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TOPOGRAPHIC AND SITE INFLUENCES ON VEGETATION, SOIL AND THEIR NUTRIENTS EAST OF THE MACKENZIE DELTA

by

ARNOLD JACOB JANZ

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
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DEPARTMENT OF BOTANY

EDMONTON, ALBERTA

FALL, 1974

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Topographic and site influences on vegetation, soil and their nutrients east of the Mackenzie Delta" submitted by Arnold Jacob Janz in partial fulfilment of the requirements for the degree of Master of Science.

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ABSTRACT

Three topographic positions (hilltop, midslope and depression) at three locations on the treeless uplands east of the Mackenzie Delta, were compared for differences in vegetation and soil characteristics.

Moderately well drained to imperfectly drained soils on hilltops and midslopes, dominated by low shrub-heath vegetation are associated with 30% deeper active layers, 30% shallower surface organic horizons and 50-100% greater concentrations by weight of available phosphorus and potassium than poorly drained depressions dominated by sedge-heath vegetation. Exchangeable calcium and pH in the organic horizon, which are highly correlated with each other, are both significantly higher at Tununuk Point than at the other two sites and are thought to be partly responsible for the significantly lower phosphorus and potassium concentrations found there. Total and available soil nitrogen concentrations are similar among study sites and topographic positions.

The nutrient content of the standing crop is generally greatest on hilltops, decreasing downslope and being least in depressions. For nitrogen, phosphorus and potassium, the differences between hilltops and depressions are statistically significant. Nitrogen and phosphorus contents are 30% greater while potassium contents are 14% greater on hilltops than depressions.

The phosphorus content of standing crop is 10 and 14% greater and potassium is 10 and 30% greater at the Caribou Hills and Tuktoyaktuk respectively, than at Tununuk Point. The calcium content is more than 100% greater at Tununuk Point than at the other two sites.

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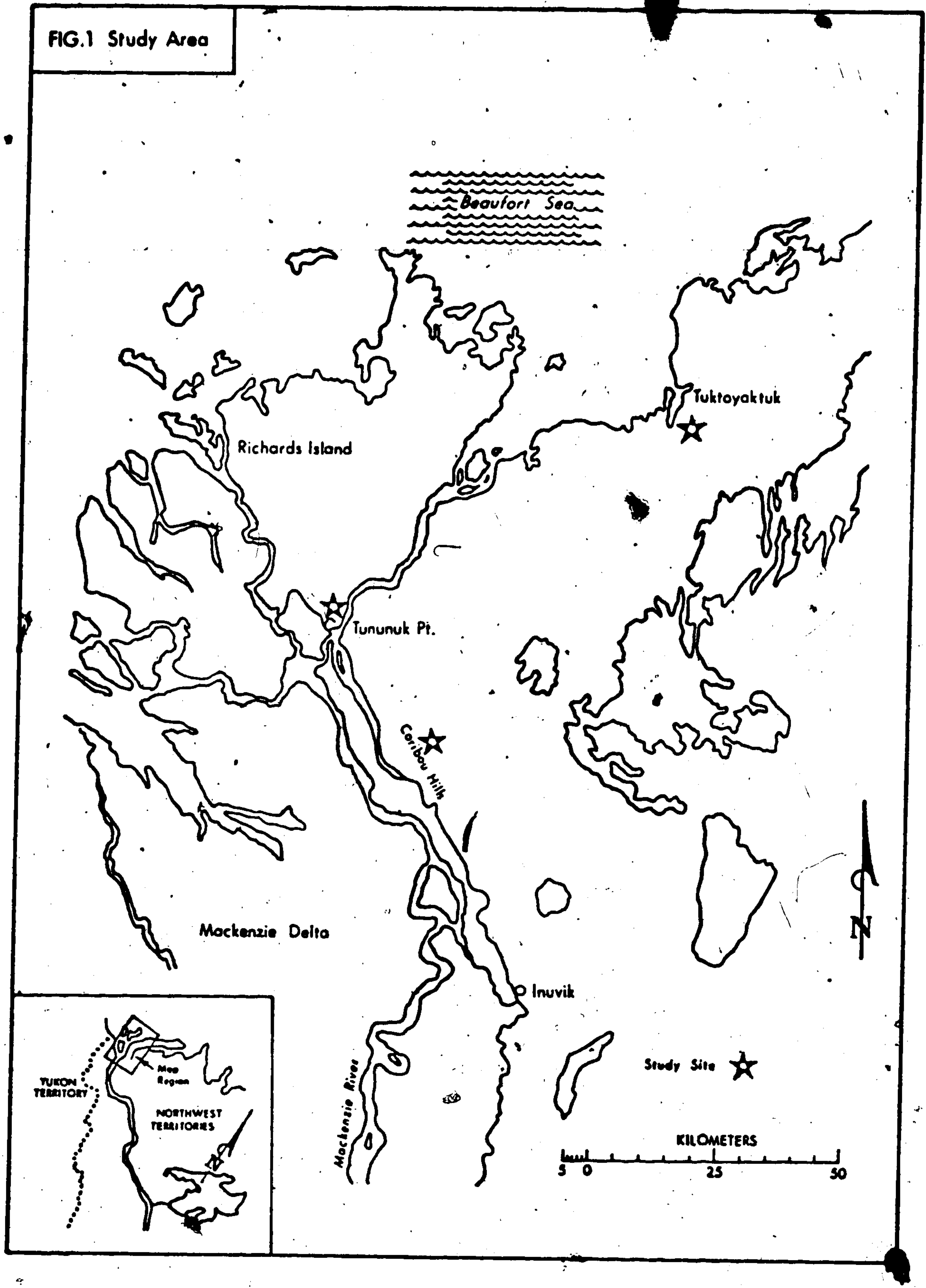
1.0 INTRODUCTION

Topography, and its effect on drainage, is commonly recognized as the major factor influencing local variations of soil and plant community patterns. Drew and Shanks (1965), in the northwestern part of the Yukon Territory, attributed soil and plant community patterns to the effects of soil drainage, land surface age, snow cover, soil reaction and micro-relief. Tedrow *et. al.* (1958), classified soils of the north slope of Alaska on a drainage catena.

In the Arctic, influences of topography are somewhat accentuated by the presence of permafrost, which impedes vertical while encouraging lateral drainage. Drainage is generally a function of slope and soil particle size, but in regions underlain by permafrost, slope becomes more important because of the barrier to drainage by permafrost. As a result, the water table generally fluctuates seasonally within the active layer, a layer which seldom exceeds a depth of 60 cm by late August in the upland study area east of the Mackenzie Delta (Fig. 1).

Increased industrial activity in this area due to recent oil and gas discoveries, has prompted interest in natural, physical and biological processes. With this in mind, a study was conducted in 1971 and 1972 to identify and quantify changes in several vegetation and soil physical and chemical parameters along topographic gradients, and to suggest how these changes may be responsible for the distinct soil and plant community patterns.

FIG.1 Study Area



2.0 DESCRIPTION OF STUDY AREA

The study area lies within the Arctic Coastal Plain physiographic region, and Marine Tundra Climatic zone (Burns, 1973). Low precipitation (10 to 20 cm annually), and short growing seasons are characteristic of this area which lies within the continuous permafrost zone above the Arctic Circle. Inuvik and Tuktoyaktuk report a mean annual precipitation of 26 and 12 cm, mean annual temperatures of -10 and -11°C and frost-free periods of 96 and 88 days repsectively (Burns, 1973). Break-up of river and lake ice occurs about mid-June and the area remains relatively cloud-free in spring till the end of June. July and August experience frequent cloud and fog along the coast and inland.

The gently rolling landscape east of the Mackenzie Delta has a maximum relief of 100 m (Mackay, 1971) and consists of Pleistocene fluvial, marine and lacustrine sediments from two glaciations (Fyles, 1966; Rampton, 1971), except for the northern Caribou Hills which have sediments composed of Tertiary gravels.

Steep slopes, and relatively flat hilltops and depressions are the result of thermokarst lakes. These lakes cover 30 to 50% of the land surface (Mackay, 1963) (Fig. 2). Areas occupied by the formerly thermally eroding lakes are presently occupied by sedge-heath vegetation. Low shrub-heath vegetation (Corns, 1974) commonly occupies tills on hilltops and midslopes.

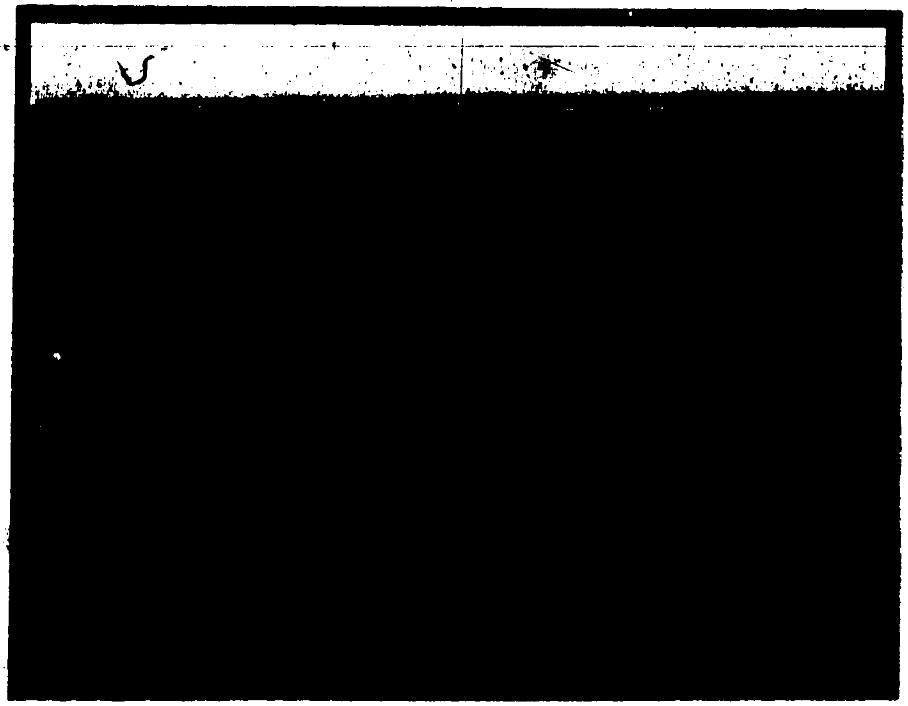


Figure 2. General topography of the study areas (this photo was taken approximately 60 km north of Inuvik).

The study area near Tuktoyaktuk has 0.7 to 2.5 m of interbedded sands and gravels (Bouchar *et al.*, 1967). Soils are coarse textured, mostly sandy loams and slopes range from 6 to 14% with a relief of 15 to 25 m.

Glaciofluvial sands and gravels, possibly up to 10 m thick, cover most of the Tununuk Point area. In places they are capped by till (Rampton, 1971). Soils are slighlty coarser textured here than at Tuktoyaktuk but topogaphic relief is similar with slopes of 5 to 15%.

The study area in the Caribou Hills consists of gravels and sands dissected by meltwater channels some of which are presently occupied by lakes (Mackay, 1963). Broad hills and more gentle slopes are characteristic of this area. Slopes range from 4 to 12% with a relief of 30 to 40 m.

In all study locations, hilltops and midslopes with dwarf shrub-heath vegetation are more subject to frost heaving than depressions with sedge-heath vegetation. Frost boils or earth hummocks range from 0.5 to 2 m in diamteter with a microrelief of 5 to 20 cm and are separated by 0.5 to 1 m wide moss-filled depressions. Occasionally, mineral soil which has been expelled upwards by the forces of frost action, has buried former surface organic horizons. Soils in the Caribou Hills are generally finer textured and hills are broader than those at Tuktoyaktuk or Tununuk Point so that the mineral soil is exposed more frequently and therefore the microrelief is more pronounced. On slopes the processes of frost heaving and downward movement of the active layer over permafrost combine to create solifluction features.

3.0 METHODS

Sampling areas were selected near Tuktoyaktuk, Tununuk Point, and the Caribou Hills. Sampling was done within the first week in August to reduce seasonal phenological variation. At each location, three areas were chosen from air photos and ground reconnaissance, each of which had a sequence of low shrub-heath hilltop and midslope, and sedge-cottongrass-heath bottomland. The 27 topographic positions are referred to as stands.

A 30 m baseline was laid out in each stand, and three randomly placed 0.25 m^2 quadrats were then placed on the line. Live plant cover was estimated by species and clipped within each quadrat. The clipped material included all attached vascular plants and cryptogams which were clipped at 2 cm below the cryptogam surface. Litter material was then gathered from the same quadrat. After clipping, a soil pit was dug to permafrost under each quadrat and the profile described according to Canada Department of Agriculture (1970). Ten soil samples were taken within each stand from all important horizons. These were then composited for one representative sample. Active layer depth measurements were made with a graduated (1 cm) steel rod at 1 m intervals along the 30 m baseline.

Soil and vegetation samples were frozen and shipped to Edmonton to be dried. Plant material from each quadrat was dried at 80°C and then weighed. Soils were weighed, air dried, then weighed again for field moisture determination. Plant material was ground to pass through a 60 mesh sieve and sent to the Alberta Department of Agriculture Soil and

Feed Testing Laboratory in Edmonton for analyses of nitrogen, phosphorus, potassium and calcium. Analyses followed a modified procedure of Horitz (1965).

Soil samples were evaluated for color (Munsell color charts), then ground to pass through a 2 mm sieve. Part of each sample was sent to the above named laboratory for analyses of available and total nitrogen, available phosphorus and potassium. Laboratory analyses followed a modified procedure of Jackson (1958).

Other soil analyses included texture by the hydrometer method (Bouyoucos, 1951); loss on ignition (3 hours at 450°C); pH (soil paste-glass electrode); the exchangeable cations calcium, potassium and magnesium by atomic absorption spectrophotometer after extraction with ammonium acetate; total exchange capacity by atomic absorption spectrophotometer analysis of sodium after successive extractions with ammonium acetate, sodium chloride and ammonium acetate; and available water after ceramic plate extraction at 1/3 and 15 bars.

Statistical analyses of the data including Duncan's multiple range test, Student's t-test and the simple correlation coefficient follow those described in Steel and Torrie (1960).

4.0 RESULTS

4.1 Topographic and site influences on vegetation

4.1.1 Plant communities

In the uplands east of the Mackenzie Delta, plant communities consistently reflect the influence of the rolling topography. They are the major visible expression of changes in topography. Other parameters, such as depth of the active layer, and soil moisture, also reflect topographic changes and appear to be more directly responsible for plant community variation.

As this study was closely related with the general vegetation survey of Corns (1974), his vegetation classification is used. His study demonstrates the effect of topography on the distribution of vegetation types within this study area. He indicates that the dominant vegetation type is the low shrub-heath, which is characteristic of hilltops and gentle slopes. The sedge-heath subgroup which is part of the herb-low shrub-heath type, is usually situated on level to gentle slope areas below the low shrub-heath type in topographic position. The medium shrub (*Alnus*) -heath type described by Corns, was not included in this study due to its less extensive distribution.

In the Tuktoyaktuk region, *Vaccinium vitis-idaea* ssp. *minus*, and *Eriophorum vaginatum* ssp. *spissum* are the dominant vascular species in sedge-heath depressions while *Empetrum nigrum* ssp. *hermaphroditum*, *Vaccinium vitis-idaea* ssp. *minus*, *Betula nana* or *glandulosa* and *Salix glauca* ssp. *acutifolia* dominate low shrub-heath units in midslope and hilltop positions.

Dominant species in sedge-heath depressions at Tununuk Point are *Vaccinium uliginosum* ssp. *alpinum, Arctostaphylos rubra, Dryas integrifolia* ssp. *integrifolia, Carex* spp. and minor amounts of *Eriophorum vaginatum. Vaccinium uliginosum, Dryas integrifolia* and *Arctostaphylos rubra* are dominant in low shrub-heath types in midslope and hilltop positions.

Vaccinium uliginosum is present in all topographic positions in the Caribou Hills. Other important species include *Vaccinium vitis-idaea* and *Betula nana* or *glandulosa* in most topographic positions, while *Eriophorum vaginatum* along with *Vaccinium vitis-idaea, Empetrum nigrum* and *Carex* spp. occupy bottom positions. *Ledum palustre* ssp. *decumbens* is fairly common in midslope and hilltop low shrub-heath positions and often occurs in bottom positions as well.

The moss component, having total cover values ranging from 15 to 80%, is the major component of the vegetation in all topographic positions. In depressions, *Sphagnum* spp. predominate, growing mainly in micro-depressions around *Eriophorum vaginatum* tussocks. Tussock sides and tops appear to be favorable microhabitats for heath species such as *Ledum palustre* and *Vaccinium vitis-idaea.* On midslopes and hilltops, mosses occur mostly in hollows or micro-depressions surrounding and separating earth hummocks. Here they provide insulation and aid in the formation of ice wedges between hummocks. Mosses on midslopes and hilltops do not form as thick an insulation layer as do mosses in depressions. Vascular species prefer habitats of higher micro-topographical positions and as such are found on the sides and tops of earth hummocks and solifluction features.

Several vascular species including *Ledum palustre*, *Vaccinium vitis-idaea*, and *Betula nana* growing in depression positions are noticeably chlorotic when compared to the same species in higher topographical positions.

One other difference among topographic positions is the relatively low cover of woody shrub species in depressions compared to the other positions, and the low cover of herbaceous species including sedges such as *Carex* spp. and *Eriophorum vaginatum* on midslopes and hilltops.

4.1.2 Tissue nutrient composition

Several investigations have been done concerning nutrient composition on arctic and subarctic vegetation. Kellogg and Nygard (1951) have analyzed several forage species from alpine, arctic tundra and forest regions in Alaska for crude protein, phosphorus and calcium, to determine possible deficiencies for native animals. Pieper (1963) near Pt. Barrow, Alaska and Scotter (1972) in the Reindeer Grazing Preserve north of Inuvik, N.W.T. have reported seasonal nutrient changes of some major tundra species. Haag (1974) investigated the influence of fertilizers on nutrient content of native species from hilltop and bottom positions near Tuktoyaktuk, N.W.T. In the same area Younkin (1973) investigated differences in nutrient contents of *Arctagrostis latifolia* and *Calamagrostis canadensis* from disturbed and undisturbed tundra habitats.

In this study, four major nutrients, nitrogen, phosphorus, calcium and potassium are examined and their function briefly described according to Tisdale and Nelson (1966).

Nitrogen is an essential constituent of protein and chlorophyll in temperate plants. The forms most commonly assimilated by plants are the nitrate and ammonium ions. Phosphorus is required in much smaller amounts by plants and occurs mainly in the inorganic orthophosphate ion form (H_2PO_4), which is also the most abundant form found in some northern areas (Saebø, 1968). A sufficient supply of the orthophosphate ion seems to aid root growth, and protein synthesis (Tisdale and Nelson, 1966). Potassium is absorbed by plants as the potassium ion. It does not form an integral part of plant constituents, but its function appears to be catalytic. Calcium is absorbed as the cation and is required by all higher plants, and is related to protein syntheses by its enhancement of nitrate nitrogen uptake. It may also be associated with activity of enzyme systems and ion uptake.

.1 Nitrogen (Crude Protein/6.25)

Analysis of the data reveal significant differences in standing crop, litter and *Betula nana* leaf tissue nitrogen among topographic positions (Table 1). Concentrations of nitrogen are greatest in hilltop materials, intermediate in midslope positions and least in depression positions.

.2 Phosphorus

Significant differences in standing crop and *Betula nana* leaf tissue phosphorus content occur between low shrub-heath types in

Table 1: Nitrogen ($\frac{\text{crude protein}}{6.25}$), phorphorus and potassium contents of standing crop, *Betula nana* leaf tissue and litter material among topographic positions from all study locations (n = 9 ± SE).

Nutrients and Vegetation Components	Topographic Positions Hilltop	Midslope	Depression
<u>Nitrogen</u> (%)			
Standing Crop	1.1 ± 0.05 a[1]	0.99 ± 0.02 a	0.84 ± 0.03 b
Litter	1.38 ± 0.03 a[1]	1.23 ± 0.04 b	1.05 ± 0.02 c
Betula nana leaf	1.83 ± 0.06 a[1]	1.76 ± 0.05 a	1.61 ± 0.05 b
<u>Phophorus</u> (%)			
Standing Crop	0.104 ± 0.003 a[1]	0.094 ± 0.003 a	0.082 ± 0.004 b
Litter	0.107 ± 0.002 a[2]	0.096 ± 0.003 ab	0.084 ± 0.004 b
Betula nana leaf	0.25 ± 0.014 a	0.23 ± 0.014 a	0.22 ± 0.026 a
<u>Potassium</u> (%)			
Standing Crop	0.28 ± 0.013 a[2]	0.25 ± 0.007 b	0.24 ± 0.01 b
Litter	0.15 ± 0.005 a	0.14 ± 0.008 a	0.15 ± 0.01 a
Betula nana leaf	0.64 ± 0.022 a[2]	0.60 ± 0.026 a	0.53 ± 0.026 b
<u>Calcium</u> (%)			
Standing Crop	0.99 ± 0.19 a	0.96 ± 0.16 a	0.75 ± 0.12 a
Litter	1.50 ± 0.23 a[2]	1.54 ± 0.24 a	0.88 ± 0.16 b
Betula nana leaf	0.68 ± 0.03 a	0.77 ± 0.04 a	0.73 ± 0.06 a

[1] Any two means in a row not followed by the same letter are significantly different at p = 0.01 (determined by Duncan's multiple range test).

[2] Any two means in a row not followed by the same letter are significantly different at p = 0.05.

all study sites (Table 1). Phosphorus contents are highest in hilltop and midslope materials and lowest in depressions.

Differences also occur among study sites, phosphorus being lowest in materials from Tununuk Pt. and highest at Tuktoyaktuk (Table 2).

.3 Potassium

Potassium in standing crop, litter and *Betula nana* leaf tissue is greatest on hilltops and least in depressions (Table 1). Slight differences also occur among study sites, potassium being least in material at Tununuk Pt. and greatest at Tuktoyaktuk (Table 2).

.4 Calcium

No differences in standing crop and *Betula nana* leaf tissue calcium occur among topographic positions, but this element occurs in much greater amounts in material at Tununuk Pt. than at the other two study sites (Table 2).

Litter materials from depression positions contain much less calcium than those from midslopes or hilltops (Table 1). Calcium concentrations are also significantly greater in litter material at Tununuk Pt. than at Tuktoyaktuk and Caribou Hills (Table 2).

Table 2: Phosphorus, potassium and calcium contents of standing crop, *Betula nana* leaf tisue and litter material among study sites from all topographic positions (n = 9 ± SE).

Nutrients and Vegetation Components	Locations		
	Tuktoyaktuk	Tununuk Pt.	Caribou Hills
<u>Phosphorus</u> (%)			
Standing Crop	0.096 ± 0.003 a*	0.084 ± 0.006 a	0.092 ± 0.005 a
Litter	0.095 ± 0.003 a	0.083 ± 0.006 a	0.097 ± 0.005 a
Betula nana leaf	0.28 ± 0.005 a	0.18 ± 0.01 b	0.23 ± 0.016 a
<u>Potassium</u> (%)			
Standing Crop	0.303 ± 0.059 a	0.228 ± 0.037 b	0.249 ± 0.022 b
Litter	0.16 ± 0.011 a	0.13 ± 0.003 b	0.15 ± 0.003 a
Betula nana leaf	0.63 ± 0.065 a	0.53 ± 0.056 b	0.617 ± 0.09 a
<u>Calcium</u> (%)			
Standing Crop	0.71 ± 0.086 a	1.4 ± 0.15 b	0.58 ± 0.03 a
Litter	1.15 ± 0.18 a	1.99 ± 0.20 b	0.78 ± 0.05 a
Betula nana leaf	0.66 ± 0.01 a	0.85 ± 0.05 b	0.67 ± 0.02 a

* Any two means in a row not followed by the same letter are significantly different at $p = 0.05$.

4.2 Topographic and site influences on soil characteristics

4.2.1 Soil morphology

The dominant feature of soils in this study is the presence of permafrost underlying the active layer. This frozen barrier inhibits drainage, thereby inducing anaerobic and gleyed profile conditions in all topographic positions. In addition, imperfectly drained conditions are responsible for frost heaving within the active layer, especially in midslope and hilltop positions where the active layer is deeper and total mineral soil volume greater than in depressions. Because of these frost processes, soil forming processes are masked, making classification difficult.

Several soil classifications have been formulated for other tundra areas. These classifications have been based on general vegetation and drainage characteristics (Kellogg and Nygard, 1951; Tedrow *et. al.*, 1958 and Tedrow and Cantlon, 1958). Under the classification system used by Tedrow and associates in Alaska, depression soils in this study could be classified as Meadow Tundra soils. Hilltop and midslope soils become Upland Tundra soils.

The Canadian system (C.D.A., 1970) is inadequate to describe hilltop and midslope soils in this study, because of the rapid horizontal profile variations and frequent burial of surface and other horizons due to frost heaving. The most useful classification is a recent tentative system devised to include soils under the influence of frost heaving (Canada Soil Survey Committee, 1973). Under this system, depression soils are classified as Gleysolic Turbic and Static Cryosols while hilltop and midslope soils become Regosolic Turbic Cryosols. The discontinuous Bm in the hummocks of hilltops and midslopes is responsible for the Regosolic Subgroup classification of these soils. Occasionally, hummocks with a Bm of greater than 10 cm thickness were encountered and fall into the Brunisolic Turbic Cryosol Subgroup.

Several soil profiles have been described by Tarnocai (1972) north of Inuvik, N.W.T., in an intensively frost disturbed area. These soils have been called Cryic Dystric Brunisols under the C.D.A. (1970) system and would now be called Brunisolic Turbic Cryosols. Day and Rice (1964) have described two hummock profiles in the Caribou Hills using the Canadian system. The moderately well drained and imperfectly drained hummocks were classified as Subarctic Orthic Regosol and Subarctic Gleyed Acid Brown Wooded respectively.

The most extensive soils over permafrost in Alaska have been classified as Histic Pergelic Cryaquepts by Allen *et. al.*, (1968), under the 7th approximation soil classification system (Soil Survey Staff, 1960 and 1967). These soils are comparable to many soils underlain by permafrost in Canada and Eastern Siberia, U.S.S.R. Thick organic horizons, gleyed mineral horizons, the presence of permafrost at shallow depths, loamy or silty textures, and buried organic horizons are a few common features of these soils (Allen *et. al.*, 1968).

Using the 7th approximation, soils in depressions could be called Histic Pergelic Cryaquepts because of their thick organic horizons, gleyed mineral horizons and the presence of permafrost at shallow depths. Hilltop and midslope soils contain thinner organic horizons than depression soils, so could be called Pergelic Cryaquepts, but this usually applies only to hummock soils. No nomenclature exits in this classification which describes the total soil pedon including the complete cycle of hummock and hollow.

.1 Depression positions (Figures 3 and 4)

Thick undecomposed organic horizons (10 to 30 cm), and shallow active layers (Table 3), are characteristic of soils in depressions dominated by sedge-heath vegetation. A slightly decomposed layer usually lies under the upper fibric layer. A thin (1 cm) brownish horizon of mixed partially decomposed organic and mineral material within a gleyed matrix may be present as the top mineral horizon. Usually the structure is amorphous but may be fine to medium granular. The lower part of the soil profile is nearly always a thin (10 to 15 cm) mineral horizon above the frozen zone which is gleyed with some mottles, and is saturated throughout the growing season (Figure 5). Often the remains of a buried fossil tussock may be preserved at or below the freeze-thaw zone.

Roots of low shrubs and heaths when present are restricted to the top 10 cm of the organic horizon, but herbaceous species such as *Eriophorum vaginatum* and the *Carex* species extend their roots to the bottom of the active layer.

On gentle slopes where soil movement may occur but moisture is high, mineral soils may be exposed and the active layer is more variable

Figure 3: Diagramatic soil profile for depression positions (August 5).

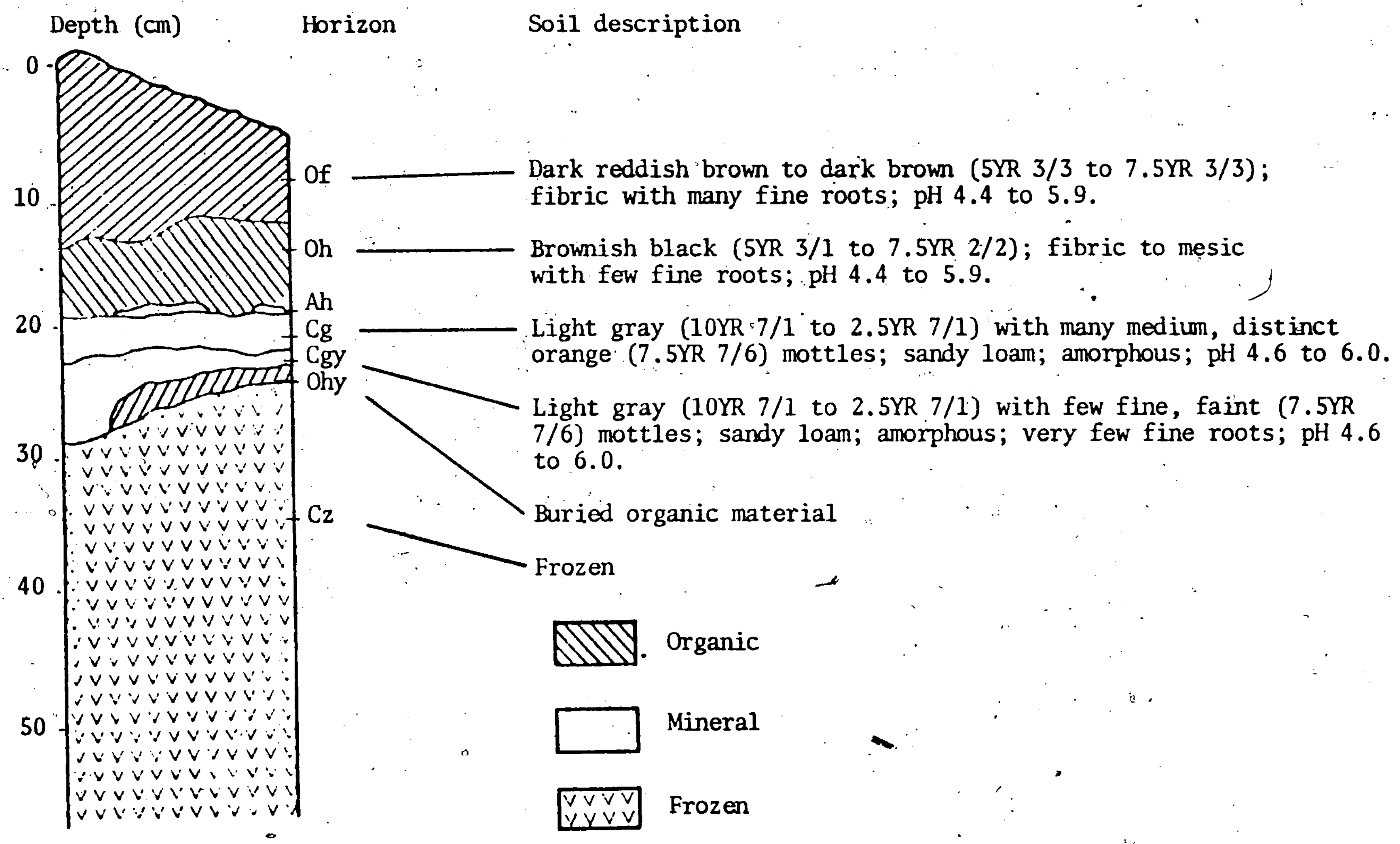


Figure 4: Soil cross section in a depression topographic position (August 15)

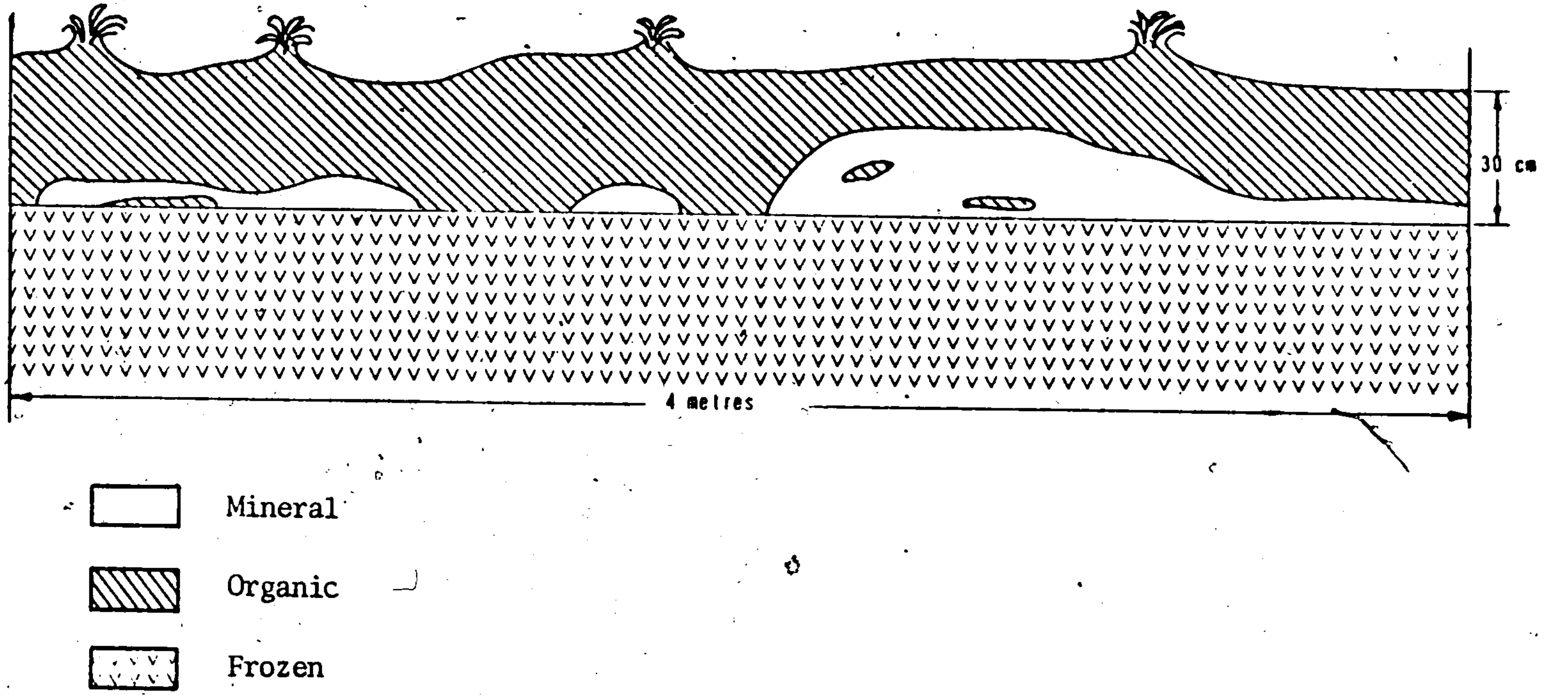


Figure 5. Typical soil profile in a depression position.

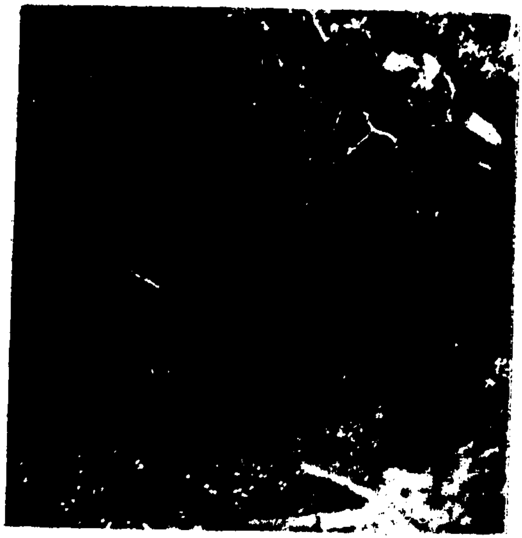


Figure 5. Typical soil profile in a depression position.

Table 3: Active layer depths (cm) among topographic poisitions from all study sites (Aguust 5) (n = 30 ± SE).

Locations	Topographic Positions		
	Hilltop	Midslope	Depression
Tununuk Pt.	40 ± 2.2	49 ± 3.7	28 ± 0.4
Caribou Hills	46 ± 5.9	41 ± 3.5	29 ± 1.9
Average	40 ± 2.7 a*	41 ± 2.8 a	28 ± 1.2 b

* Any two means in a row not followed by the same letter are significantly different at p = 0.01.

in depth. This situation exists in one stand in the Caribou Hills.

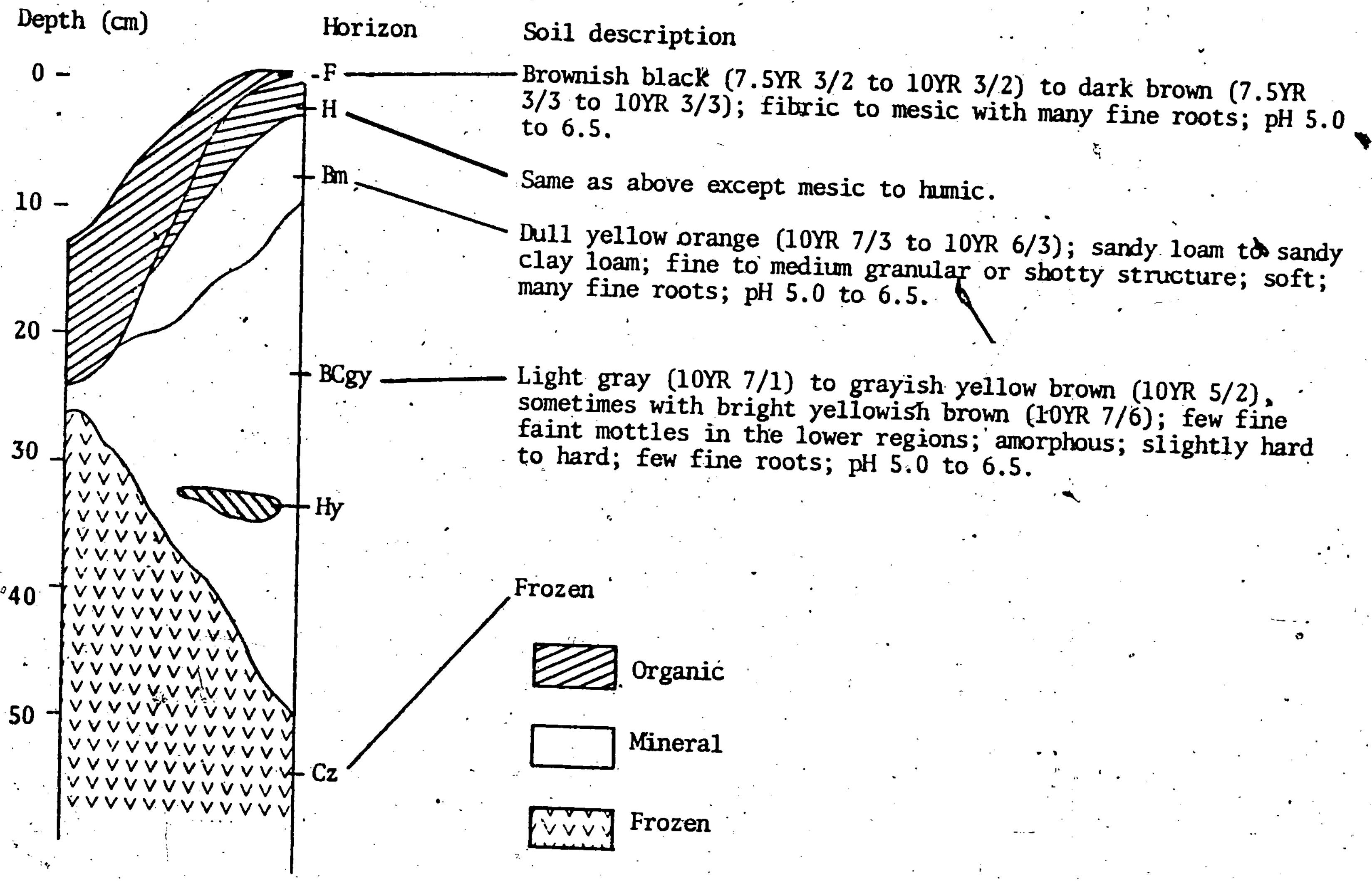
The organic horizon pH in these bottom positions ranges from 5.4 to 6.0 at Tununuk Pt. and from 4.4 to 4.9 at Tuktoyaktuk and the Caribou Hills. Mineral horizons have a pH of 5.1 to 5.9 at Tununuk Pt. as opposed to 4.0 to 5.0 at Tuktoyaktuk and Caribou Hills.

In these sedge-heath depression positions, frost induced surface features are absent, indicating that frost processes are not as intensive as in the better drained hilltops and midslope positions. The only evidence of frost induced disruption within the active layer is the occasional buried fossil tussock or other organic material occurring in the mineral region at the base of the active layer. Several reasons may be given to explain this relative active layer stability. First of all, the active layer is shallow, allowing only a small volume to be influenced by frost processes. Secondly, about 75% of the active layer volume consists of organic material, which is fairly compressible when subjected to frost forces. The remaining saturated mineral position constitutes only 25% of the active layer volume, which is too small a volume to participate in active frost heaving.

.2 Midslope and hilltop positions (Figures 6 and 7)

There is no typical soil profile for midslope or hilltop positions because of the extreme variation caused by frost heaving. A few characteristics are typical though. The active layer is usually deepest through hummocks or frost boil tops where the organic horizon is shallowest or

Figure 6: Diagramatic soil profile for hilltop and midslope positions (August 5).



F — Brownish black (7.5YR 3/2 to 10YR 3/2) to dark brown (7.5YR 3/3 to 10YR 3/3); fibric to mesic with many fine roots; pH 5.0 to 6.5.

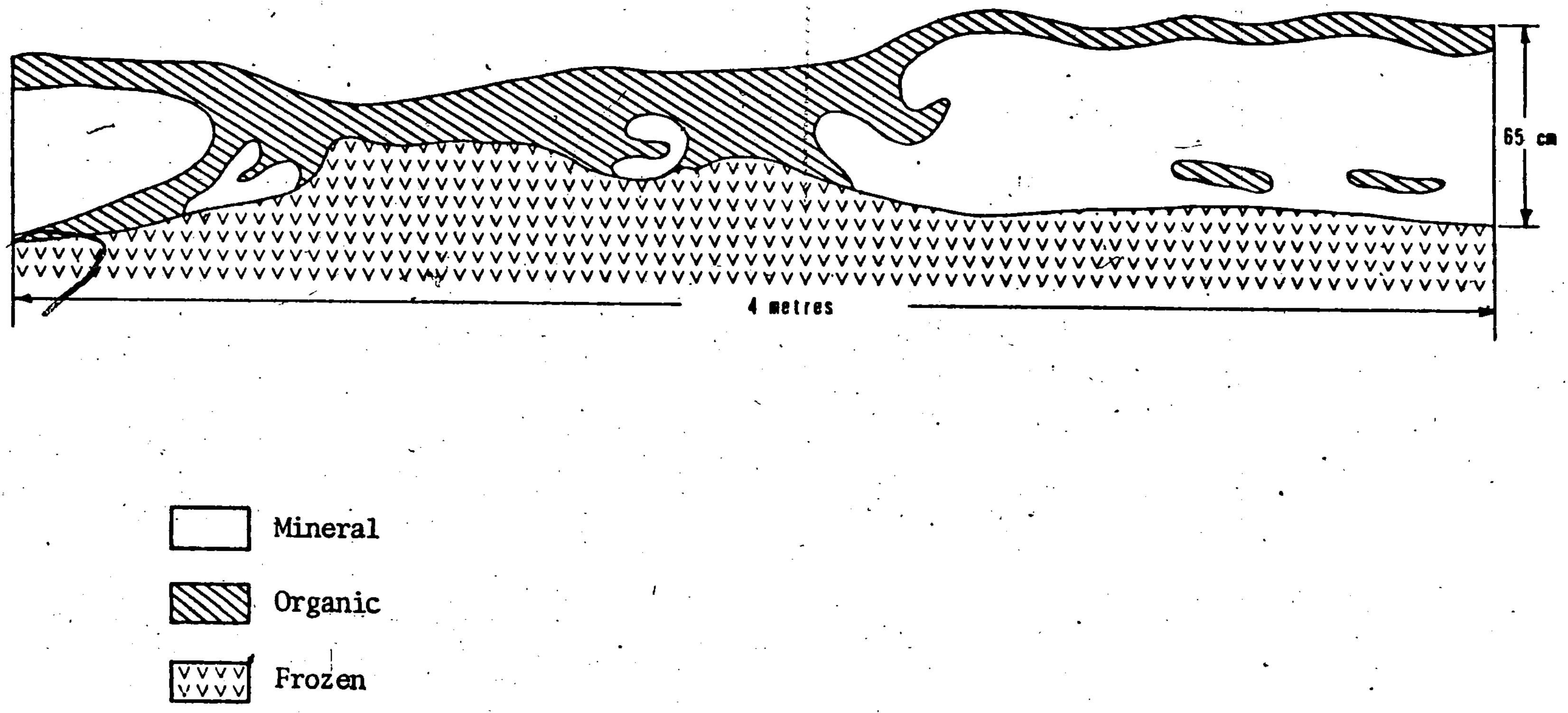
H — Same as above except mesic to humic.

Bm — Dull yellow orange (10YR 7/3 to 10YR 6/3); sandy loam to sandy clay loam; fine to medium granular or shotty structure; soft; many fine roots; pH 5.0 to 6.5.

BCgy — Light gray (10YR 7/1) to grayish yellow brown (10YR 5/2), sometimes with bright yellowish brown (10YR 7/6); few fine faint mottles in the lower regions; amorphous; slightly hard to hard; few fine roots; pH 5.0 to 6.5.

Cz — Frozen

Figure 7: Soil cross section in hilltop and midslope topographic positions (August 15)



missing, and shallowest in hollows surrounding the hummocks where the partly decomposed horizon is thickest and least dense.

In all study locations, hilltops and midslopes with low shrub-heath vegetation are more subject to frost induced surface disturbances than depression positions. This is indicated by the abundance of surface features such as earth hummocks, and solifluction stripes and lobes on these higher topographic positions.

Earth hummocks are most abundant on hilltops where they vary considerably in composition. They range in size from 0.5 to 2 m in diameter with a microrelief of 5 to 20 cm and are separated by 0.5 to 1 m wide moss filled depressions (Figure 8).

The rooting zone of low shrubs and heaths is generally restricted to the organic horizon, which may extend to or below the permafrost table. However, many roots extend partway into the mineral soil just under the organic horizon, and are probably partly repsonsible for the fine to medium granular structure often observed there. Soil frost processes may also cause this structure.

An amorphous horizon extends down to permafrost. Organic stains or buried organic matter may be scattered throughout this horizon as is documented by Brown (1969) and Tarnocai (1972). Roots are scarce in this amorphous region of the active layer.

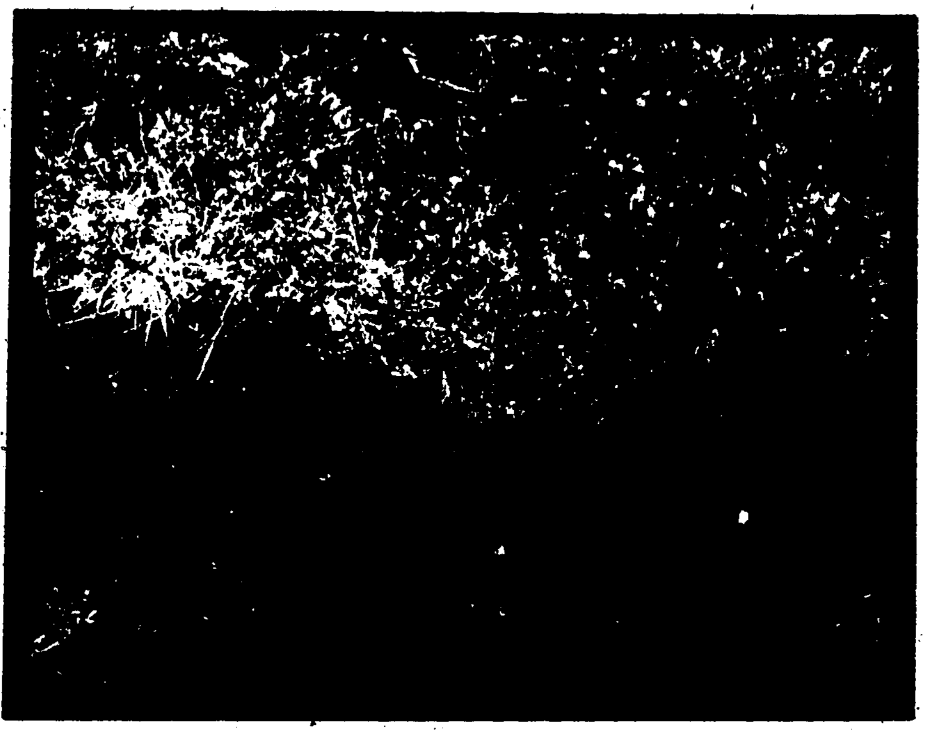


Figure 8. Typical soil profile in hilltop topographic positions. This one includes a hummock (on the right) and interhummock or hollow (on the left). Note the buried organic material throughout the hummock.

The soil pH of hilltops and midslopes is 4.8 to 6.1, 5.8 to 6.5 and 4.0 to 6.0 in organic horizons, and 5.0 to 5.5, 6.1 to 6.6 and 4.6 to 5.9 in mineral horizons at Tuktoyaktuk, Tununuk Pt. and Caribou Hills respectively.

Organic horizons at Tununuk Pt. are more humified than those at the other two locations, possibly due to greater decomposition rates because of higher pH and exchangeable calcium. However the nutrient status of soils and plants is generally lower there than at Tuktoyaktuk and Caribou Hills where organic matter is not so decomposed.

The organic section of nearly all profiles is composed of at least two horizons, each characterized by its decomposed condition. The majority of profiles examined contain mesic surface horizons and humic subsurface organic horizons. On the other hand, soils in depression positions have predominantly fibric surface organic horizons with mesic subsurface horizons.

4.2.2 Soil moisture

Escessive water in soils is deleterious to bacterial activities because the oversupply limits gaseous exchange and lowers the oxygen supply. It has been shown that optimum moisture levels for aerobic bacteria activities are at 50 to 75% of the soil's water holding capacity (Alexander, 1961). Douglas and Tedrow (1959) found that respiration of soil samples was more highly correlated with temperature than moisture.

Soil moisture is commonly expressed on a dry weight basis, however, it has been suggested that a better evaluation of soil moisture content is given when moisture is expressed on a volume basis because it more closely defines the moisture conditions encountered by plant roots (Boetler, 1968). This is only possible when bulk density of the soil material is known. In this study bulk density is not known, but the dry density of the 2 mm fraction is known, which at least provides a relative estimate of variation of organic-horizon density and moisture among topographic positions.

Table 4 indicates that soil moisture in relation to the volume and weight of dry soil is much greater in organic horizons of bottom positions than in mid and hilltop positions.

Table 4: Organic horizon field moisture on a volume and weight basis among topographic positions from all study sites.

Soil Moisture	Topographic Positions		
	Hilltop	Midslope	Depression
Volume basis (%)	58 ± 4.5 a*	57 ± 7.8 a	79 ± 3.8 b
Weight basis (%)	157 ± 13 a	165 ± 7 a	282 ± 15 b

* Any two means in a row not followed by the same letter are significantly different at $p < 0.01$.

Variation of water retention properties of the surface organic horizons accompany variations in topography. At 1/3 bar tensions, the water retained is 99, 114 and 123% of the dry soil weight in hilltop, midslope and depression positions respectively. At 15 bar tensions, water retained is 88, 99 and 112% of dry weight in hilltop, midslope and depression positions respectively. Differences between hilltop and depression positions are significant at $p = 0.01$ for both tensions. Although the greatest water holding capacities are found in organic horizons of depressions, available water, as measured by the difference between the amount of water held at 15 and 1/3 bars, does not vary among topographic positions. No consistent variation in the water holding capacities of the mineral portion of the active layer is evident. It appears that field moisture (%) on a weight basis is much greater than that retained at 1/3 bar, indicating that in the organic horizon at least, soil moisture is above field capacity at the beginning of August.

4.2.3 Soil organic matter

Low organic matter decomposition rates in northern regions, resulting in thick organic horizons and shallow active layers, are thought to be due to low temperatures and high soil moistures. Tedrow *et. al.* (1958) indicated that in northern regions, organic matter accummulation was greater than its decomposition. Douglas and Tedrow (1959) found that soil temperature was the factor that principally controls the rate of organic matter decomposition in the Arctic. They reported that the highest rates of decomposition occurred in Half Bog soils and lowest in the Arctic Brown soils. Thicker organic layers were associated with decreased organic matter decomposition rates due to lower temperatures when compared to habitats with higher soil temperatures (Douglas and Tedrow, 1969 and Vassiljevskaya *et. al.*, 1972).

Alexander (1961) attributed low decomposition rates in saturated anaerobic soils to the oxygen deficient environment in which aerobic decomposition was much less significant that anaerobic decomposition. Ponomereva (1964) stated that decomposition of taiga vegetation was slow because of its low concentrations of nutrients such as calcium and nitrogen, and its high content of resistant compounds such as lignins, waxes and resins. Wilde and Krause (1960) speculated that cold boreal environments are conducive to moss growth, and that the rate of growth depends on the degree of paludification. Heilman (1966) agreed with this and attributed the paludification to the low density and substantial insulating properties of mosses.

Buried organic horizons are common in tundra soils. Brown (1969) postulated that buried organic materials in tundra soils are a result of lake erosion, wind deposition and cryopedological processes. On level areas organic matter becomes buried by the upward movement of mineral soils and subsequent burial of the surface horizon. On slopes, saturated soils move downslope over the frozen interface and in so doing, fold under and bury the surface horizon.

Organic horizons are thickest in depression positions but similar in midslope and hilltop positions. They are also thicker at Tununuk Pt. than at the other two stations. On hilltops and midslopes, organic matter in in micro-depressions or hollows surrounding hummocks is significantly thicker at p = 0.01 (12 ± 1.2 cm) than on hummocks (6.8 ± 0.66 cm).

Organic matter, as measured by weight loss on combustion at 450°C, is greatest in surface horizons of depression positions, and least in organic horizons of midslope and hilltop positions (Table 5). Bulk density of the organic horizons was not determined, instead, the density of the 2 mm fraction was measured and indicates that hilltop organic horizons have the greatest density while those in depression positions are the least dense. Both density and loss on ignition are significantly correlated with pH and with each other (at p = 0.05).

Table 5: Organic matter depth (cm), content (%), and 2 mm fraction density among topographic positions from all study sites (n = 9 ± SE).

Organic Horizon Characteristics	Topographic Positions		
	Hilltop	Midslope	Depression
Depth (cm)	10 ± 2.5 a*[1]	9.3 ± 2.2 a	15 ± 3 b
Loss on ignition (%)	57 ± 3 a [1]	64 ± 3 ab	71 ± 4 b
Density (g/cc)	0.37 ± 0.02 a [2]	0.35 ± 0.026ab	0.29 ± 0.01 b

* Any two means not followed by the same letter are significantly different at: 1 - p = 0.01
2 - p = 0.05

4.2.4 Soil Nutrients

Numerous reports about low availability of mineral nutrients in subarctic and arctic soils are available (Russell, 1940; Sorensen, 1941; Kellogg and Nygard, 1951; Dadykin, 1958; Bliss, 1962; Korovin, 1963). This low availability has been attributed to factors such as low nitrogen fixation rates (Bliss, 1971), low decomposition rates (Douglas and Tedrow, 1959), the relatively unweathered state of most arctic soils (Hill and Tedrow, 1960), high soil moisture or poor aeration (Paul and Delong, 1949; Glentworth, 1947; Loach, 1966), evacuation of nutrients by acid leaching (Ponomarev, 1964), increased separation of mineral soil and nutrients from the root zone because of the increased organic layer thickness (Heilman, 1966 and 1968), immobilization of nutrients by permafrost (Pruitt, 1970), and by organic compounds (Salisbury, 1959).

Precipitation, electrical discharges and biological fixation by symbiotic or free-living bacteria and algae are the usual means of nitrogen input into the soil. However, the two former processes are minor in northern regions, so the greatest nitrogen input factor is probably biological fixation. This fixed nitrogen may be mineralized into soluble forms such as NO_3 - and NH_4 + which are used by plants (Tisdale and Nelson, 1966).

In natural systems $NH_4 \pm N$ is by far the most abundant form of mineral nitrogen, ranging from 25 to 350 ppm in organic horizons and from 2 to 5 in mineral horizons in a number of samples from Tununuk Pt. This compares to a range of 0 to 7 ppm in organic horizons and 0 to 1 ppm in mineral horizons of NO_3 - N in the same samples. Levels of less than 10 ppm NO_3 - N are considered low and levels greater than 20 ppm considered adequate for most crops in agricultural soils in Alberta (D.H. Laverty, Alberta Soil and Feed Testing Laboratory - personal communication).

Soil parent material is the ultimate source of phosphorus. In most soils, phosphorus availability is at a maximum in the pH range of 5.5 to 7.0, (Tisdale and Nelson, 1966). Below this range, phosphorus tends to be removed from the soil solution by complexing with iron and aluminum, while in conditions where the pH is greater than 7.0, calcium, magnesium and carbonates tend to precipitate with phosphorus. In Alberta agricultural soils, levels of available phosphorus below 10 ppm are considered low while levels greater than 20 ppm are considered adequate for most crops.

Potassium, like phosphorus, originates in the parent materials, but is found in much larger concentrations than phosphorus. Potassium is considered to be readily available when found in the soil solution, or on the exchange complex. In Alberta agricultural soils, levels of available potassium below 50 ppm are considered low while those above 100 ppm are considered adequate for most agricultural crops.

Analyses of samples in this study indicate that available nutrients are low on a soil dry weight basis. Low concentrations have also been reported by Heilman (1966 and 1968), Brown (1969), Haag (1974) and Babb (1974). In this study total N and available NO_3 - N in both the organic and mineral portions of the active layer, are so negligible that no differences are observed among study sites or topographic positions (Table 6). Since the NO_3 - N form of nitrogen is a product of certain decomposition processes which convert NH_4 - N to NO_3 - N, the low amounts of NO_3 - N gives a slight indication of the decomposition rate, yet it must be kept in mind that NO_3 - N is a "luxury" form of nitrogen, being taken up immediately by plant roots and microorganisms when made available.

Phosphorus and potassium, on the other hand, show some differences among study sites and topographic positions. Both of the latter nutrients show the greatest availability in soils on hilltop positions and the least availability in depression positions (Table 6). Among study sites, available phosphorus and potassium occur in greatest amounts in soils on the Caribou Hills and in least amounts in Tununuk Pt. soils (Table 7).

Exchangeable cations, including calcium and magnesium, appear to be most abundant in hilltop positions. Exchangeable calcium and soil pH are highest in Tununuk Pt. soils (Table 7), and are also strongly correlated ($r = 0.89$ at $p = 0.01$) in all study locations.

From the information about adequate and inadequate soil nutrient levels in Alberta agriculture soils it appears that only available NO_3 - N and phosphorus levels are inadequate for plant growth (in terms of agricultural crops) whereas potassium levels appear to be adequate for crop production. Since nutrient requirements for native species in the study area are not known, it is difficult to determine if nutrient levels are actually inadequate.

Table 6. Some major soil nutrients in the organic and mineral horizons among topographic positions from all study areas (n = 9).

Nutrients	Topographic Positions		
	Hilltop	Midslope	Depression
Total N (%)[a]			
Organic	1.4 ± 0.07 a*	1.55 ± 0.07 a	1.5 ± 0.1 a
Mineral	0.18	0.21	0.29
Available N (ppm NO_3 - N)[b]			
Organic	0.5 a	0.5 a	0.5 a
Mineral	0.0	0.0	0.0
Available P (ppm)[c]			
Organic	5.92 ± 1.1 a	3.58 ± 0.06 ab	2.75 ± 0.5 b
Mineral	0.83	1.0	0.83
Available K (ppm)[d]			
Organic	169.0 ± 20.0 a	130.0 ± 17.0 ab	90.0 ± 19.0 b
Mineral	130.0	108.0	71.0
Exchangeable Ca (meq/100g)[e]			
Organic	51.0 ± 5.0 a	50.0 ± 6.0 a	40.0 ± 7.0 a
Mineral	10.4	11.4	11.6

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* Any two means in a row not followed by the same letter are significantly different at p = 0.01

[a] Kjeldahl nitrogen

[b] $CuSO_4$ and Ag_2SO_4 soluble nitrogen

[c] NH_4F and H_2SO_4 soluble phosphorus

[d] NH_4 acetate soluble potassium

[e] NH_4 acetate soluble calcium

Table 7: Available soil phospohorus and potassium and exchangeable calcium and pH in the organic horizons among study sites averaged over all topographic positions (n = 9 ± SE).

Nutrients	Locations					
	Tununuk Pt.		Tuktoyaktuk		Caribou Hills	
Phosphorus (ppm)	0.77 ± 0.35	a*	3.44 ± 0.65	b	4.72 ± 0.77	b
Potassium (ppm)	82.00 ± 15.00	a	132.00 ± 16.00	b	175.00 ± 20.00	b
Calcium (exchangeable) (meq/100 gm)	61.00 ± 4.00	a	33.00 ± 4.00	b	47.00 ± 7.00	b
pH	6.37	a	5.2	b	4.9	b

* Any two means not followed by the same letter are significantly different at: p = 0.05.

5.0 DISCUSSION

5.1 Parameters unaffected by change in topographic position

Several important parameters show no significant differences among topographic positions. These include soil texture, soil pH, total cation exchange capacity, and total and available soil nitrogen. As a result they are not considered as being influenctial in promoting differences in vegetation and nutrients.

Texture of the parent material in all positions and study areas, ranges from loamy sand to sandy clay loam. All study sites have some variation in texture, but this slight change does not seem to induce vegetation changes.

Soil pH tends to be lower in depression positions, but the differences are not significant statistically. As mentioned earlier though, pH of Tununuk Pt. soils is significantly higher than at the other sites, being highly related to the calcareous parent material there.

The total cation exchange capacity of the sampled organic horizons is highly variable. Means of 96, 97, and 103 meq/100 gm dry soil for hilltop, midslope and depression positions respectively were obtained. These differences are not significant enough to explain differences in plant and soil nutrients among topographic positions.

Data for total and available nitrogen data in the organic horizons indicate no differences among topographic positions. Several explanations can be given. Alexander and Schell (1973) working at Barrow, Alaska, have found that nitrogen fixation by organisms in association with tundra vascular plants is not nearly as significant as fixation by the lichens *Peltigera* spp., *Stereocaulon* spp. and the blue green algae *Nostoc* spp. in association with some mosses. Wetter sites were always associated with greater fixation rates. In a Swedish subarctic mire, Granhill and Selander (1973) found that nitrogen fixing blue green algae associated with *Sphagnum* spp. and *Drepanocladus* spp. are resonsible for higher plant production.

From this it appears that the input of nitrogen by nitrogen fixation is greater in depression positions than midslope and hilltop. However, since decomposition rates are greater in the upper positions, mineral nitrogen release would appear to be greater there. This combination of higher fixation rates in depressions but greater decomposition rates on hilltops may explain the similarity of available soil nitrogen among topographic positions.

Soil temperature would be expected to be greater in higher, better drained positions than in depressions. However, Younkin (1972) in the Tuktoyaktuk Peninsula, has demonstrated that at a 10 cm depth on a clear mid July day, soil temperatures were similar in hummocks from hilltop and bottom positions. Hollows surrounding hummocks on hilltops were even slightly cooler than hollows in depressions. Hollows in all positions were found to be 4 to 6°C cooler than adjacent hummocks.

5.2 Parameters influenced by changes in topographic position and site

5.2.1 Vegetation

Corns (1974) has indicated for this study area, that the major difference between vegetation on drier habitats, low shrub-heath type, and wetter habitats, herb-low shrub-heath type, is the dominance of shrubs on hilltops and slopes, and of herbs in depressions. According to Billings and Mooney (1968), the most obvious adaptations of plants to severe tundra or alpine environments are the reduction in plant height and the tendency toward a herbaceous habit. They observed that a greater proportion of herbaceous species occur beyond the timberline, indicating that conditions there are less than optimum for shrubs.

Herbaceous species appear to have special adaptations for their growth in shallow, saturated, nutrient deficient soils. Firstly, roots of grasses and sedges in both low shrub-heath and sedge-heath types in this study were found to extend down to the bottom of the active layer in the first week of August. On the other hand, deciduous shrubs and evergreen heath species have long roots or rhizomes which are concentrated near the surface 15 cm, but in hummocks, often penetrate somewhat into the mineral portion, thereby creating a fine to medium granular soil structure in the top 5 to 10 cm of the mineral section. However, in depressions, the roots of heaths and other shrubs remain within 10 cm of the soil surface, never penetrating the mineral portion of the soil. Roots of sedges, however, in these depressions, often penetrate the mineral portion of the active layer. In fact, species such as *Eriophorum vaginatum* have root tips that have a unique tendency of actively growing at the permafrost surface.

Similar observations have been made at other locations. At Umiat, Alaska, Bliss (1956) classified root systems of 13 species into two groups; shrubs with rhizomes from which shallow adventitious roots arise, and grasses and sedges with primary or adventitious roots which penetrate the soil and peat to greater depths than shrubs. *Eriophorum vaginatum* ssp. *spissum* and *Arctagrostis latifolia* roots were found within 0.5 to 1.5 cm of the retreat of the permafrost table. Younkin (1973) on the Tuktoyaktuk Peninsula has made similar observations for *Arctagrostis latifolia.* Dadykin (1958) reported that Serebryakov (1952) has found root tips of this species 3 to 5 cm in frozen soil at the end of the growth period.

Secondly, root systems in arctic regions are large in comparison to those in temperate regions. Billings, (1973) and Sorensen (1941) attributed this to a lack of soil nitrogen. Dennis and Johnson (1971) concluded that arctic above ground environments are more severe than below ground environments, and thereby explain the high root:shoot ratios. Others (Billings and Mooney, 1968; and Hadley and Bliss, 1964) have observed that most of the standing crop is underground in arctic and alpine regions because of the substantial energy storage capacity required below ground for plant survival during the long winter period and during rapid shoot growth the following spring. The large below to above ground ratio of living mass of arctic species appears to be an adaptive mechanism to cope with other factors such as water relations and mineral nutrition, in addition to the maintenance of carbohydrate reserves for early spring growth (Billings, 1973).

In the present study, the factors for which plants seem to be well adapted, are factors associated with poorly drained habitats so common in depressions, and include higher moisture contents, thicker and less dense organic layers within shallower active layers, and lower available phosphorus and potassium contents.

5.2.2 Soil moisture

No single factor directly controls the distribution of plant communities although certain factors may indirectly control parameters which may be responsible for this distribution. Soil moisture is commonly recognized as controlling most local environmental and vegetation gradients both in alpine and arctic regions (Tedrow and Cantlon, 1958; Billings and Mooney, 1968; Bliss, 1971; Billings, 1973). In permafrost regions, soil moisture changes occurring in response to topographic changes, influence differences in active layer depth and organic matter decomposition, density and thickness. Together with active layer conditions and organic matter properties, soil moisture is thought to be responsible for available mineral nutrient differences among topographic positions within the study areas and on similar parent materials. These differences in available nutrients may be responsible for differences in the nutritional status of plant and litter material, and also for differences in the herbaceous and shrubby habits of plants in depressions and hilltops respectively.

Soil moisture as evaluated on a volume and weight basis is highest in sedge-heath dominated depression positions as reported above (Table 4). On a dry weight basis, soil moisture among topographic positions in the organic layer to some extent varies inversely as the active layer depth ($r = -0.88$ at $p = 0.01$) indicating that topographic differences alone may not control soil moisture differences.

In depression positions, soil water moves very slowly, if at all, through the shallow active layers. As a result, gaseous exchange becomes limited and oxygen decreases as carbon dioxide concentration increases. Remezov *et. al.*, (1965) states that growth of most plants was inhibited under conditions where the soil air was composed of less than 9 to 12% oxygen and greater than 1% carbon dioxide by volume. Under these conditions, anaerobic decomposition becomes more important than aerobic, and toxic by-products such as H_2S, CH_4, and H+ are evolved during incomplete metabolism of organic carbon (Alexander, 1961; Geisler, 1965; Armstrong and Boatman, 1967). Remezov *et. al.*, (1965) states that these gases, especially H_2S are toxic to most plants except those such as *Alnus* spp., *Spirea* spp. and bog mosses. Further, most plants respond to good aeration by root ramification and lengthening and to poor aeration by decreasing root length and ramification and increasing root thickness. Geisler (1965) found a linear positive correlation between aeration and root lengthening but a negative correlation between aeration and root ramification. In this way, only those species survive in anaerobic habitats which are able to overcome the oxygen deficiency either by having the ability to supply their roots with an internal oxygen supply, or by extending their roots laterally for long distances above the oxygen deficient zone.

Armstrong and Boatman (1967) have shown that oxygen translocation from shoot to root occurs in species such as *Eriophorum angustifolium*. The roots of this species are often surrounded by ferric oxide which has been oxidized and precipitated around the oxygen rich roots. They concluded that the internal supply of oxygen also oxidizes toxins such as H_2S, thereby preventing the death of the plant. In this study, reddish brown iron precipitates have been noticed around dead *Eriophorum vaginatum* roots, indicating that a similar mechanism may take place in this species also. Other species such as *Rubus chamaemorus* roots, so common in depressions of this study contained aerenchymous cells which allowed the plant to survive on oxygen deficient environments (Saebø, 1970).

Another adaptation of plants growing in low topographic positions is the ability to maintain shallow root systems, enabling them to grow as near to the soil surface as possible. This mechanism has been postulated by Dennis and Johnson (1971) as a means by which roots may avoid low soil temperatures. However, it may also be a mechanism by which plants occupy only the oxygen sufficient zones such as those found in higher microtopographical sites. Wright (1959) found the rooting zone of trees to be restricted to the surface of saturated peats in Europe. Tamm (1950) indicated that trees on Swedish swamp soils usually have a very superficial root system because of higher oxygen concentrations near the surface. Saebø (1970) found that *Rubus chamaemorus* usually occupied hummocks rather than hollows on wet Norway bogs.

In depression positions in this study, shrubby species such as *Betula nana* and *Ledum palustre* extend their roots only 5 to 10 cm into the organic layer, and often grow on tussock sides, possibly contacting a more oxygen rich zone there. However, species adapted to this anaerobic habitat, such as *Eriophorum vaginatum* and *Carex* spp. extend their roots completely into the anaerobic zone. This has also been observed by Chapin (1972) in northern Alaska.

5.2.3 Soil organic matter

The degree of organic matter decomposition, as indicated by organic horizon density is somewhat related to soil moisture perecentage (on a dry weight basis) at $r = 0.6$ at $p = 0.01$. This is in agreement with Alexander (1961) who states that the decay of the major plant constituents is depressed as the supply of oxygen diminishes. Further, a depression of decay rates results in the accummulation of organic materials being greater than loss by decomposition.

Table 5 indicates that the surface organic horizon is deeper, less dense and contains more organic matter in depression positions than in midslope or hilltop positions. Of the total soil volume within the active layer, the organic portion occupies 40% of a typical hilltop profile and 75% of a typical depression profile. Of the two transects illustrated (Figures 4 and 6), the hilltop transect active layer occupies 31% more of the cross sectional area than the depression active layer transect. This indicates the importance of the organic layer on active layer properties. It is also evident that organic insulation properties have a much greater effect on variation of active layer depths on hilltops and midslopes than on active layer depths in depressions. The reason for this is the regulatory effect on soil temperatures imposed by the high moisture regimes in depression positions. The result is an active layer of fairly uniform depth in depressions, whereas on hilltops, although soil temperatures may not be any higher than in depressions at 10 cm (Younkin, 1973), drier conditions exist which allow a more rapid thaw of hummocks with low ice and water contents, and very slow thaw rates of hollows under the influence of enhanced insulation properties due to thick organic layers.

Two important conditions are imposed on plants occupying soils with thick organic horizons such as those in depression positions and in hollows surrounding hummocks on hilltops. Firstly, plants growing on thick organic horizons are somewhat elevated above the mineral soil, thereby being separated from the mineral soil. The degree of separation depends on the organic layer thickness. Since the mineral soil is the major source of several major nutrients such as phosphorus and potassium, plants which can not extend their roots into this zone because of their elevated positions, must derive those nutrients from the organic layer. Secondly, thick organic horizons of low density, which are responsible for shallow active layers by virtue of their insulating properties, occupy the major portion of the active layer, leaving only the remaining minor portion to be occupied by mineral material. As a result of the decreased mineral volume, smaller amounts of nutrients from this region can be released by weathering, and taken up by roots to be eventually deposited on or within the surface organic horizon. These processes have been shown by Heilman (1966 and 1968) to be responsible for paludification of forests in central Alaska.

Organic horizons on hilltops and midslopes are alternately shallow on hummocks and deep in hollows. Also, mineral soil which occupies approximately 60% of the active layer, is slowly being circulated inside the hummocks by frost processes, aiding in the weathering processes. Since shrubs are common in these topographic positions, and their roots extend laterally for long distances (Bliss, 1956), their chances of contacting the mineral zone are high.

The combination of thick organic horizons and high moisture contents would seem to be partially responsible for the low occurrence of shrubby species in depression positions. Adapted sedges and grasses, though, are not only able to cope with the anaerobic conditions imposed by these high moisture regimes, but also to penetrate through thick organic horizons into mineral portions of the active layer, thereby tapping the most important source of several major mineral nutrients, and aiding in the upward movement and cycling of those nutrients. This is especially true of *Eriophorum vaginatum*, which is ideally adapted to soils with reduced temperatures, low nutrient contents, shallow active layers and low oxygen concentrations.

This species extends its roots deep into the active layer, thereby contacting nutrients such as phosphorus which move only slowly by diffusion. Secondly, Chapin (1972) has demonstrated that *Eriophorum* has the ability to produce roots at 40% of maximum production at soil temperatures as low as 5°C, while a temperate species, *Scirpus* under similar conditions could only produce roots at 15% of maximum production. Thirdly, the *Eriophorum* tussock has been called a self sustaining "island" because of its efficiency in translocating nutrients from leaves to rhizomes and roots, before annual leaf die back (Goodman and Perkins, 1959). These adaptations, plus the tussock form of this species, makes it important in depression positions, because of the ability of its root mass to contact a large soil volume, thereby contacting and transferring nutrients to the upper portion of the active layer where they are then concentrated.

Heath species occur on all topographic positions because they do not seem to be limited to any particular moisture conditions, perhaps because they are well adapted to low nutrient conditions and have shallow root systems which occupy regions of highest oxygen concentrations.

5.2.4 Soil and plant nutrients

The release of mineral nutrients into the soil environment in the form available to plants, depends on the rate of weathering of the parent material, and the rate of decomposition of the organic portion of the soil profile. Since both these processes are retarded in arctic regions, available nutrients are generally low in comparison to temperate agricultural soils. Low concentrations have been reported by Kello[illegible] and Nygard (1951), Heilman (1966 and 1968), in central Alaska, Brown (1969) in northern Alaska, Haag (1974) in the Tuktoyaktuk Peninsula and Peters and Walker (1972) on Devon Island.

Most nutrients, when released in the decay or weathering process, are used by microorganisms and plants, or become unavailable by complexing with organic compounds or metallic ions. Nutrients such as NO_3 - N are fairly mobile, and may be supplied by mass flow to the plant root from the total soil volume within the root zone. However, less mobile nutrients, such as adsorbed phosphate, may be supplied to the plant root by diffusion only from the immediate vicinity of the root surface (Bray, 1967 and Nye, 1968). In addition, since most of the phosphorus absorption occurs in the root tips, the greater the exploitation of the soil volume by the roots, the greater the amount of phosphorus absorbed (Tisdale and Nelson, 1966).

In this study, of the three major nutrients, nitrogen, phosphorus and potassium in the organic horizon, differences in the availability of soil phosphorus and potassium are most pronounced. These differences occur among study areas as well as topographic positions. The availability of these two nutrients varies at the same rate ($r = 0.82$ at $p = 0.01$), indicating that conditions, such as weathering and decomposition rates controlling their release and availability, are similar. The differences in the availability of these two nutrients seem to influence differences found in live standing crop nitrogen and phosphorus among topographic positions. Available soil phosphorus is correlated with standing crop nitrogen ($r = 0.50$ at $p = 0.05$), and with phosphorus ($r = 0.58$ at $p = 0.01$) while available soil potassium is correlated with standing crop nitrogen ($r = 0.57$ at $p = 0.01$) and with phosphorus ($r = 0.58$ at $p = 0.01$). However, no relationship exists between total or available soil nitrogen and standing crop nitrogen, phosphorus or potassium.

It has been suggested by various researchers in the past (Russell, 1940; and Sorensen, 1941) that meager plant growth in the Arctic is related to low levels of soil nitrogen. Investigations by several workers in the Northwest Territories and Alaska have not identified any single nutrient as being most limiting to plant growth in the Arctic. Both nitrogen and phosphorus and occasionally fertilizer applications have initiated responses in plant growth.

Work on the Tuktoyaktuk Peninsula by Haag (1974) has demonstrated that additions of nitrogen alone to native plant systems had a significant positive effect on plant production in two habitats, whereas the addition of phosphorus had no significant effect on plant production, except in combination with nitrogen, when evaluated during one growing season.

Others, though, have found that additions of phosphorus initiate a greater growth response in introduced and native grasses than additions of nitrogen (Laughlin, 1969; Younkin, 1972; Mitchel, *et. al.*, 1973), and that greatest responses occur with addition of nitrogen and phosphorus in combination. Younkin's plots, which were monitored for three seasons at Inuvik and Tuktoyaktuk, N.W.T., indicated that plant height, biomass and seed head production of several introduced grasses, were increased with phosphorus additions alone, and also in combination with nitrogen and lime. But nitrogen and lime alone had no beneficial effect (Younkin, 1972 and Hernandez, 1973).

Laughlin (1969), working in south central Alaska, demonstrated that over a four year period, phosphorus applications alone increased production of native *Calamagrostis canadensis* more than high levels of nitrogen application alone, and that additions of nitrogen and phosphorus in combination initiated the greatest responses. Additions of potassium were beneficial only in combination with phosphorus.

Mitchell (1973), also working in Alaska with various introduced grass species, indicates that plant growth benefitted from phosphorus and potassium additions, but not from nitrogen applications alone.

Phosphorus deficiencies have been associated with cold, saturated organic soils by some European and Russian workers. Salisbury (1959) has indicated that phosphorus deficiencies are characteristic of organic soils, since phosphorus in combination with organic matter is not very available to plants. Zhurbitsky and Shtrausberg (1957), Shtrausberg (1958), and Korovin *et. al.* (1963), have indicated that phosphorus uptake by plants was limited by low soil temperatures, thereby inhibiting assimilation of nitrogen into nucleoproteins. Glentworth (1947) and Paul and DeLong (1949) indicate that under waterlogged conditions, available soil phosphorus was often low because of loss due to its solubility in the gley zone of the soil profile. In addition to low phospohorus contents in waterlogged soils, Pearsal (1950), Armstrong and Boatman (1967), and Loach (1968), indicate that the uptake of phosphorus was often reduced by ferrous iron precipitatates around oxygen rich roots of plants.

Others have attributed phosphorus deficiencies in arctic and subarctic soils to conditions associated with the organic horizon thickness. Heilman (1966 and 1968) has demonstrated that the ability of black spruce to extract nutrients from the soil decreases as the organic horizon thickens. In other words, as plants become elevated above the mineral soil by the thickening organic layer, their roots become more and more isolated from the source of several major and minor nutrients. This problem becomes accentuated in permafrost regions where the volume of mineral soil decreases as the organic layer thickens, further reducing the potential of nutrient release. Low phosphorus levels have also been associated with shallow soils or low soil volumes in California (Jenny, *et. al.*, 1950).

Tamm (1965) substantiates this in his study on drained peatlands and well drained forests in Sweden. He found that forests on well drained mineral soils responded to nitrogen fertilization but not to phosphorus and potassium, whereas trees on drained peatlands, which were well elevated above the mineral soil, responded to phosphorus and potassium to a greater extent than to nitrogen application. Wright (1959), investigating water-logged deep peats in Britain, indicates that young trees showed much greater responses to phosphorus applications than any other nutrient. He found that nitrogen deficiencies in tree needle tissues could be corrected by phosphorus applications.

From the literature it appears that the phosphorus and potassiumm status of soils depends largely on the mineral soil volume available to supply these nutrients. Heilman (1968) demonstrates that the total quantity of nutrients on a soil volume basis to a depth of 50 cm was much greater in mineral than organic soils in central Alaska. In this study the total quantity of nutrients in the mineral portion of the active layer is generally greater than that found in the organic horizon, litter and standing crop combined (Table 8) assuming that the total soil phosphorus content of a sample is at least fifteen times greater than the available phosphorus content as demonstrated by Heilman (1968). It would appear that the removal of the standing crop, litter and organic horizon, followed by a deepening active layer, would serve to expose a large nutrient reservoir to colonizing plant species. This large nutrient reservoir may be partly responsible for the increased vigor of colonizing species observed by Hernandez (1973) and Younkin (1973) in various disturbed areas on the Tuktoyaktuk Peninsula.

Having established that soils in depression positions have lower levels of phosphorus and potassium than soils on hilltops and midslopes and that mineral horizons generally contain more total nutrient quantities than organic horizons, attention should be directed to the response of vegetation to these situations. It is recognized that plants growing in depression positions are adapted to a nutrient and oxygen deficient environment. Heath species have adapted to the oxygen deficiency by being very shallowly rooted. This makes them susceptible to nutrient deficiencies, especially phosphorus, because of their separation from the mineral soil. Their high degree of sclerophylly may be an adaptation towards this phosphorus deficiency. Herbaceous species, on the other hand, such as *Eriophorum*, have adapted to the oxygen deficiency by providing an internal oxygen supply to the roots which extend deep into the anaerobic region. Their large root system which penetrates through the organic horizon into the

Table 8: Dry weight and total nutrients of the standing crop, litter, and organic and mineral horizons among topographic positions from all study sites. Data are based on all material within the active layer on August 5, under a surface area of 1 m^2.

Topographic positions and plant and soil components	Dry Weight (g)	Total nutrient weight (g)		
		N	P	K
Hilltop				
Plant[a]				
Standing Crop	891	9.8	0.93	2.5
Litter	656	9.1	0.70	1.0
Total	1547	18.9	1.63	3.5
Soil[b]				
Organic	37,000[c]	518 (total)	0.22 (available)	6.3 (available)
Mineral	450,000[d]	810	0.37	58.5
Total	487,000	1328	0.59	64.9
Midslope				
Plant				
Standing Crop	887	8.8	0.83	2.2
Litter	687	8.5	0.66	1.0
Total	1547	17.3	1.49	3.2
Soil				
Organic	32,500	504	0.12	4.2
Mineral	475,500	998	0.47	51.4
Total	508,000	1502	0.59	55.5
Depression				
Plant				
Standing Crop	775	6.3	0.62	1.8
Litter	211	2.2	0.18	0.3
Total	986	8.5	0.80	2.1
Soil				
Organic	43,500	652	0.12	3.9
Mineral	225,000	630	0.18	15.9
Total	268,500	1282	0.30	19.8

[a] Standing crop and litter N, P and K are based on data from Table 1.

[b] Total soil N (Kjeldahl) and available soil P (NH_4F and H_2SO_4 soluble) K (NH_4 acetate soluble) are based on data in Table 6.

[c] Organic horizon weights = density x thickness (Table 5).

[d] Mineral horizon weights = density (1.5 g/cc) x [organic horizon thickness (Table 5) - active layer depth (Table 3)].

shallow mineral region is an adaptation to the immobility and deficiency of phosphorus. Younkin (1974) working in the Tuktoyaktuk Peninsula, speculates that the ability of *Arctagrostis latifolia* roots to penetrate and take up nutrients in cold mineral regions of the active layer, may permit it to extend its geographical range well north of *Calamagrostis canadensis*, which has its roots restricted to the warmer surface organic horizon where competition for nutrients may be greater.

In other regions, slow rates of plant growth, nitrogen deficient soils and sclerophyllous vegetation have been associated with phosphorus deficient soils (Loveless, 1961; Clarkson, 1967). Watt (1966) working in northern Minnesota peatlands, found that both nitrogen and phosphorus applications produced growth responses in black spruce leaders, but this response was markedly increased when these elements were applied in combination. Work in Australia by Beadle (1953 and 1954), demonstrates that floristics and community structure were determined either directly or indirectly by soil phosphate content, rather than by soil depth and nitrogen. He indicates that sclerophyllous vegetation commonly occurs on phosphorus deficient soils and that these soils were often nitrogen deficient as well because of the influence of soil phosphorus on the growth of nitrogen fixing organisms associated with legumes.

In the tropics, Loveless (1961) has found that sclerophyllous vegetation is usually associated with phosphorus deficient soils, rather than any specific wet or dry habitat. He has demonstrated that the distinct negative correlation which exists between the degree of sclerophylly of species ($\frac{\text{crude fibre \%}}{\text{crude protein \%}}$ x 100) was associated with low phosphorus contents in leaves of some tropical species, and the suggestion is made that the ability to tolerate low phosphate and nitrogen levels could be a characteristic of sclerophyllous vegetation. He indicated that the degree of sclerophylly was associated with protein rather than fibre content, and that the correlation between crude protein and tissue phosphate was significant.

When these concepts are applied to data in this study, similar results are observed. The degree of sclerophylly is significantly lower in the Caribou Hills vegetation than at the other two sites, being greatest at Tununuk Pt. This corresponds favorably to data on available soil phosphorus which is highest in Caribou Hills and lowest in Tununuk Pt. soils. Lowest concentrations of phosphorus and potassium are also evident in Tununuk Pt. plant tissue (Table 3). Furthermore, a significant negative correlation exists between vegetation sclerophylly and tissue phosphorus content (r = 0.54 at p = 0.01). Loveless has indicated that these relationships do not necessarily provide proof for the dependence of sclerophylly on soil phosphorus levels. He and others indicate though, that sclerophyllous vegetation in other areas of the world, irrespective of habitat, is often associated with soil phosphorus deficiencies (Caughey, 1945 and Beadle, 1954).

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A significantly greater degree of sclerophylly exists in Tununuk Pt. than in Caribou Hills standing crop (909 vs. 684 at $p = 0.01$). Tununuk Pt. is the most calcareous site of the three, having the highest soil pH with the lowest phosphorus content, while Caribou Hills soils have much lower soil pHs and the highest soil phosphorus contents. *Dryas integrifolia* is quite abundant at Tununuk Pt. This species possibly contributes to the high degree of sclerophylly observed there as it occurs in all topographic positions indicating that it is not restricted to one habitat or drainage type. Kellogg and Nygard (1951) have reported that *Dryas* plants from alpine meadows in Alaska are found on soils high in calcium, and the plants themselves are high in calcium but very low in phosphorus, the imbalance possibly contributing to nutritional disturbances in Dall sheep.

Differences in degree of sclerophylly among topographic positions are not significant, but indicate that lower phosphorus concentrations in depression positions may be partly responsible for the higher degree of sclerophylly found there (775 ± 44), than on higher topographic positions (874 ± 66) when averaged over all study sites.

It appears then, that low available soil phosphorus concentrations may be partly responsible for the vegetation distribution within the study area. Locally, depression positions are most deficient in phosphorus and usually contain sedges and heaths which are adapted to phosphorus deficient environments by virtue of deep soil penetration by their roots (sedges) and by their sclerophyllous nature (heaths). Regionally, Tununuk Pt. parent materials are calcareous with the most phosphorus deficient soils, and support more sclerophyllous vegetation than Tuktoyaktuk and the Caribou Hills. Perhaps, as has been shown by Korovin *et. al.*, (1963) and Dadykin (1958), a phosphorus deficiency limits the uptake and assimilation of nitrogen by plant roots. Consequently, evergreen heath species are favored in these sites because of their low photosynthetic rates (Hadley and Bliss, 1964) and slow growth rates which enable them to conserve and translocate amino acids, rather than producing annually new, high protein leaf tissue as deciduous species do. Clarkson (1967) has suggested that low rates of protein synthesis are an adaptation of species adapted to phosphorus deficient soils. Deep rooted sedges are also favored in these sites because of their ability to overcome the phosphorus deficiency by extending their roots beyond the organic horizon into the cooler, denser mineral regions of the profile where closer root-soil contact may enable them to take up required nutrients such as phosphorus more efficiently.

SUMMARY AND CONCLUSIONS

Significant changes in several parameters occur locally between upper and lower topographic positions, and regionally among study sites. They are illustrated in Tables 9 and 10.

1. Differences between topographic positions

Table 9: Comparison (in terms of percentage change in major parameters) of depression positions with hilltop positions in all study areas.

Parameters	Change (± %)
Soil moisture (volume in organic horizon)	+ 36
Loss on ignition (organic matter)	+ 25
Organic horizon thickness	+ 50
Mineral horizon thickness	- 57
Organic horizon density	- 22
Active layer depth	- 30
Available soil phosphorus (organic horizon)	- 53
Available soil potassium (organic horizon)	- 46
Standing crop nitrogen	- 24
Standing crop phosphorus	- 21
Standing crop potassium	- 14

a. It appears that the 36% increase in soil moisture between hilltop and depression positions is ultimately responsible for changes in several dependent variables between hilltops and depression positions. The increase in soil moisture retards decomposition of the surface organic horizon, allowing this horizon to maintain a lower density and a resulting greater thickness in depression positions. The lower density and greater thickness in turn combine with the high soil moisture in these depression positions to retard active layer depth increases in comparison to hilltop positions.

b. The 57% decrease in the mineral horizon thickness, which is a result of the increase in organic horizon thickness and decrease in active layer thickness between hilltop and depression positions, is largely responsible for the 53 and 47% decrease in dry weight available soil phosphorus and potassium respectively because this horizon is the only absolute source of these nutrients.

c. Decreased levels of soil phosphorus, potassium and oxygen (saturated, anaerobic conditions), in combination with increased organic and decreased mineral volumes are responsible for decreases in standing crop nitrogen, phosphorus and potassium between hilltop and depression positions.

d. In terms of vascular species, the visible expression of the above differences is the predominance of shrubs on hilltops and sedges in depressions. Since deciduous shrub roots tend to avoid oxygen deficient regions of the active layer by extending laterally for long distances [illegible] shallow depths instead of downward, they survive best on sites such as hilltops where the organic horizon contains higher levels of nutrients than depression positions, and where their roots can readily contact the near-surface mineral horizon.

Sedges, on the other hand, have roots which are able to utilize all portions of the active layer, mineral as well as organic, by being tolerant to oxygen deficiencies.

Heath species appear to survive on both hilltop and depression habitats although in depressions, they appear slightly chlorotic when compared to those on hilltops. Their success in both environments, despite the tendency of their roots to occupy only the surface 10 cm of the active layer, is possibly related to their slow growth rates, which in other species and regions have been related to phosphorus deficiencies (Clarkson, 1967). In addition, they are evergreen, so do not need to produce annually large amounts of photosynthetic material, which would require large amounts of available soil nutrients.

2. Differences among study sites

Table 10: Significant changes in major parameters between study sites averaged over all topographic positions.

Parameters	Changes due to location (± %)	
	Tuktoyaktuk to Tununuk Pt.	Caribou Hills to Tununuk Pt.
Exchangeable soil calcium (organic horizon)	+ 84	+ 30
Soil pH (organic horizon)	+ 23	+ 30
Density (organic horizon)	+ 23	+ 26
Available soil phosphorus (organic horizon)	- 77	- 84
Available soil potassium (organic horizon)	- 38	- 53
Standing crop calcium	+ 97	+ 140
Standing crop phosphorus	- 12 (n.s.)	- 8 (n.s.)
Standing crop potassium	- 25	- 8 (n.s.)
Standing crop sclerophylly	+ 11 (n.s.)	+ 33

n.s. = not significant

Tununuk Pt. parent material, which is high in calcium and has a high pH, is responsible for lower soil phosphorus and potassium levels there than at the other two study sites. As a result, standing crop phosphorus and potassium concentrations at Tununuk Pt. are lower than at the other two sites. These lower concentrations may be responsible for higher standing crop [illegible] at Tununuk Pt. and may also explain the abundance of the evergreen species *Dryas integrifolia* there compared to the other two sites.

The significantly higher organic horizon density at Tununuk Pt. reflects possible higher decomposition rates there due to high calcium concentrations in plant tissue as has been suggested by Ponomereva, (1964). However, these higher decomposition rates do not appear to be responsible for higher soil nutrient levels. Also, greater organic horizon density conditions do not appear to initiate a greater degree of active layer melt-out.

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