal regeneration of spruce seedlings. However, although the *environmental* conditions might be adequate for regeneration under such a program, a fundamental question remains unanswered, and this concerns the availability of white spruce seed. Good seed years appear to be few in the Mackenzie Delta as has been shown for interior Alaska (Werner 1964; Brink and Dean 1966; Zasada and Viereck 1970; Zasada 1971). Such factors as disease (*Chrysomyxa pirolata*), frost, insects, and the red squirrel (*Tamiasciurus hudsonicus*) all cause reductions in the cone crop of white spruce (Zasada and Viereck 1970), and all these factors are present in the Mackenzie Delta. Therefore, even if spruce were selectively logged, there might not be a sufficient cone crop for a number of years to permit regeneration. This is but one of the questions that should receive critical attention before extensive commercial logging is begun in the Mackenzie River Delta.

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