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ANTHROPOGENIC TUNDRA DISTURBANCE
AND
PATTERNS OF RESPONSE
IN THE
EASTERN CANADIAN ARCTIC

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for the degree of Doctor of Philosophy

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ABSTRACT

The literature of disturbance ecology reveals that, under present climatic conditions, non-native plants have little or no role in high arctic tundra revegetation. Rather, it has been suggested that indigenous flora, especially long-lived perennial graminoids, are crucial to recovery. However, few long-term data are available on past impacts within productive sedge-meadows in the High Arctic, and none which consider the non-vascular flora.

This thesis combines biogeographical and patch dynamics perspectives to focus on ≥21 yr of natural and assisted recovery of vegetation and soils from a wide range of dated anthropogenic surface disturbances at three Canadian Arctic sites. Empirical, experimental and archival investigations were made among climatically similar, but widely disjunct, coastal lowlands of contrasting geologies on Baffin, Devon, and Cornwallis Islands. These data encompass minerotrophic and oligotrophic wetlands in which the vascular floras show minimal differentiation yet the sampled bryofloras share only 31.8% of their total taxa. The occurrences chosen for study are representative of the most widespread, small-scale human impacts in the North, including vehicular, pedestrian, construction, and pollution disturbances.

It was determined that rutting from even a single passage of a tracked vehicle in summer resulted in significant reductions in species richness and biomass. On slopes ≥2°, these same small ruts have drained large areas of peatlands, a serious cumulative impact. Long-term effects of drainage include the local extinction of populations of <u>Sphagnum</u> spp. and rhizomatous vascular aquatics, and changes in the chemistry and thermal regime of drained mineral soils. Other effects include significant changes in biomass and the concentrations of macronutrients in the leaves of dominant species. These effects were magnified in peatlands drained where multi-pass vehicle movements occurred.

Species richness displayed an inverse relationship with trampling intensity and the soils of heavily trampled ground remained severely compacted after 21 years. These patches were dominated by dense swards of ruderal grasses. Nutrient concentrations in the leaves of the latter and other colonizing and surviving species tended to increase with trampling intensity. Trampled patches and archaeological sites appeared selectively grazed by several herbivores. Although humans initiated the disturbances within these patches, it is the animals which are responsible for many of the dynamics of patch change over the long-term.

Classification and ordination procedures revealed linkages between the floristic associations of trampled meadows on Baffin Island and archaeological sites on Devon and Cornwallis Islands. One critical implication is that even low levels of human impact may give rise to ruderal plant communities which are extremely persistent. These patches are poor in terms of species richness, but contribute to habitat heterogeneity at the landscape level and comprise preferred forage for local vertebrate herbivores.

Archaeological excavation and restoration revealed that at least some stores of viable seed exist in both mesic and wet tundra soils and point to the importance of initial floristic composition (*sensu* Egler 1954). From a long-term perspective, the data establish that mesic tundra vegetation and soils are easily disturbed and recover much more slowly than their low arctic counterparts under similar disturbance regimes.

RÉSUMÉ

La littérature sur l'étude écologique des régimes de perturbations révèle que, dans les conditions climatiques actuelles, les plantes non-indigènes ne jouent pas un rôle important dans la recolonisation végétale de la toundra du Haut Arctique. Il a plutôt été suggéré que la flore indigène, surtout les plantes herbacées vivaces, est cruciale pour le rétablissement de la végétation. Cependant, peu de données à long terme sont disponibles sur l'impact de perturbations antérieures sur la végétation actuelle des prairies à carex du Haut Arctique, et aucune ne considère la flore invasculaire.

Cette thèse combine des perspectives biogéographiques et de dynamiques de parcelles pour se concentrer sur plus de 21 ans de rétablissement naturel et assisté de la végétation et des sols de trois sites de l'Arctique Canadien ayant subit une gamme de perturbations anthropogéniques de surface. Des recherches empiriques, expérimentales et archivistiques furent effectuées parmi de basses terres côtières climatiquement semblables mais de géologies contrastantes, sur l'Ile de Baffin, l'Ile Devon et l'Ile Cornwallis. Ces données incluent les milieux humides minérotrophes et oligotrophes où la flore vasculaire montre une différenciation minimale, tandis que les bryophytes échantillonées ne partagent que 31.8% de tous leurs taxa. Les perturbations choisies pour l'étude sont représentatives des impacts humains à petite échelle les plus répandus dans le Nord. Celles-ci incluent les perturbations causées par les véhicules, les piétons, la construction, et la pollution.

Il fut déterminé que l'ornière causée par le simple passage d'un véhicule chenillé durant l'été résultait en des réductions significatives de la biomasse et de la diversité végétale. Sur des pentes ≥2°, ces petites ornières ont drainé de grandes portions de tourbières, ce qui représente un impact cumulatif sérieux. Les effets à long terme du drainage incluent l'extinction locale de populations de Sphagnum spp. et d'espèces vasculaires aquatiques à rhizomes, en plus de changements dans la chimie et le régime thermique de sols minéraux drainés. D'autres effets incluent des changements significatifs de la biomasse et de la concentration de macroéléments dans les feuilles d'espèces dominantes. Ces effets furent amplifiés dans les tourbières drainées où des déplacements de véhicules tout-terrain eurent lieux.

La diversité végétale a montré une relation inverse à l'intensité du foulement. Les sols des sites fortement piétinés demeurèrent très compactés même après 21 ans. Ces parcelles étaient dominées par des tapis denses de plantes herbacées rudérales. Les concentrations d'éléments nutritifs dans les feuilles de ces dernières et d'autres espèces colonisatrices et survivantes tendaient à augmenter avec l'intensité du foulement. Les parcelles foulées et les sites archéologiques semblaient être sélectivement broutés par plusieurs herbivores. Bien que des humains eurent initiés les perturbations à l'intérieur de ces parcelles, ce sont surtout les animaux qui, à long terme, sont les responsables de la dynamique des changements dans les parcelles.

Des liens entre les associations floristiques des prairies foulées sur l'Ile de Baffin et des sites archéologiques sur les Iles Devon et Cornwallis ont été révélés à l'aide de classifications et d'ordinations. En conséquence, même un faible niveau d'impact humain peut donner lieu à des communautés de plantes rudérales extrêmement persistantes. Ces parcelles sont pauvres en terme de nombre d'espèces présentes, mais elles contribuent à l'hétérogénéité de l'habitat et comprennent du fourrage prioritaire pour les herbivores vertébrés locaux.

Des excavations et des travaux de restoration archéologiques ont révélé qu'il existe un certain nombre de graines viables dans les sols de toundra mésiques et dans ceux de toundra humides. Ils ont aussi démontré l'importance de la composition floristique initiale (*sensu* Egler 1954). A long terme, les données présentées ici démontrent que la végétation de toundra mésiques et les sols mésiques du Haut Arctique sont facilement endommagés et se rétablissent beaucoup plus lentement que leurs équivalents du Bas Arctique.

РЕЗЮМЕ

В современных климатических условиях адвентивные виды не принмают участия или имеют очень небодьшую роль в восстановлении растительности нарушенных высоко арктических тундры. Скорее можно предположить, что в этом случае решающее значение имеют вилы местной флоры, особенно долгоживущие многолетние злаки. Вместе с тем, для Высокой Арктики имеется немного данных долгосрочных наблыдений зарастания после нарушений, они касаытся продуктивности осочниковб и нет сведений о других растениях кроме сосудистых.

В представленнов исследовании из широкого диапазона датированных антропогенных повсрхностных нарушений рассматриваются изменения нарушенных участковб происходившие в течене 21 и более лет как в ходе естественного, так и включающего вмешательство человека восстановления растительности и почв. Исследования были проведены в трех районах высокоарктической Канадской тундры. Они сходны климатически, но значительно удалены друг от друга и расположены на прибрежных низменностях островов Баффинова Земля, Девон, Корнуоллис, имеющих контрастные геологические условия. Тем самым, полученные данные дают возможность сравнить минератрофные и олиготрофные заьолоченные территории, на которых флора сосудистых растений имеет минимадьную дифференциацию, в то время как бриофлора составляет только 31.8% от общего чусла видов. На участках, выбранных для изичения было представлено большинство широкораспространенных на Севере антропогенных воздействий, включая влияние вездеходов, вытаптывания, строительства и загрязнения.

Выли проведены многофакторные анализы и обобщения данных по биотическим и абиотическим компонентаи примерно на 400 площадках. Выли использованы количественная классификация и ординация как для видов, так и для взаимосвязей видов и факторов среды. Параметры случайного варьирования рассматривались отделно с применением однофакторного анализа. Исследовали химизм почв и растений, чтобы выявить местные и географические вариации в круговороте питатеьных веществ.

Было установлено, что колен возникающие после даже одного проезда гусеничного вездехода летом приводят к заметной редукции видового богатства и биомассы, что сохраняется в течение более двух декад. На склонах крутизной более 2° такие слабые следы вездеходов способствуют дренированию значительных площадей торфяников и серьезному нарушению аккумуляции веществ. Долговременрос вздействие дренажа приводит к вымиранию популяций сфагновых (*Sphagnum*) мхов и корневищных

сосудистых водых растений, к изменению химизма и температурого режима на дренированных минеральных почвах. Другие воздействия включают заиетные изменининя в биомассе и концентрации макрозломоитов, прусутствующих в листьях доминирующих видов. Наибольшие воздействия были замсчены на торфяниках, дренирусмых более глубокими колеями, возникшими после неоднократного проезда гусеничого транстпорта.

Видовое богатство демонстрирует обратную связь с интенсивностью вытаптывания. Почвы там, где грунт подвергался сильному давлению, остаются сильно уплотненными и после 21 лет. Такие участкие покрыты плотной дерниной из рудеральных трав. Концентрация питательных веществ в листьях последних, а также других поселяющихся или сохранившихся там растений имеет тененцию возрастать с усилением вытаптывания. Вытоптанные участки и археологические места стоянок кажутся выборочно выеденными некоторыми травоядными. Хотя именно человек был первоначальной причиной нарушений на этих участках, животные во многом определяют динамику изменений растительности здесь в течение долгого времени.

Процедуры классификации и ординации обнаружили связь между флористическими ассоциаями вытоптанных луговин на Баффиновой Земле и археологических мест стоянок на островах Девон и Корнуоллис. Можно сделать заключение, что даже низкие уровни вовдействия человека могут дать начало для формирования рудеральных сообществ, являющихся чрезвычайно стойкими (долговременно существуюшими). Эти участки бедны в отношении видового разнообразия, но порышают разнообразние ландшафта и предетавляют собой пастбища предпочитаемые местными травоядными позвончными.

Археологические раскопке и попытки реконеструкции выявили, что по крайней мере некоторые запасы жизнеспособных семян существют как в умеренно влажных, так и в сырых тундровых почвах, и показали важность исходого флористического состава (в смысле Egler 1954). Процессы и скорость естественного восстановления растительност в Высокой Арктике не имеют прямых аналогов. В частности почвы и растительность умсренно влажных тундр легко нарушаются и восстакавливаются гороздо медленное, чем в аналогичных местообитаниях низкоширотной Арктики при сходных режимах нарушений.

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CHAPTER I. INTRODUCTION

1. Introduction

i. Rationale and background

The literature of high arctic disturbance ecology provides an extremely limited amount of data on responses to anthropogenic disturbances of any scale, intensity or age. Particularly lacking are long-term data on the community-level recovery potential of the most productive wet and mesic sedge-moss meadow habitats. These habitats occur mainly in coastal lowlands, and although limited in spatial extent they are of critical importance to the region's herbivores (Anonymous, 1972; Babb & Bliss 1974a). While it is well known that the High Arctic differs considerably from the Low Arctic in terms of its floristics, vegetation, climate, soil development and hydrology (Young 1971; Moore 1978; Maxwell 1981; Woo 1986; Edlund 1986), we have no long-term data on anthropogenic disturbance by which to compare these two regions.

One of the central assumptions of tundra disturbance ecology has been that recovery from human impact in the Arctic is slow (Oechel 1989). Moreover, it is also thought that the process of recovery in the Low Arctic is essentially similar to that exhibited in the High Arctic, except that the latter is slower (Babb & Bliss 1974a). This assumption by Babb & Bliss is based mostly on data from two essentially short-term (≤10 yr) studies, one near Tuktoyaktuk by Hernandez (1973) and another on Truelove Lowland, northern Devon Island, by Babb (1972), with ancillary data from other Queen Elizabeth Islands. Based on the results of these two studies, Babb & Bliss

(1974a:557) concluded that recovery in the High Arctic "was clearly proceeding much more slowly than in the Low Arctic".

There are numerous recent examples of multivariate analyses treating tundra and/or northern wetland plant communities. However, only three of these studies are derived from high arctic vegetation (Bergeron 1988; LaFarge-England 1989; Muc et al. 1989), and only two are from sites within the Low Arctic (*sensu* Bliss 1990) (Ovenden & Brassard 1989; Kincheloe & Stehn 1991). Only the works of Ebersole (1985) and Moen (1990) deal with anthropogenic vegetation of any kind, and these are in areas far richer floristically than the sites encompassed in the present study. There is a need for empirical as well as theoretical consideration of the effects of different patches and disturbances at a single site and among high arctic sites.

Taken together, the applied studies of disturbance in the High Arctic of North America treat mostly short-term vehicle damage and fertilization effects (Kevan 1971b; Babb & Bliss 1974a; Barrett 1975; Addison & Bell 1976; Henry et al. 1987). Only Kevan (1971b) provides data on vascular composition and cover of tracks ≥ 10 years old, but these are limited mostly to mesic-xeric Dryas-dominated communities, which are not analagous to those reported here. Bliss & Grulke (1988) provide long-term data on high arctic fertilization experiments, but their efforts were aimed chiefly at assisted revegetation programs and also have little direct applicability to this study which focusses on natural (unassisted) recovery. Other aims of tundra fertilization experiments have been to determine the nature and extent of individualistic responses within and among species, growth forms and communities (Shaver & Chapin 1980, 1986; Lechowicz & Shaver 1982; Chapin & Shaver 1985b; Henry et al. 1987).

Of equal or greater ecological importance, relative to fertilization effects and the direct effects of vehicle damage, are the direct and indirect or cumulative impacts related to pedestrian and vehicle traffic, such as altered hydrology. Bellamy et al. (1971: 432) speculated that even by artificially seeding simple vehicle ruts we "could turn what are, in the time scale of tundra, ephemeral scars into permanent biotic features". In the same year, Kevan (1971a) speculated that "on gently sloping wet meadows vehicles *may* (italics mine) press the vegetation into shallow troughs, which then direct water that would normally percolate over a wide area, thus draining all or part of the meadow and reducing its biotic productivity over many years". To date, however, there have been no data to either support or refute such predictions; the only such studies from Alaska (Walker et al. 1987a, b) are of an entirely different scale in a different biogeographic region. Although England (1982) observed that human footpaths remain visible and largely devoid of vegetation two decades after they were created on northern Ellesmere Island, there are no data on how or if such trampling disturbances may eventually recover if left unto themselves.

Another important component of transient human occupation is the construction of temporary housing. There are very few data on what the long-term effects of temporary 'modern' construction may be in the High Arctic. There are also few data on the vegetation and soils associated with palaeosettlements, with the only comprehensive Canadian study being that of McCartney (1979) in the Low Arctic. McCartney and others (e.g. Lutz 1951; Moore 1986; Moore & Denton 1988) have reported persistent effects on soil properties such as phosphorus content. In temperate, boreal and alpine zones, abandoned settlements, campsites and pedestrian-trampled areas have been shown to exhibit excessively compacted soils for periods ranging up to several decades (Kellomäki & Saastamoinen 1975; Liddle 1975; Monti & Mackintosh 1979; Stohlgren & Parsons 1986; Knapp 1991). Similar effects have been observed, but not quantified, from zoogenic disturbances (Pegau 1970), which have been considered by some to be natural analogs for vehicle tracks (McKendrick 1981; Racine & Johnson 1988; Walker & Walker 1991). Gersper & Challinor (1975) reported that soils remained significantly compacted after six years in vehicle tracks through low arctic tundra. Such soils effects are typically in addition to those reported for the vegetation.

Regarding the lowlands of northern Devon Island, it was suggested during the International Biological Programme (IBP) that "documentation on the rate and type of regeneration processes associated with terrain damage in the area may increase the understanding of the impact of man on the arctic environment" (Nettleship & Smith, 1975:79). Since the close of the IBP, the ecological importance of the Arctic has remained undiminished and even appears to have increased (Chapin et al. 1992). Indeed, the 1980 World Conservation Strategy designated the Arctic as "a priority region due to unique ecosystem characteristics such as low productivity and species diversity, and slow recovery-from-disturbance rates" (Hanson & Lamson 1990:357). Throughout this period, long-term attempts at assisted revegetation through seeding and fertilization of disturbed sites have met with limited success (Bliss & Grulke 1988) and long-term data on the nature and pattern of natural (unassisted) recovery in the region have not been forthcoming. As the old pressures from non-renewable resource development remain (Hazell 1990), and new ones arise (England 1982; MacLachlan 1988; Hazell 1991), we have yet to understand how these systems respond to the most basic and widespread small-scale impacts, such as vehicle and pedestrian traffic, human-modified slope hydrology, temporary housing construction and chemical dumping.

In response to this situation, I initiated field work on a series of dated, mostly uncontrolled anthropogenic disturbances at sites on three different islands. Widely dispersed and geobotanically distinct sites were purposely selected to test hypotheses regarding the spatial and temporal patterns of long-term, unassisted recovery of tundra vegetation and soils. This thesis has been structured to illuminate any existing local and regional patterns of recovery through sampling within and among coastal lowland landscapes at: (i) 'Old' Clyde River, Baffin Island (70°35"N, 68°40'W) (CR), (ii) Truelove Lowland, Devon Island (75°33'N, 84°40'W) (TL), and (iii) Resolute Bay, Cornwallis Island (74°41'N, 94°57') (RB) (**Fig. 1.1**). These sites are considered representative of two distinct physiographic regions: (i) the gently-sloping and hummocky lowlands of eastern Baffin Island, and (ii) the more level, but also partially hummocky lowlands of the north coast of Devon Island and some adjacent Queen Elizabeth Islands. All three sites lie within the 4°C (July) bioclimatic zone.

The bedrock and surficial geology of CR is typical of much of eastern Baffin (Sempels 1982). The Kogalu Lowland on which the study site lies is underlain by the same igneous and metamorphic rocks that form the adjacent hills and highlands. It is covered by ground moraine and drift material, with fluvioglacial, fluvial and marine deposits occuring locally. Substrates tend to be acidic (**Fig. 1.2**) and where oligotrophic fens develop, such as those which were sampled, they may be classified as 'poor' or 'transitional poor fens' according to the ranges of soil pH, conductivity and plant species present (Sjörs 1952; Crum 1988). By comparison, the surfaces of the much of lowlands at TL and RB are dolomitic or dolomite-derived and where fens develop they

Fig. 1.1 - Map of the Canadian Arctic Archipelago showing the locations of the study sites. Source: Dept. of Indian and Northern Affairs.

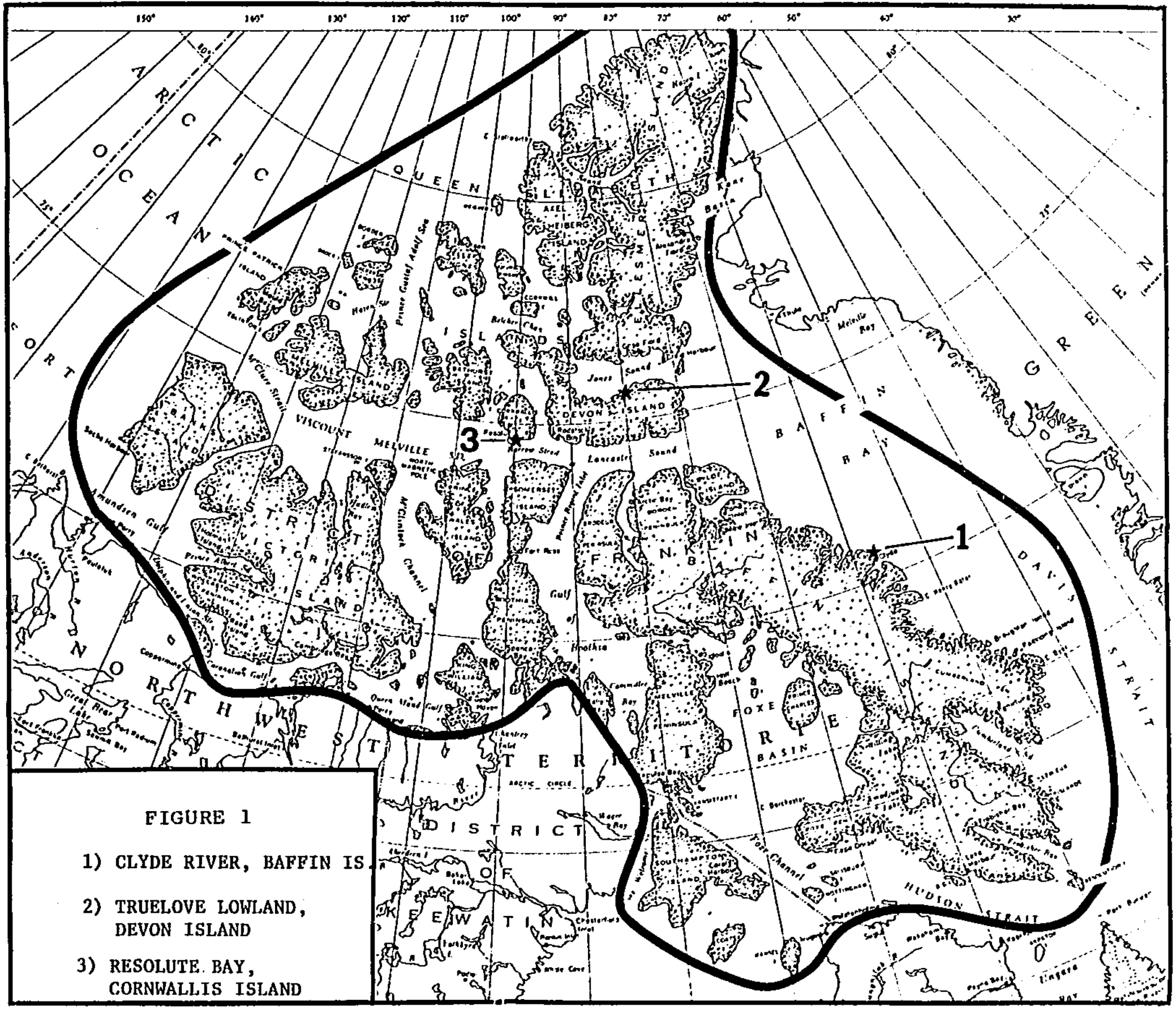


FIGURE 1

1) CLYDE RIVER, BAFFIN IS.

2) TRUELOVE LOWLAND,
DEVON ISLAND

3) RESOLUTE BAY,
CORNWALLIS ISLAND

Fig. 1.2 - Map of pH for surficial materials for the Canadian Arctic Archipelago. Modified from Edlund (1986).

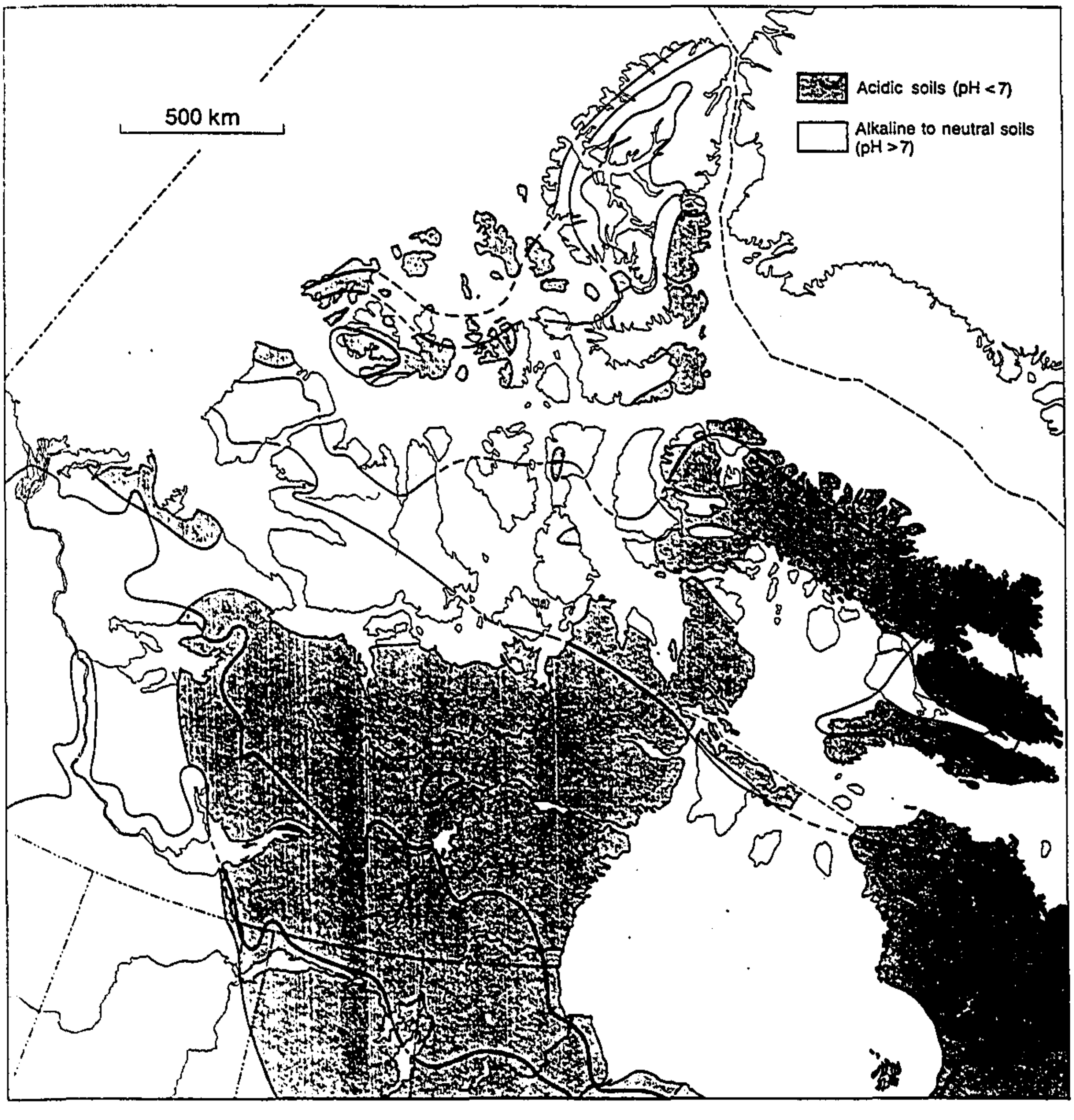
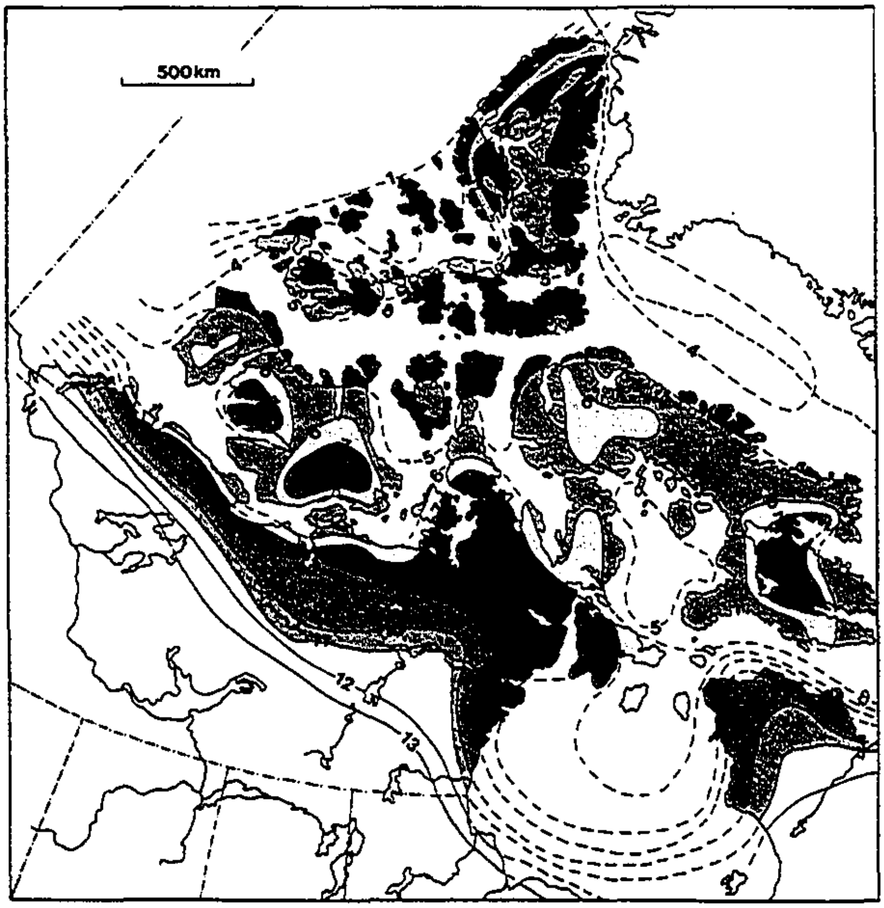

500 km
▨ Acidic soils (pH < 7)
☐ Alkaline to neutral soils (pH > 7)

Fig. 1.3 - Map of bioclimatic zones (mean July isotherms) for the Canadian Arctic Archipelago. Source: Edlund (1987). Used with permission of the author.


500 km
1
2
3
4
5
6
4
5
6
4
5
12
13

tend to be minerotrophic or 'rich' fens based on the criteria mentioned above. Given these bioclimatic similarities and geobotanical differences, the sampled vascular floras of the most extensively surveyed lowlands at TL and CR share 82.5 % of their taxa, yet the bryofloras of these same sites share only 31.8 % of their taxa.

Study sites were chosen among abandoned settlements and long-disused patches associated with active settlements within coastal lowlands which all lie within a single 'bioclimatic zone', as mapped by Edlund (1987) **(Fig. 1.3)**, meaning that that the mean July air temperature is approximately 4°C at each site. Summer warmth is considered the dominant macroenvironmental control delimiting gross distributions of vascular plants in the Arctic (Young 1971; Tuhkanen 1980; Edlund 1986), although it seems that a mosaic rather than a zonal pattern is most appropriate to understanding regional and subregional biological diversity (Matveyeva 1988; Bliss 1990).

Within a given zone, factors such as moisture, nutrient status and wind become important controls, as evidenced by change along local catenas in a number of landscapes (Reznicek & Svoboda 1982; Edlund 1983; Sohlberg & Bliss 1984). Gross distributional patterns among arctic cryptogams are not so easily explained, although there can be prounounced differences between both cryptogamic and non-cryptogamic floras of adjacent areas where substrates vary even slightly in age since deglaciation or chemical status. This is often the case among bryophytes, which may be sensitive to subtle spatial and temporal changes in factors such as soil texture, moisture and pH (Sjörs 1952; Elvebakk 1982; LaFarge-England 1989; Vitt & Chee 1990; Gignac et al. 1991).

Despite the acknowledged importance of bryophytes to tundra ecology and productivity, especially in relatively lush lowland landscapes (Vitt 1975; Longton 1988; Russell 1990), comprehensive bryophyte floristics have only rarely been coupled with either pure or applied ecological studies of high arctic vascular plants (see Barrett 1972; Sheard & Geale 1983a, b; Bliss & Svoboda 1984; Forbes 1992a, b, c). Recent applications of multivariate statistics in the region have included bryophytes only in terms of their total ground cover (Bergeron 1988; Muc et al. 1989), or in the absence of the vascular component of the vegetation at a given site (LaFarge-England 1989). Bliss & Svoboda (1984) used polar ordination to analyze whole, naturally occurring plant communities in the western Queen Elizabeth Islands, but included only one site of 'wetland grasses and sedges' which was dominated by Dupontia fisheri and apparently not analagous to those reported here.

It has long been held that tundra plant communities intergrade so readily as to make classification difficult at best (Beschel 1970). This contention was supported by the recent use of multivariate analysis in a high arctic lowland which revealed considerable floristic overlap among the most widespread plant communities (Muc et al. 1989). The authors also noted the wide ecological amplitude of the most prominent vascular plant species. On the other hand, workers in North America and Europe have shown that even high arctic communities can be formally and rigorously classified in the manner of Braun-Blanquet, through exploiting the often narrow ecological amplitudes of the regional cryptogamic flora (Barrett 1972; Elvebakk 1985; Hadac 1989). However, comprehensive surveys of high arctic bryophytes *and* vascular plants have not yet been coupled to investigations of human impact, thus limiting our ability to predict 'patch' or circumscribed community-level responses to disturbance.

At present, published studies of patch dynamics are derived mostly from natural disturbance regimes in temperate and tropical ecosystems (Pickett & White 1985), although some recent manipulations have sought to mimic natural disturbances in mixed prairie grasslands (Umbanhowar 1989). Fertilization experiments have been undertaken in the High Arctic (Henry et al. 1987), as have investigations of seed banks in natural and anthropogenic patches (Freedman et al. 1982). However, there have been no detailed, long-term studies of the vegetation and soils of anthropogenic surface disturbances within a single landscape, nor comparisons among physiognomically similar but geobotanically distinct and geographically disjunct landscapes. Only through comparative geographic analyses can we begin to understand the range of potential reponses within such a large region.

To summarize, we have a limited understanding of anthropogenic disturbance and recovery in the High Arctic, which is distinct from the Low Arctic in terms of climate, vegetation and soils, and where recovery is assumed to be functionally similar although slower as a result of these differences. In the context of the most widespread mechanical disturbance regimes (e.g. trampling, vehicle traffic, transient construction, etc.) we have no long-term data on community-level productivity, no details on cryptogamic floristics and few data on the role of cryptogamic vegetation, no comparisons among similar bioclimatic zones, and few detailed comparisons between areas of differing surficial geology. There is limited information available on the long-term effects of chemical dumping on vegetation (Smith & James 1979; French 1980, 1985). We also lack regionally applicable data on indirect or cumulative impacts, such as spatial variation in nutrient cycling, since much of the extant data are derived from studies in the Low Arctic (Chapin et al. 1992), nor do we have data on the community effects of cumulative hydrological changes (Woo 1986). Some aspects of patch-level dynamics in the High Arctic have been briefly discussed (see Freedman et al. 1982), but dealt mostly with natural disturbance (i.e. fox denning, bird manuring). Fertilization effects, both natural and experimental (Henry et al. 1987; Bliss & Grulke 1988) have been discussed, but the potential effects on patch-level grazing dynamics have not, nor has long-term change among floristics, vegetation and soils.

This research aims primarily to elucidate patterns of tundra response to a much wider spectrum of anthropogenic surface disturbance regimes than has previously been considered within the region, and to compare results from similar disturbances in different geobotanical areas within similar bioclimatic zones. Together these criteria account for much of the variation in potential small-scale human impact to be expected in the coming decades over a large portion of the Canadian Arctic Archipelago. This research seeks to add significantly to our knowledge of the potential for unassisted community recovery by investigating dated patches representative of uncontrolled impacts which are at least twice as old as those currently appearing in the literature. By examining both vascular and non-vascular components of the vegetation this study aims to expose spatial and temporal shifts in community composition and dynamics in detail.

There remain several important issues on which the literature provides equivocal answers. First, it has long been assumed that anthropogenically disturbed high arctic tundra recovers more slowly than similarly disturbed patches in the Low Arctic, but that the processes directing recovery are generally analagous. Second, the relationship of compacted soils to the recovery of vegetation has been made clear in studies of temperate ecosystems, but the importance and role of compaction have not been elucidated from arctic ecosystems. Third, patterns of assisted tundra regeneration have been contrasted within different bioclimatic zones, but there have been no comparisons of natural recovery within similar bioclimatic zones. Without such examples, there are severe limits to our ability to extrapolate from existing studies. Fourth, the great majority of disturbance studies to date have focussed on vascular plants only. From a review of such studies, it is apparent that there are few species which are either resistant or resilient in the face of anthropogenic surface disturbance. There are a far greater number of potential responses within the large non-vascular flora of the High Arctic, yet none have been addressed in any detail. Most studies have been from the minerotrophic and neutral to mildy alkaline substrates of the Queen Elizabeth Islands. To understand the relative importance of the role of non-vascular vegetation during recovery there is a need to include comparisons with more acidic, oligotrophic substrates. Finally, there have been few data published to determine whether or not cumulative impacts result from small-scale anthropogenic disturbances. Short-term studies have indicated little or no cumulative impact, although hydrologists and ecologists have cautioned that long-term effects may be significant. Based on the findings of previous investigations of the disturbance regimes studied here, both within and outside the Arctic, I have formulated the following four working hypotheses:

Hypothesis I. Unassisted or natural 'recovery' within the plant communities of anthropogenic patches will, depending on the nature, intensity and age of the original disturbance, exhibit a characteristic pattern of species composition, vegetation cover and biomass compared to adjacent undisturbed ground.

Hypothesis II. Common high arctic plant communities that have undergone similar disturbance events are marked by comparable recovery sequences among both vegetation and soils.

Hypothesis III. Soil compaction is a key factor associated with the spread of the adjoining flora into anthropogenic habitats.

Hypothesis IV. The spatial and temporal 'signatures' of the vegetation associations of the various disturbances will be best distinguished by their non-vascular floristics.

In addition to providing insight into these questions, there are ample data here suitable for testing current hypotheses on arctic succession (Svoboda & Henry 1987) and patch dynamics (Pickett & White 1985), as well as for providing the first detailed, regional synthesis of anthropogenic disturbance from a patch dynamics perspective. Palaeohuman (Thule culture) sites have provided the opportunity to compare physical and biological properties of soil and vegetation anomalies which have persisted for decades and perhaps several hundreds of years (Helmer 1991). Using the same methodology in an examination of recent (3-4 yr old) disturbances, such as 'young' vehicle tracks and archaeological excavation and reconstruction sites (Park 1986), has provided the chance to determine patterns among the early phases of resistance and/or colonization.

ii. Theoretical considerations

a. General successional theory

Efforts to understand, to generalize and to predict trajectories of vegetation change have a long and contentious history. Early in this century two views of vegetation change dominated vegetation science in North America. Clements (1916, 1936) viewed the plant community as a 'superorganism', the development of which was largely predetermined and resulted in one 'monoclimax' in a given region. This view is now largely discredited (Whittaker 1975; Miles 1979; Odum 1989). Opposing Clements' theory was the 'individualistic hypothesis' of Gleason (1926), who was skeptical that there was any organizational strategy at the community level. He argued instead that ecological succession resulted from the interaction of individuals and species as they struggle to occupy and hold space. Both Gleason and Clements assumed that plants were entirely or mostly responsible for successional changes, although it is now clear that animals and microorganisms play vital roles in the process (Odum 1989).

Another early and popular treatment of plant communities which developed, quite apart in theory and practice from that of the North Americans, was the European Zürich-Montpellier (ZM) approach exemplified by Braun-Blanquet (1932). North Americans eventually showed interest and awareness of this school and its methods (Becking 1957; Whittaker 1962), but few adopted its organizing principles. The ZM approach, which is essentially floristic in nature, was developed as an alternative to the classification of vegetation based on physiognomy (Westhoff & van der Maarel 1978), for example that of Raunkiaer (1934). The ZM approach deals mainly with the distinction and classification of plant communities necessary for vegetation inventory and mapping, and adopts neither Clements' organismal nor Gleason's individualistic approach. Instead, succession is treated in terms of an alteration of floristically distinguished plant communities.

Gleason's individualistic concept, together with the observation of multidimensional variability in a vegetation continuum, have been used as an argument against the classification of vegetation (Whittaker 1962, 1978). This multidimensionality does not deny the the possibility of a hierarchical classification of plant communities, but it does present some difficulties, as has been discussed by Moravec (1992). It is interesting to note that, contrary to the North Americans (Odum 1989), the Europeans incorporated 'animal sign' (i.e. evidence of grazing, trampling, manuring, etc.) into the sampling of vegetation from the outset (Braun-Blanquet 1932; Westhoff & van der Maarel 1978). Despite its apparent advantages over physiognomic and other approaches to vegetation classification, critics of the ZM approach have cited the subjectivity of sampling within supposedly 'homogeneous' vegetation units. However, an attempt to overcome the subjectivity of structuring Braun-Blanquet-style hierarchies has been manifest in the recent, more objective multivariate approaches to classification, discussed in Chapter III (Gauch & Whittaker 1981; Mucina & van der Maarel 1989).

Since the North American theories were first put forth, there have been some avowed and credible skeptics of community-level prediction (Golley 1977 in McIntosh 1980b: 53) who claim that "a simple mechanistic explanation of succession is not possible. Truly there is a rich array of possible mechanisms to explain succession". That this view is echoed by such an active executor of ecological experimentation as Egler (1954; 1977; see also Kenfield 1991) lends credibility to the argument. His contributions to community ecology are based on a combination of meticulous observation and manipulation spanning several decades and his concept of 'initial floristics' is among the most basic and contested tenets of successional theory (Wilson et al. 1992). Egler (1968:263) has complained that "one of the man-made laws of science is that the world be orderly and predictable". Based on his work in old-fields, rights-of-ways, and many other vegetation types, Egler concluded (in McIntosh 1980: 53) that, "ecology may not only be more complicated than we think, it may be more complicated than we can think". Miles (1979:16) also argues that, "any given succession is the resultant of a large number of probabilities" and that (p. 14), "the composition of no two patches of vegetation is precisely the same [and] neither are the seed banks. Succession on different patches of disturbed ground in the same locality frequently proceeds quite differently because of such differences".

Some early ecologists rebelled against the urge to generalize. Cooper (1926:403) found it "more helpful to clear thinking to treat succession simply as change, without saddling upon it the subjective concepts of progression and retrogression and their boon companion, 'development' ". At the same time, Gleason (1926 in Egler 1968) asked the question "are we not justified in coming to the general conclusion . . . that an association is . . . merely a coincidence" (see also McCune & Allen 1985)? Nonetheless, it has been observed that repeated species assemblages can be recognized for any particular region with a recurrent pattern of landscape (Henry 1992). Many phytosociologists would recognize such associations as noda within a 'continuum' (Ellenberg 1988). Labelling these communities is useful for communication and research (Walker 1992), but extrapolation of these communities to other regions will be accurate only if the regions have similar patterns of environment and climate at several scales (Westhoff & van der Maarel 1978; Austin & Smith 1989).

Watt (1947) observed that natural vegetation is comprised of 'a mosaic of patches', which was the product of cyclic changes within the plant community, and noted that 'patchiness . . . is widespread'. Soon after, Hutchinson (1951) coined the term 'fugitive species' to describe that class of competitively inferior species which survive by colonizing newly disturbed patches. Since then, various theories have appeared attempting to explain patterns of species composition in disturbed areas including, but not limited to, the 'intermediate disturbance hypothesis' (see below). Horn & MacArthur (1972:752) ventured that "there is no formal limit to the number of species that can be fitted into a given patchy environment, as long as local extinctions of each species, or regeneration of patches provides a supply of unoccupied patches". The sole constraint Horn & MacArthur placed on this statement concerned the possibility that the supply of patches may be insufficient to maintain some species (Abugov 1982). Similarly, Crawley (1986) observes that the best correlate of high invasibility in plant communities is the inverse of plant cover; low cover is associated with high invasibility. In each of these views, it seems, an open patch will not remain open for long; bare soil is simply not an option. Few of these hypotheses, however, have been tested with data from tundra environments (see, however, Fox 1981).

b. Patch dynamics

It is now generally accepted that predictions based on first principles which encompass all taxa, ecological systems or situations, are unlikely to be productive in the development of theory relating to disturbance because of the variable nature of species, populations, communities and ecosystems (Pickett & White 1985). Pickett & White's argument is that the sorts of predictions we can make about disturbance are mechanistic - those that take into account the peculiarities of a particular system and situation. This view is echoed by Austin & Smith (1989: 37) who argue that, "the concept of a community of co-occurring species can only be relevant to a particular landscape and its pattern of combinations of environmental variables; community is a landscape property".

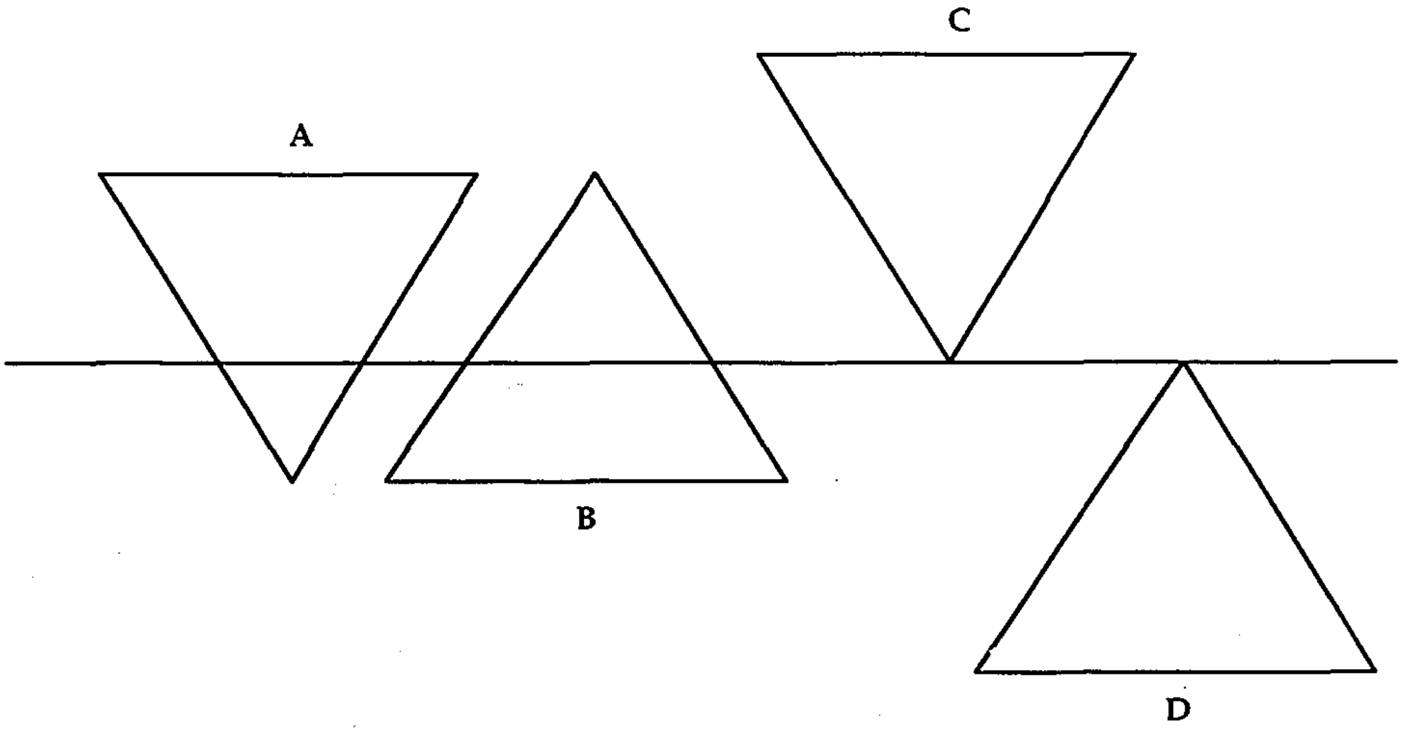
These views are central to the theory of patch dynamics - the interpretation of patch change. Patchiness, according to Pickett & White, implies a relatively discrete spatial pattern, but without constraint on patch size, internal homogeneity or discreteness. A patch implies a relationship of one patch to another in space, where other patches exist, and to the surrounding unaffected or less affected matrix. Patch formation and disturbance are often linked, but disturbance may not always produce a patch and a patch is not always the product of disturbance. In Miles' view (1979), all patches are different and unique, yet some subsets are more similar than others such that vegetation can be classified into different types, which are of great practical utility. This is a fundamental tenet of patch theory, and one that is well-suited to testing with the present data set.

The question which emerges is: how similar is the vegetation which develops on similarly disturbed patches in the same locality? Or in a different locality? Given the limited extent of the local and regional high arctic floras, and the relatively similar climatic regimes shared by the different study sites, it seems that we can effectively limit at least a portion of the 'large number of probabilities' (Miles 1979) responsible for patch composition. If so, we may effectively increase the 'practical utility' of the analysis as measured by our capacity for meaningful prediction.

Two major 'hypotheses' current in the literature of disturbance ecology are of interest in this study. The better known is the 'intermediate disturbance hypothesis', which states that species richness will be greatest in communities experiencing some intermediate level of disturbance (Loucks 1970; Connell 1978b; Huston 1979; Denslow 1980). Pickett & White (p. 378) acknowledge that, "the statement leaves much unspecified. First, which community and ecosystem parameters will behave in the expected way? For example, will intermediate disturbance enhance nutrient retention or productivity as well as richness"? They note that the maximum level of disturbance needs to be explicitly defined for the system at hand. They also raise the issue of quantification. How should the impact of disturbance be measured? Destruction of biomass is an oft-used and reasonable parameter, "but structural disruption of the community, substrate disruption, or in some cases the area of the disturbed patch may be appropriate measures" (Pickett & White, p. 378). Because disturbance may be subdivided into the components of magnitude, frequency, and size, intermediacy in each of these variables may mean different things (Peet et al. 1983). The second major hypothesis relates disturbance frequency to species richness. It holds that where disturbance recurs more frequently than the time required for competitive exclusion, species richness should be maintained (Huston 1979). Pickett & White (p. 379) consider this, "an important generalization with clear implications for the intermediate disturbance idea".

In their synthesis, Pickett & White draw attention to several other generalizations derived from the literature of patch dynamics and they outline the principle unresolved questions. They begin by generalizing about

Fig. 1.4 - Diagram of four contrasting sorts of community structure showing disposition of biomass relative to the substrate and degree of attachment of the organisms to the substrate. (a) Shoot-biased community having the preponderance of biomass above the substrate. Resource levels and community attributes are altered most by disturbances that disrupt the above-ground portion of the community. (b) A root-biased community having the majority of biomass arrayed within the substrate. Disturbance to the within-substrate component will influence resources and community structure most significantly. Many tundra communities are root-biased. (c) A surface-attached community having all biomass above the substrate and superficial attachment to the substrate. Although the terminology relies on plant structure, animal communities can have analagous structures; indeed, surface-attached communities are common among invertebrate animals. Communities of burrowing animals would form a fourth type, (d) substrate contained. Modified from Pickett & White (1985).



physiognomic system structure as a context for disturbance. Of the four contrasting sorts of community structure (**Fig. 1.4**), tundra would be considered as 'root biased'. This distinction is important because the structure of a system will determine (a) what sorts of disturbance may have an impact, (b) the threshold of intensity that is effective and (c) the dependence of species coexistence on disturbance. They contend that disturbance of insufficient intensity to open the root mat in 'root biased' systems will have little impact on species coexistence.

Pickett & White assert that the rate of regrowth after disturbance is determined by the resource base and concede that the effect of disturbance of a given intensity and frequency may be different in resource-limited systems than in resource-rich sites. Species richness may be reduced in systems experiencing a severe disturbance regime but having low resource base. Since environmental stress may, by affecting resource uptake and productivity, also govern system structure, its role may be similar to that of the resource base. In general, species' growth form, growth rates, longevity, dispersal, and other life history characteristics are important in determining disturbance as well as in responding to it. A key issue (Pickett & White 1985: 381) is, "whether species have discrete regeneration niches (*sensu* Grubb 1977) or are randomly and interchangeably mixed after disturbance". The authors conclude (p. 384) that, "an explicit statement of the parameters that respond to disturbance, the variables that determine the impact of disturbance, and consideration of the context and constraints of disturbance, can form the basis of a theory of disturbance. Placing studies of disturbance in various systems, *particularly understudied ones* (italics mine), in this framework will further our ability to generalize and make appropriate predictions about disturbance".

c. Succession in the Arctic

The Arctic has long been of special interest to ecologists and geographers. In most cases the High Arctic has been considered distinct from the Low Arctic in studies of both biotic and abiotic pattern and process. Early observations of arctic plant succession often emphasized the instability of a variety of sloped and level soil surfaces, due mainly to frost action (Elton 1927; Griggs 1934; Polunin 1934). Thus, where development of a closed vegetation cover was perennially inhibited, some researchers began to doubt the very existence of 'stable' arctic plant communities (Griggs 1934; Raup 1951; Sigafoos 1952; see Churchill & Hanson 1958 for an opposing view). Several others have also acknowledged the strong relations between vegetation and periglacial geomorphology (Wiggins 1951; Bliss & Cantlon 1957; Drury 1962; Viereck 1966; Lambert 1976; Jonasson 1986). Still others, concentrating on studies of vascular vegetation, have cited the difficulty of discerning discrete plant communities, particularly in the High Arctic (Beschel 1970; Webber 1978; Bergeron & Svoboda 1989; Muc et al. 1989).

Recent important works to include critical discussion of disturbance and/or succession in the Arctic include Batzli et al. (1980), Billings & Peterson (1980), Ebersole (1985), Billings (1987), Cargill & Chapin (1987), Svoboda & Henry (1987), Walker et al. (1987), Walker & Chapin (1987), Matveyeva (1988), and Bliss & Peterson (1992). Three of these are of particular interest because each provides graphic models which are suitable for testing with the present data. Svoboda & Henry (1987: 380) set out hypotheses about the 'driving forces' and 'resistances' which direct succession in 'marginal arctic environments'. Their discussion focusses mainly on vegetation within polar deserts and semi-deserts, following Bliss & Svoboda's (1984) definition of lands having <5% total plant cover and 5 to 20% vascular plant cover respectively. However, much of the discussion by Svoboda & Henry regarding the effects of stress, competition, and species replacement is also directly relevant to tundra areas with more complete vegetation, especially where disturbance has significantly reduced plant cover and, hence, competition. The second model, discussed by Cargill & Chapin (1987), is more empirical in nature. It is derived from mostly short-term (≤7 yr) studies in low and subarctic Alaskan sites and specifically addresses the effects of vehicle tracks on tundra plant productivity (see also Chapin & Shaver 1981: 615). A third, more general model of disturbance and vegetation response developed in Alaska is presented by Walker et al. (1987: 6).

There is now a wealth of information on tundra disturbance and succession in general. In his recent review of contraints to arctic plant growth, reproduction and establishment, Billings (1987: 362) observed that, "arctic plants, in general, have not yet evolved much resistance to impacts by people, the relative newcomers to the Arctic . . . arctic plant species can tolerate the cold climate, but they have not yet evolved a temperate toughness against trampling". This view appears to ignore the long-standing role of Inuit and their impacts within and among arctic ecosystems (see Freeman 1984; Wenzel 1991). However, it does point to the importance of the consideration of endemic tundra disturbance regimes under which the vegetation has evolved and the utility of searching for natural analogs among them (Walker et al. 1987; Walker & Walker 1992).

The complexity and number of potential interactions among processes controlling successional change are discussed in some depth by Batzli et al. (1980) and Walker & Chapin (1987), who observed interplay among natural disturbance regimes. Batzli et al. (1980) review the effects of frost-patterned ground on local vegetation development (see also Jonasson 1986) and how it affects the nesting and feeding habits of tundra grazers such as lemmings. They also highlight the significant effects these grazers have on the local redistribution of plant materials and nutrients and, consequently, the long-term patterns of composition and productivity of the vegetation. Walker & Chapin (1987), in their investigation of successional processes on Alaskan floodplains, note a pattern of preferential grazing upon early successional species by snowshoe hares which is thought to be critical in directing the course of local vegetation change.

Models such as those developed by Chapin & Shaver (**Fig. 1.5**) and Walker et al. (1987) (**Fig. 1.6**) are useful in visualizing the possible scenarios of tundra vegetation change resulting from human impact but, to date, remain untested outside the low arctic region within which they were originally designed. Conversely, the model by Svoboda & Henry (**Fig. 1.7**) was developed specifically to treat succession within high arctic ecosystems, but has not been tested with data from dated, patch-level anthropogenic disturbances. Instead, the model has been applied to natural disturbance of a different scale, specifically revegetation since deglaciation and, more recently, questions of macroclimatic change (Bliss & Peterson 1992). Together these three models provide a suitable framework within which to consider the present data set and to draw conclusions about the geographic variability of tundra responses to patchy anthropogenic disturbance and the extent to which such variation is predictable.

Fig. 1.5 - Diagrammatic representation of causal relationships among factors linking vehicle passage in tundra to increased plant productivity. Unbroken arrows indicate effects demonstrated in low arctic research; broken arrows indicate suggested effects. Source: Chapin & Shaver (1981). Used with permission of the author.

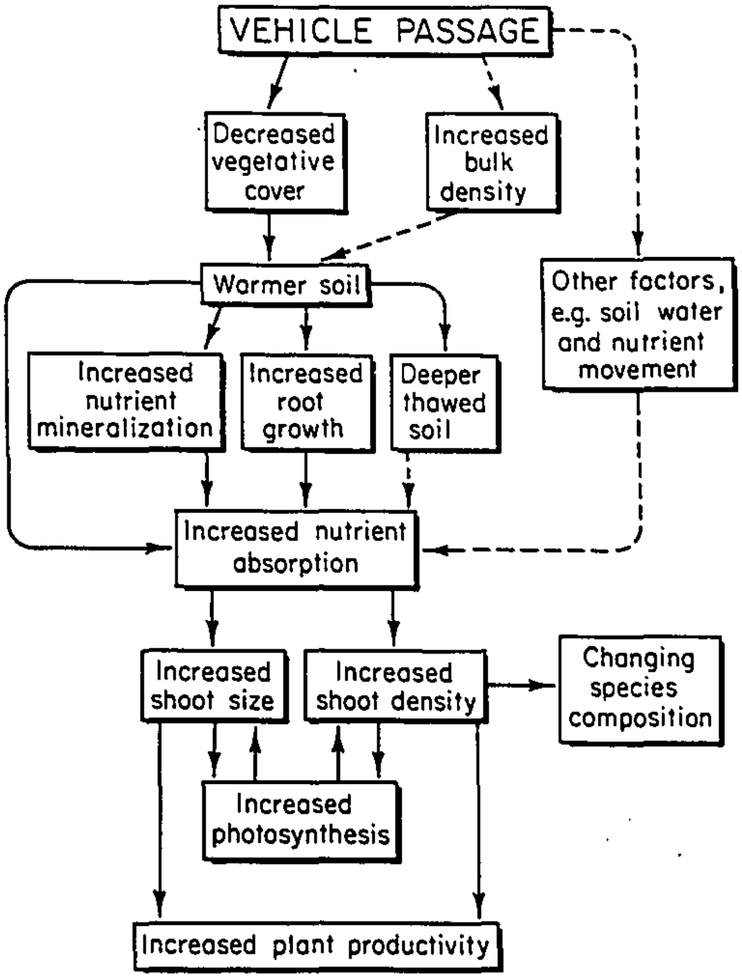

VEHICLE PASSAGE
Decreased vegetative cover
Increased bulk density
Warmer soil
Other factors, e.g. soil water and nutrient movement
Increased nutrient mineralization
Increased root growth
Deeper thawed soil
Increased nutrient absorption
Increased shoot size
Increased shoot density
Changing species composition
Increased photosynthesis
Increased plant productivity

Fig. 1.6 - Diagrammatic representation of general pathways of tundra recovery following disturbance. Source: Walker et al. (1987a). Used with permission of the publisher.

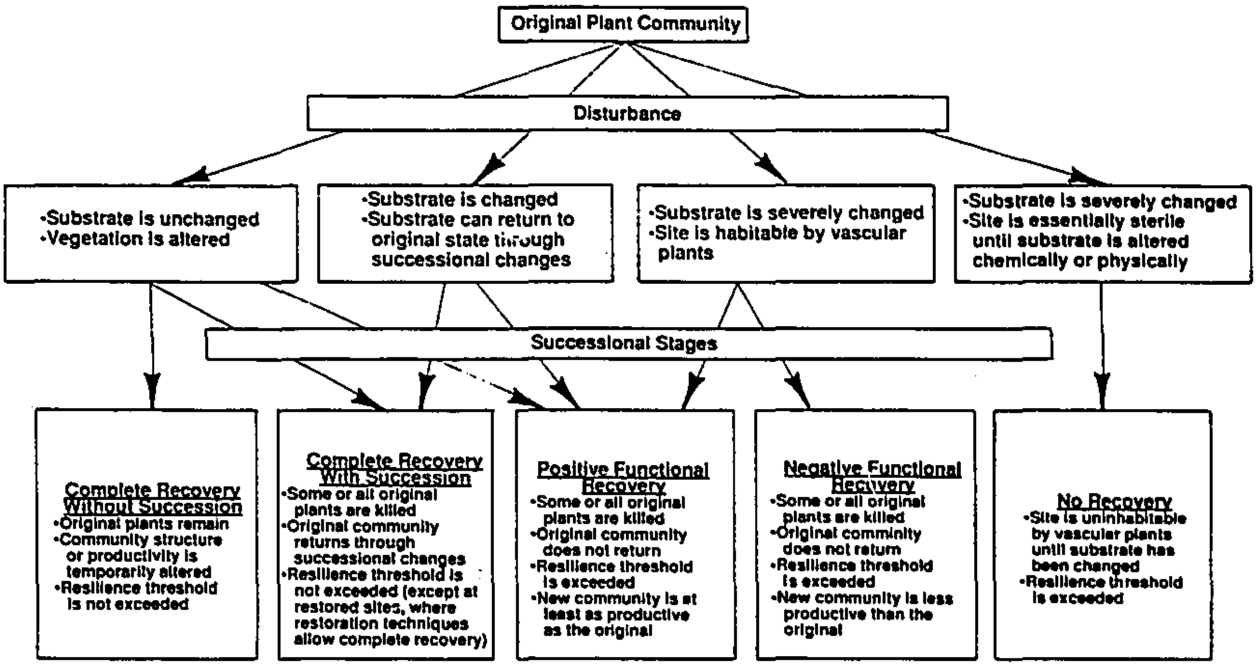
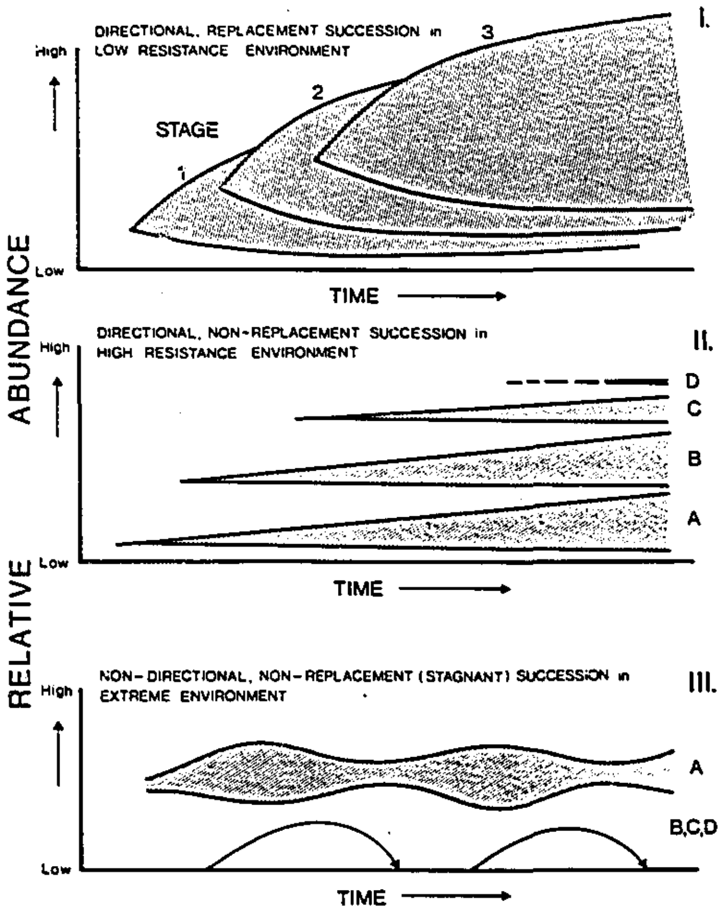

Original Plant Community
Disturbance
•Substrate is unchanged
•Vegetation is altered
•Substrate is changed
•Substrate can return to original state through successional changes
•Substrate is severely changed
•Site is habitable by vascular plants
•Substrate is severely changed
•Site is essentially sterile until substrate is altered chemically or physically
Successional Stages
Complete Recovery Without Succession
•Original plants remain
•Community structure or productivity is temporarily altered
•Resilience threshold is not exceeded
Complete Recovery With Succession
•Some or all original plants are killed
•Original community returns through successional changes
•Resilience threshold is not exceeded (except at restored sites, where restoration techniques allow complete recovery)
Positive Functional Recovery
•Some or all original plants are killed
•Original community does not return
•Resilience threshold is exceeded
•New community is at least as productive as the original
Negative Functional Recovery
•Some or all original plants are killed
•Original comminity does not return
•Resilience threshold is exceeded
•New community is less productive than the original
No Recovery
•Site is uninhabitable by vascular plants until substrate has been changed
•Resilience threshold is exceeded

Fig. 1.7 - Diagrammatic representation of succession in environments of varying resistance. Source: Svoboda & Henry (1987). Used with permission of the author.


I.
DIRECTIONAL, REPLACEMENT SUCCESSION in LOW RESISTANCE ENVIRONMENT
High
Low
STAGE
1
2
3
TIME
II.
DIRECTIONAL, NON-REPLACEMENT SUCCESSION in HIGH RESISTANCE ENVIRONMENT
High
Low
D
C
B
A
TIME
III.
NON-DIRECTIONAL, NON-REPLACEMENT (STAGNANT) SUCCESSION in EXTREME ENVIRONMENT
High
Low
A
B,C,D
TIME
RELATIVE ABUNDANCE

iii. Terminology and concepts

Several terms central to vegetation science and disturbance ecology have been variously defined, often in a confusing and tautological manner. 'Succession', for example, lacks a concrete meaning and this study will adopt Cooper's (1926) view that it is better to refer simply to vegetation change. Though variously defined, disturbance is perhaps the one process which is inimical to each of the theoretical frameworks and concepts discussed in this thesis. Over the years there has been a good deal of debate over whether natural (and even some anthropogenic) disturbance regimes are endogenous or exogenous agents of change. That is to say, has disturbance played an integral role in the evolution of the community or ecosystem under consideration? How does disturbance affect the structure, composition and maintenance of the community? At what scale(s) does it occur? Are its effects of importance?

White (1979: 241) argued persuasively that "disturbances and the vegetation responses they initiate seem to be an integral part of the pattern in most landscapes. The kinds of natural disturbance vary regionally and also within one landscape as a function of topography, substrate, and the vegetation present". Similar points were made by Sousa (1984). The theoretical role of disturbance and its effects on 'mosaic phenomena' (*sensu* Watt 1947) have also been discussed by Whittaker & Levin (1977). The latter considered the following three groups of interrelations in natural communities: (1) microsite or population-level interrelations. The microsites for a community form a mosaic that is differentiated by physical environment or biological effects or both; (2) community-level relations. Most communities are subject to disturbance followed by succession; (3) really a sub-group of (2), including inter- and intracommunity relations. Intracommunity patterns relate to microsite differentiation and species-level responses. Intercommunity successional mosaics are spatial complexes within which community disturbance is a major force.

Each of these groups is in part defined by its scale - spatial, temporal, and ecological (Mohler 1983; Wiens et al. 1986; Addicott et al. 1987; Auerbach & Shmida 1987; Pielou 1988; Fortin et al. 1989; Økland 1990b). If one is attempting to characterize anthropogenic disturbance effects, knowledge of natural variation at several scales is a prerequisite to interpretation of mosaic phenomena. Related questions include: to what extent are the signatures observed the result of the underlying original or 'undisturbed' formation(s)?; and at what scales do each occur?

Because disturbance is a scale-variable phenomenon, our observations and conclusions must be appropriately scaled to the systemic level under investigation. In this study, the non-random and local nature of the various anthropogenic disturbance types must be considered in the context of local and landscape-level biotic and abiotic patterns. One or more passes of a tracked vehicle may be catastrophic to an association of mesic-xeric hummock-top plants, but may not affect an adjacent association occupying a mesic-hydric hollow. A bit further inland, where slope and insolation are reduced and snow lies until quite late in the growing season, there is no hummock-hollow complex to interact with the same vehicle, no matter how many times it passes. These are examples of the types and scales of natural mosaics which must be considered before the effects of disturbance can be interpreted.

The importance of characterizing the disturbance itself is not to be overlooked. As a term, some authors have used disturbance interchangeably with perturbation and stress, occasionally confusing cause and effect (McIntosh 1980; Rykiel 1985; van Andel & van den Bergh 1987). Perturbation has a rigid definition within physics and its use will be avoided here. Stress, such as that imposed by climate, will be considered separately from disturbance and then only in an ecophysiological sense (Svoboda & Henry 1987; Chapin et al. 1992).

Arctic vegetation and soils have often been considered particularly susceptible to disturbance, or 'fragile' (Billings 1973; Babb & Bliss 1974b; Banfield 1975; Barnett et al. 1975; Eckhardt 1988), but fragility is ill-defined and perhaps, in use, has come to be an oversimplification. In the present study, unless othewise specified, disturbance will be considered a human-induced change in conditions, which interferes with the normal functioning of a biological system (van Andel & van den Bergh 1987). Within a given system or 'interrelational group' (*sensu* Whittaker & Levin 1977), a disturbance regime has four basic dimensions: frequency, intensity, scale (extent), and timing (season) (Connell & Slatyer 1977; Sousa 1984; Rykiel 1985; White & Pickett 1985; Petraitis et al. 1989). However, other dimensions can also be important, such as pattern in space. Frequency encompasses consideration of not only the recurrent nature of a disturbance, such as trampling, but also the age of isolated and recurrent disturbances, defined as the number of years since the cessation of human activity within a given patch or set of patches. A reference state must be defined for each disturbance regime, but it need not be static.

Due to the relative heterogeneity of arctic tundra even at local scales, reference states or 'controls' have been situated immediately adjacent to each disturbance to clarify what constitutes 'normal functioning'. Natural factors which effect these controls, such as wind, frost-heave, late-lying snow, etc., are normal aspects of the reference state and these are noted where they are considered pertinent. Moderate grazing by musk-oxen, for example, is an important aspect of the structure and productivity of meadows at TL (Henry 1992), but not at CR. Snow-patches are important in some meadows at CR, but not in others.

Other key concepts include resistance, resilience, and recovery from disturbance (Oechel 1989). Resistance reflects an ability to remain unchanged by disturbance. Resilience refers to an ability to return to a predisturbance state. Both can be considered at the scale of the individual plant (Mooney & Hobbs 1986) or of the community as a whole (Grubb & Hopkins 1986). In a vegetation context, change refers primarily to community composition or productivity (Walker et al. 1987a). Disturbance often implies negative changes, such as a reduction in species richness or biomass, but any deviation from normal, or reference state, is considered disturbance. Together, resistance and resilience determine the speed, degree, and direction of recovery from a disturbance.

Recovery is the process by which a community achieves relative biological and physical stability following disturbance and it may not necessarily lead to a community similar to the one that previously existed. Complete recovery occurs only when the community has regained its original productivity and species composition (Walker et al. 1987a). Recovery may occur naturally, or it may be affected by human agency, in which case the terms revegetation and restoration may apply. There is some debate as to what constitutes fully recovered or restored vegetation (Pielou 1986; Cairns 1989). The extent of recovery in the present study will be discussed in Chapter IV. Together, different levels of resistance, resilience, and recovery are important components of the range of potential responses to disturbance within a given system. This thesis will be primarily concerned with spatial patterns of response, but will also consider the mechanisms behind these responses when sufficient evidence is available to support such a discussion.

Finally, the terms 'high arctic' and 'ruderal' are defined for the purposes of this study as follows. The 'High Arctic' is dominated by open polar desert and semi-desert vegetation (*sensu* Bliss & Svoboda 1984), but encompasses a limited number of smaller, more productive landscapes characterized by closed tundra vegetation which appears physiognomically similar to low arctic tundra. True high arctic tundra, however, lacks tussocks of Eriophorum vaginatum and upright shrubs, such as Salix and Betula spp. In accordance with the Chicago Manual of Style, 'Arctic', 'High Arctic', and 'Low Arctic' are capitalized when used as nouns. These words are not capitalized when used as general adjectives (e.g. arctic regions, low arctic vegetation).

'Ruderal' vegetation is meant here simply as that inhabiting naturally and/or anthropogenically disturbed sites and is consistent with the recent definition provided by Lincoln et al. (1992). It is not intended to imply any linkage with a particular growth strategy (*sensu* Grime 1979). Other terms in common use include 'apophyte' and 'hemerophyte' (*sensu* Porsild 1932), although definitions by Porsild and others (Lincoln et al. 1992) imply links to cultivated ground, which I wish to avoid. Ahti & Hämet-Ahti (1971: 15) define apophytes as native plants "evidently drawing benefit from human activities", an assumption beyond the simple presence of the plants I wish to emphasize. Dorogostaiskaya (1975) echoes the view of Ahti & Hämet-Ahti, although Druzhinina & Zharkova (1979: 30) provide a more suitable, unbiased definition for apophytes, as "native tundra species remaining for a long time on disturbed sites". If purposely divorced from the reference to strategies (*sensu* Grime 1979), 'ruderal' appears to be a less confused, if general, vegetation descriptor.

CHAPTER II. STUDY SITES, MATERIALS AND METHODS

2.1 Physical subsystems

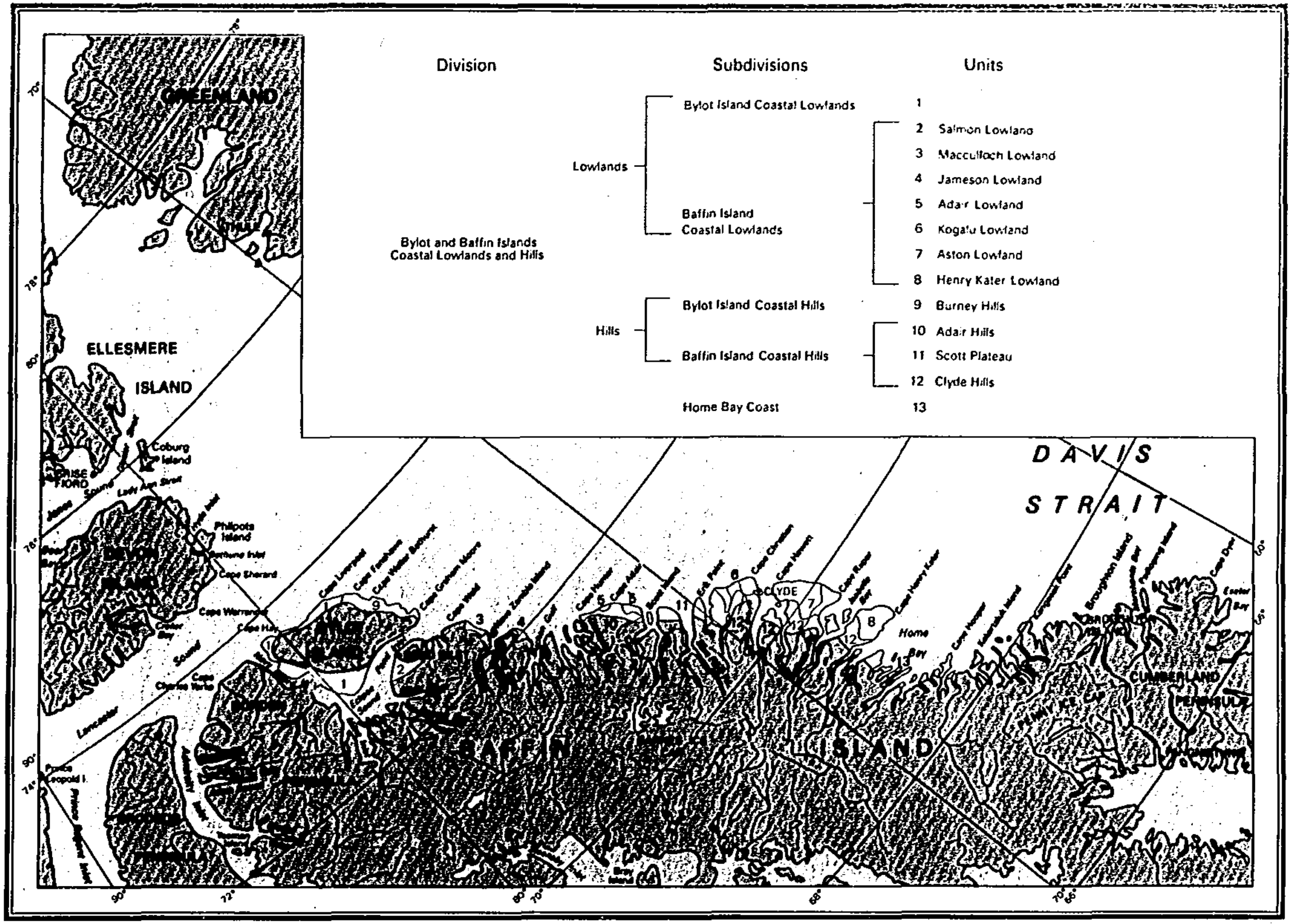
i. Geology and physiography

a. Clyde River

The physiography, surficial geology and coastlines of the eastern Canadian Arctic have been summarized by Sempels (1982). The whole of Canada has been divided into distinct physiographic units, known as the 'borderlands' and the 'shield' (Bostock 1976), the latter of which includes most of Baffin Island. The study site at CR sits near the edge of the Clyde Foreland (see Nettleship & Smith 1975; Mode 1980), on a portion of the larger Kogalu Lowland which is one of a series of nine lowlands dominating the coasts of northeast Baffin and adjacent Bylot Islands (**Fig. 2.1**). All but one of these (the Salmon Lowland near Pond Inlet) are underlain by the same igneous and metamorphic rocks that form the adjacent hills and highlands and are covered by ground moraine and drift material, with fluvioglacial, fluvial and marine deposits occuring locally.

The glacial history of this area is complex and somewhat unusual in that there is no evidence that Laurentide Ice ever reached the coast of the central Clyde Foreland (Miller et al. 1977). As a result, the area has been proposed as a glacial refugium (Løken 1966). *In situ* marine shells above and below the Ayr Lake till on the Foreland have been radiocarbon dated within a minimum range from 33000 to 47700 ybp (Miller et al. 1977). Though the history of the terrain at the actual study site is less certain (Andrews 1991,

Fig. 2.1 - Map of physiographic subdivisions of the coastal lowlands and hills of Bylot and Baffin Islands, showing the location of the Kogalu Lowland and the settlements at CR. With the exception of the Salmon Lowland, substrates are generally siliceous and range from mildly to moderately acidic. Modified from McGill University (1963a, b).



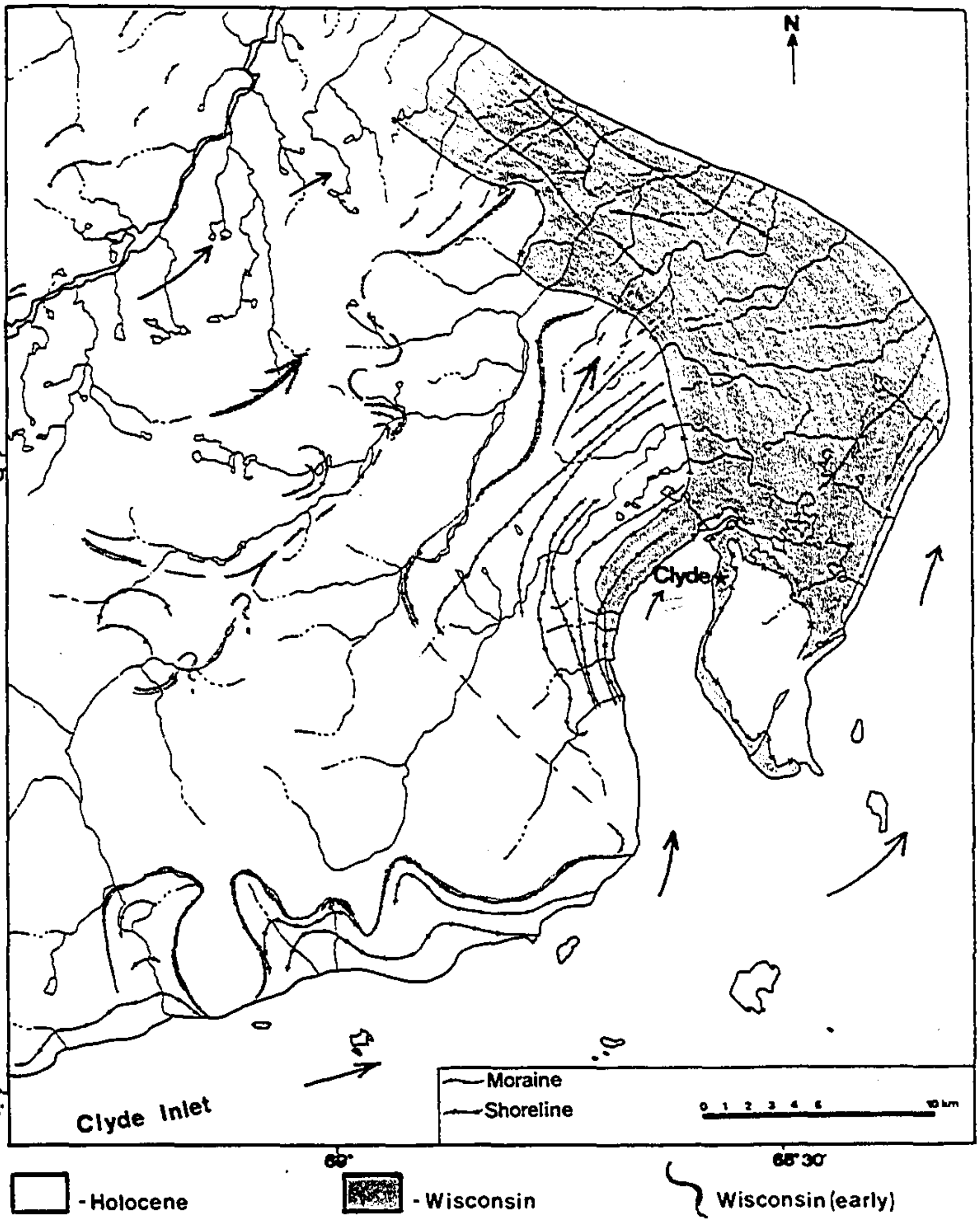
Division		Subdivisions	Units	
Bylot and Baffin Islands Coastal Lowlands and Hills	Lowlands	Bylot Island Coastal Lowlands	1	
		Baffin Island Coastal Lowlands	2	Salmon Lowland
			3	Macculloch Lowland
			4	Jameson Lowland
			5	Adair Lowland
			6	Kogalu Lowland
			7	Aston Lowland
			8	Henry Kater Lowland
	Hills	Bylot Island Coastal Hills	9	Burney Hills
		Baffin Island Coastal Hills	10	Adair Hills
			11	Scott Plateau
			12	Clyde Hills
		Home Bay Coast	13	

Figure 2.1 Physiographic Subdivisions of the Bylot and Baffin Islands Coastal Lowlands and Hills, after McGill University, 1963a and b.

pers. comm.), it appears to have been ice covered and subsequently submerged (see Miller et al. 1977 and Mode 1980 for detailed discussion). On northeast Baffin Island, the general arrangement of lateral moraines suggests that ice moving through the fiords overrode much of the forelands and continental shelf (Hodgson & Haselton 1974; Mode 1980). Lateral moraines adjacent to the site suggest that mid-Wisconsinan age ice flowed from Clyde Inlet into the trough of Patricia Bay and over onto the foreland (**Fig. 2.2**). The stratigraphy of the Clyde Foreland has been mapped by Mode (1980), and he depicts the study as having a veneer of marine deposits overlying morainal materials.

In general, the surface of the Kogalu Lowland is covered with similar layers of marine veneers and moraine deposits interspersed with pockets of meadows, marshes and ponds, and has several low, rounded hills of bedrock protruding through the drift cover (Sempels 1982). The study site has a northwesterly aspect and is on a gently sloping (1-5°) backshore of unconsolidated material ranging from boulder gravel to clay, with the surface veneer being generally fine-grained. This material is apparently thick enough (>1 m) to isolate the vegetation from the gneissic bedrock, which is deep enough to remain permanently frozen at this site. All but two of the vegetation stands sampled lie between 4 and 12 masl in elevation. Stands 3 and 4 lie slightly further upslope (ca. 16 masl) near the base of a large hill. Mode (1980:34) has reported Holocene emergence dates using ^{14}C methods at several elevations. His estimates from 9 to 10.5 masl indicate ages of 6000-6300 ybp, and one date from 20 masl indicates an age of 8100 ybp.

Fig. 2.2 - Map of moraines and shorelines on the Clyde Foreland, with emergence periods indicated. Abandoned shorelines occur at 4.5, 8, 25, 40-45, 50-55, 60-65, and 75.85 masl. Much of the Kogalu Lowland is a former marine bench where hummocky terrain and thaw ponds occur (see terrain classification map in Mode 1980). The 4.5 and 8 masl shorelines run through the study area. Source: Mode (1980). Used with permission of the author.


N
70° 30'
70° 15'
69°
68°30'
Clyde
Clyde Inlet
Moraine
Shoreline
0 1 2 3 4 5 10 km
- Holocene
- Wisconsin
Wisconsin (early)

b. Truelove Lowland

At 43 km^2, TL is the westernmost in a series of four lowlands including Skogn (13 km^2), Sparbo-Hardy (86 km^2) and Sverdrup (26 km^2). The lowlands are the result of postglacial rebound following deglaciation of this portion of the island ca. 8700 ybp (Andrews 1970; Bliss 1977). Despite its designation as an intensive high arctic study site during the IBP, adequate characterizations of the landforms and surficial deposits of TL were not included in the study program (Walker & Peters 1977). Bedrock characteristics in the vicinity of Truelove Inlet are discussed by, King (1969) and Krupicka (1977). Glenister (in Barrett 1972) reports the bedrock of the area from Sverdrup Inlet to Cape Sparbo as being composed chiefly of a Precambrian basement complex unconformably overlain by carbonate and clastic sedimentary beds. The lower sedimentary beds are sandstones and these are overlain by a series of dolomite beds followed by an upper inter-bedded series of dolomites, breccia, conglomerates and sandstone (Cowie in King 1969). The unconformity is seen clearly from the lowland, which is bordered to the east by a steep Cambrian dolomitic escarpment and to the south by a sheer scarp of Precambrian material capped by a thin sedimentary layer (Krupicka 1977).

Most of the lowland itself is covered with Pleistocene age deposits that overlay a Precambrian complex of granulites and granitic gneisses. Granitic outcrops are common across the lowland, particulary in the northern portion (Bliss 1977). With post-glacial uplift, lagoons were cut off by off-shore bars which formed beach ridges, resulting in the formation of shallow lakes. Some of these have filled in to become meadows, the dominant landform of the lowland. The beach ridges occur in a sequence of more than 20 'steps' across the lowland and effectively block the drainage of water **(Plates 2.1 and 2.2)**

Plate 2.1 - Oblique aerial view looking north showing close-up the pattern of beach ridge and meadow formation at TL, in which rising seashores block drainage and wetlands develop. Note high-center polygons in center foreground and vehicle tracks traversing beach ridge at lower right. Photo date: 2 August 1989.

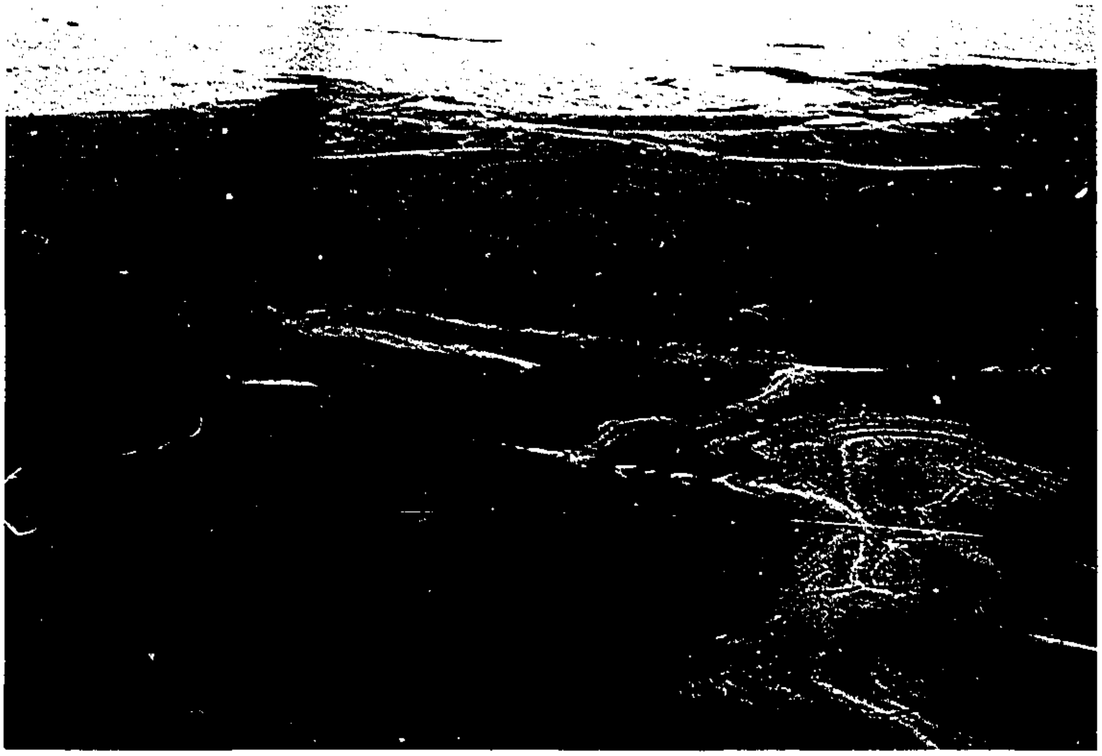


Plate 2.2 - Vertical aerial view of Truelove Lowland and vicinity showing the overall pattern of beach ridges, meadows, and lakes across the lowland, which generally slopes from east to west. The dolomitic plateau and cliffs are seen at right. Scale = 1:60000. Lowland is approximately 5 x 8 km. Photo date: 17 July 1959.

(Bliss 1977). From the coast, the lowland complex rises gradually to to ca. 45 masl at the escarpment base (Barrett 1972). King (1969) has presented evidence that the marine limit found in nearby Truelove Valley lies ca. 246 feet asl.

c. Resolute Bay

The terrain units of RB have been described by Cruickshank (1971). Evidence of glaciation is apparent and many periglacial features appear to be quite old. Frost activity in the form of poorly sorted polygons characterized the coarse gravels and cobbles of the sample stand. Surface features in and around RB are derived from Ordovician and Silurian dolomite, dolomitic sandstone, limestone cobbles and pavements, and calcareous sandstones and shales, resulting mostly in mildly alkaline substrates. The surveyed archaeological site was apparently close to the shore when built, but now sits on a raised marine terrace several hundred meters from the shore. The former shoreline has a local slope of ≤1° and conforms to Cruickshank's 'Terrain Unit 1B(+3)' just a few hundred meters from the southern shore of Resolute Lake.

ii. Permafrost

a. Clyde River

CR lies well within the zone of continuous permafrost (Linell & Tedrow 1981), although no surveys on permafrost depth, temperature or amplitude are available from this portion of Baffin Island. Detailed observations on active layer development collected for this study under a variety of undisturbed terrain conditions indicate that development is generally shallow with significant variations over short distances. These variations were often quite predictable and correlated with differences in exposure and snow cover, vegetative cover, surface moisture and soil texture. Active layer development for both disturbed and undisturbed terrain is plotted in several **Appendices (29-39 see also Section 4.2.i.a)** and shows that the thermal maximum occurs in late August.

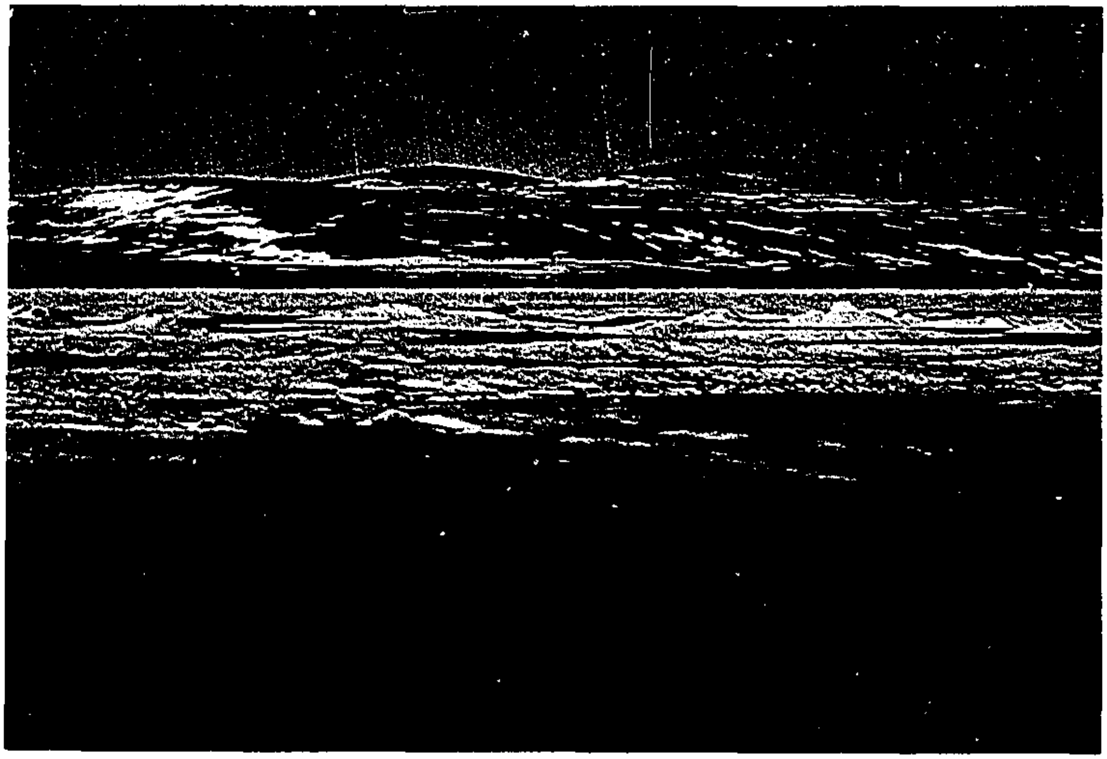
Depths exceeding 80 cm were restricted to larger exposed hummocks, beach ridges and slopes with a southwesterly aspect. As well, soils beneath poorly vegetated stands such as Nos. 3 and 4 thawed to nearly 1 m, despite the presence of late-lying snow beds (see **Plates 2.3 and 2.4**). Thaw depths were reduced beneath moist inter-hummock hollows and other microsites where fibric peat depths were substantial and ranged from 40 to 70 cm by late August (*including* fibric peat layers of up to 17 cm thick). These observations are consistent with those reported by others (Crampton 1977; Tarnocai & Zoltai 1978) for hummocky sites in the central arctic archipelago.

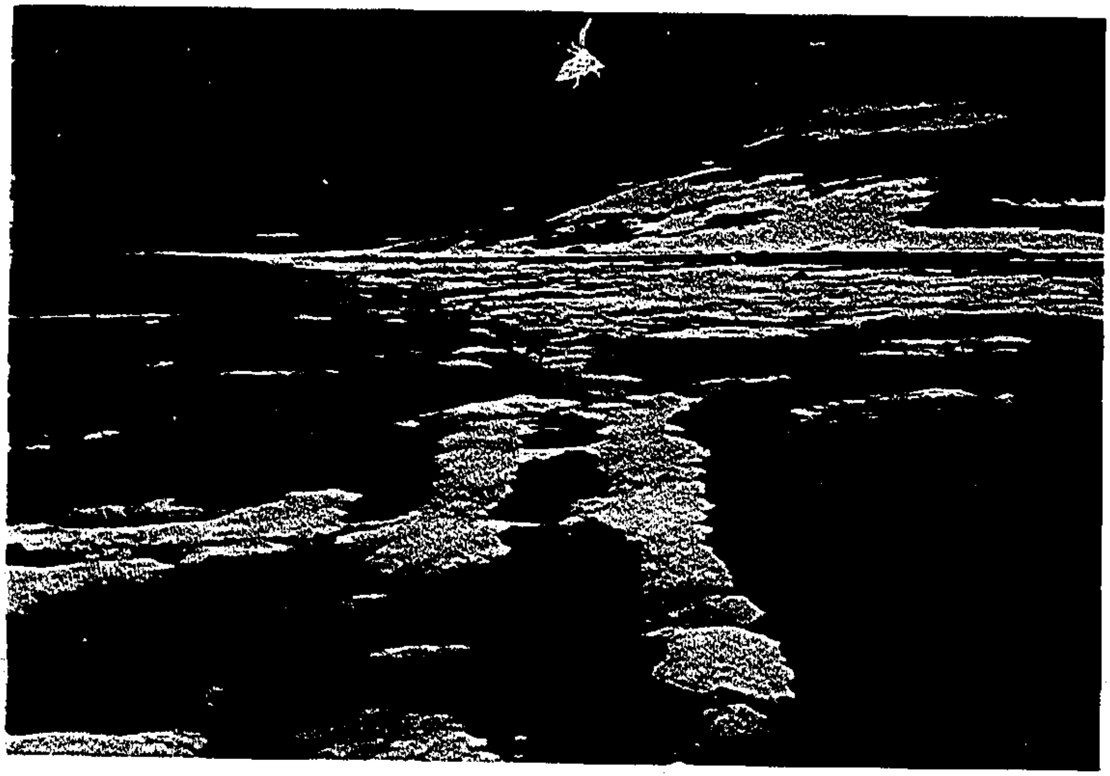
b. Truelove Lowland

Permafrost investigations were conducted at TL under the direction of Brown (1977) during the IBP. Of a number of terrain types sampled for mean annual ground temperature during 1971-73, the 'tundra-meadow site' (hummocky sedge-moss meadow) had the warmest readings (ranging from -14.75 to -13.75°C @ 0.5-2.8 m depth). Active layers depths in the same meadow site during July-August ranged from 30 cm (1972) to 70 cm (1971) (1971 was an exceptionally warm year, with 1973 being nearly as warm). In general, the active layer of soils at TL reaches maximum thickness in late July (Muc 1977).

Plate 2.3 - View from the new settlement toward 'Old' Clyde River ('akiani') showing the pattern of snow melt and the location of late-lying snow patches upslope from the old settlement, which was generally close to the shore (**see Plates. 2.7-2.14**). Photo date: 20 June 1990.

Plate 2.4 - Close-up of Stand 4 showing snow patches at and near the base of the large hill behind the old settlement. One week prior the snow had been ≥50 cm deep. Note the persistence of snow in the tracks, which resulted from a single passage of a tracked vehicle during summer 1970 or 71. The microclimate of the tracks is different than that of the adjacent controls. Photo date: 21 June 1990.





The depth of snow cover is widely variable among sites and its presence strongly affects active layer development (Brown 1977). Snowcover at the meadow site was measured monthly from May 1972 to May 1973 and ranged from 46 cm (May-June 1972) to 0 cm (July-Sept. 1972) to 30 cm (May 1973). Snow depth transects measured in late June 1968 by Barrett (1972) averaged 22 cm for snow line at beach crests and 15.5 cm for meadow sites. Along beach ridges, Barrett found foreslope habitats (Tetragono-Dryadetum) remained snow covered 1.5 weeks longer than the adjacent meadows (Caricetum stantis). In late August 1968 & 1969 he recorded active layer depths of ca. 30 cm in these meadows. For this study, 56 measurements of the active layer were made in 13 separate undisturbed meadow sites (Caricetum stantis) at the end of July 1990 and averaged 40.6 cm with a range of 25-73 cm (*including* fibric peat layers of 4-16 cm). No measurements of snow cover were made.

c. Resolute Bay

RB also lies well within the continuous permafrost zone. Active layer depths on well-drained sites can be shallow even at the thermal maximum, with the maximum depth being 63.5 cm in sandy soil, with shallower depths (13-15 cm) in organic soils (Cook 1958). Arkay (1972) reported mean depths of 62±12 cm for gravel beach ridges in polygon fissures where organic matter had collected, and depths of 72±13 cm for the polygon mounds.

iii. Soils and hydrology

a. Clyde River

There is a now a wealth of general information on the formation and classification polar soils (Tedrow 1977; Reiger 1983). However, details on the nature of certain pedogenic processes, such as rates of weathering, may be based on a limited number of examples (Ugolini 1986). Soil forming processes are affected by adverse climatic factors - particularly low temperatures, low levels of precipitation, and the limited availability of unfrozen water - that decrease biomass production, rate of organic matter decomposition, leaching potential, etc. (Ugolini 1986). The complex of tills, glaciofluvial and glaciomarine sediments of the Clyde Foreland is one of the most studied sites in the Eastern Canadian Arctic (Sempels 1982), and undisturbed pre-Wisconsinan age soils associated with the aforementioned glacial refugium have been reported from here (Andrews & Miller 1972). However, little detailed information is available on soil processes and contemporary typology for the area.

Pedologists tend to discuss genetic soil types and pedogenic gradients in terms of biogeographic or pedogenic zones that have been imposed upon the Arctic (Tedrow 1973; Walker & Peters 1977; Ugolini et al. 1982). In a latitudinal transect depicting a gradient of eastern Canadian arctic and subarctic soil formation processes, Moore (1978) describes a beach ridge profile from Clyde River as being equivalent to Tedrow's 'Polar Desert Soils'. These are poorly developed soils of the Orthic and Cryic Regosol subgroups of the Canadian classification scheme and develop under conditions of low precipitation and low biological activity. They exhibit minimal accumulation of organic matter, neutral pH values and negligible leaching. Another beach ridge profile has been similarly described from nearby Cape Christian (thin O horizon overlying oxidized sand), while more strongly developed soils were found on buried marine deposits of an earlier interglacial (Miller et al. 1977).

For this study, most profiles examined were of soils in moderately well to poorly drained meadow sites. Analyses revealed that undisturbed mineral soils in these meadows have particle size ranges as follows: sand 43-52%; silt 30.5-37%; clay 16-19.5%. Organic matter content for these same soils ranged from 1.5-5.0%, usually in relation to microtopography (see below). Gently sloping, moderately well drained terrain predominates over undisturbed portions of the study area and is characterized by hummock-hollow complexes (**Plate 2.5**). These are comprised mostly of completely vegetated turf hummocks, similar in structure and appearance to those described for other sectors of the circumpolar north (Raup 1965; Beschel & Matveyeva 1972). The hummocks are generally between 70 to (rarely) 115 cm in diameter and 20-40 cm in height and may often be slightly elongated in a downslope direction. Evidence from other workers (Crampton 1977; Tarnocai & Zoltai 1978; Mackay 1980) indicates that larger hummocks tend to develop in the Low Arctic and that, in the High Arctic, they tend to develop mainly on coastal lowlands (Tarnocai & Zoltai 1978).

Numerous peat forming mosses are present at CR and peat layers tend to be well developed on hummocky terrain and levels of pH in the undisturbed mineral layer (5-10 cm depth) are mildly-moderately acidic. Accumulation of organic matter varies considerably between hummocks and hollows, being generally ≤8 cm on hummock tops and ≥ 11 cm in hollows, which appears to level the terrain somewhat (**Plate 2.6**). Small-scale hydrology is influenced by the hummocks and a clear moisture differential exists

Plate 2.5 - General view upslope from Stands 12 and 16 of naturally occurring hummock-hollow complexes which characterize much of the undisurbed terrain in the study area. These areas are fairly moist with a low frequency of fruticose and crustose lichens on the hummocks. Note the late-lying snow in the background, the predominant source of seasonal moisture during spring runoff, and also the large proportion of dead-attached plant tissue, indicative of the lack of grazing. Sphagnum spp. provide structure for the hummocks. Photo date: 18 June 1990.

Plate 2.6 - Close-up of 'undisturbed' hummock at CR, showing fairly thick layer of peat and live bryophytes (Aulacomnium spp. and Sphagnum spp.) which is sharply separated from underlying mineral soils. Note general absence of roots in mineral layer. Hummocks are covered with Salix arctica, S. reticulata, and assorted Cyperaceae. Photo date: 9 July 1989.

V16

between the two microsites, with hummock tops often exposed and dry to the touch soon after snow melt, while hollows may stay moist, or even saturated in some water tracks or channels, late into the summer. Internal moisture gradients are equally apparent in hummocks of this type (Tarnocai & Zoltai 1978). Vegetation, soil and active layer (see above) development are strongly affected by this moisture differential. In general, moist soils beneath hollows tend to be organic, while drier soils within the central and upper portions of the hummock tend to be mostly mineral, where some sorting of particles may occur (Tedrow 1974; Walker & Peters 1977; Tarnocai & Zoltai 1978). Classification of high arctic meadow soil-vegetation patterns according to subgroups of the Canadian Soil Survey Committee has proven quite predictable, even at small scales, except under the wettest conditions (Walker & Peters 1977). Soil profiles from CR are seen in Chapter IV (**Plates 4.1-4.11**) and show distinct patterns related to microtopography, soil drainage conditions, and disturbance regime. Most undisturbed soils appear to fall into one of the following subgroups, in order of (generally) increasing moisture or reduced drainage: (1) Brunisolic Turbic Cryosol; (2) Gleysolic Static Cryosol; or (3) Gleysolic Turbic Cryosol.

As has been reported for the meadow systems at TL (Rydén 1977), surface moisture and drainage appears to be related more to the pattern of snow accumulation and runoff than moisture derived from the thawing active layer. Evidence for this at CR is that artificial channelling of spring runoff has substantially dessicated select downslope portions of the meadows, as will be discussed. Studies elsewhere in the region have found that as much as 80% of the annual precipitation can be lost into the atmosphere through evaporation, leaving only 20% for runoff, which occurs mostly during and immediately after the melt period (Rydén 1977; Ohmura 1982). However, this is not always the case (Woo 1983).

Large, late-lying snow fields upslope from the abandoned settlement provide most of the seasonal moisture for the CR lowland. Other than the beach ridge stand, soils here are the most poorly developed of those sampled, despite the relatively early emergence of substrates at this elevation (Mode 1980). Surfaces on the lower slopes can remain relatively moist well into the growing season, particularly in water channels, though 'spring' runoff had usually peaked by the last week of June and was more or less complete by the first week of July. Most hummock tops and many hollows in interfluves, were dry to the touch from this point on with the exception of precipitation events. Precipitation events were uncommon after June and typically left only traces of moisture, but there were occasional fogs. Water tracks are small, concave tracts which channel runoff, are separated by interfluves, and appear similar to those reported for northern Alaska (Kane et al. 1989; Walker et al. 1989) (see **Plate 2.9**). Recent evidence indicates that they are important in terms of local nutrient cycling (Chapin et al. 1988; Shaver et al. 1991). Their importance in terms of local vegetation development will be discussed in a later section.

b. Truelove Lowland

As on Baffin Island, tundra soils of the Queen Elizabeth Islands are mainly limited to lowland landscapes where there is a reliable source of water throughout the growing season (Tedrow 1974). The meadow soils sampled at TL generally contain more moisture further into the growing season than those at CR. Runoff hydrographs from the IBP (Rydén 1977) show that melting begins and ends later than at CR, but the reduced slopes, consistently shallower active layer and impoundment effects of the beach ridges together serve to keep considerably more moisture at the surface throughout the growing season (Bliss 1977; Brown 1977; Rydén 1977). As was discussed above, the geology of this area is more variable than at CR, with both dolomitic and granitic parent materials present. The substrates on beach ridges and in meadows sampled for this study were apparently dolomitic and Sphagnum spp. were conspicuously lacking, though perhaps more from climatic limitations. Soils fall into the same subgroups defined for CR with the addition of Fibric Organo Cryosols in some of the wettest meadows where the maximum active layer depth barely exceeded that of the organic mat, if at all. Surface waters in the meadows tended to be circumneutral or mildly alkaline, while the mineral soils beneath (5-10 cm depth) ranged from mildy alkaline to slightly acidic. Undisturbed beach ridge soils were mildly alkaline.

c. Resolute Bay

Soils in the area sampled were classified as 'polar desert' soils by Cruickshank (1971), the dominant soil type in the Queen Elizabeth Islands (McMillan 1960; Tedrow 1974). The 'soil' adjacent to the sampled Thule dwelling consisted essentially of calcareous cobbles, the interstices having collected some aeolian fines and organic matter from the minimal plant cover, most of which was accumulated in polygonal fissures. Arkay (1972) reported a pH range of 8.1 to 8.6 for gravel beach ridges similar to that which was sampled for this study. The Thule dwellings in the area are generally carpeted in a thick layer of peat with a slightly humic surface horizon

(Cruickank 1971) and a closed vegetation cover similar to those sampled at TL.

Hydrology in the nearby McMaster River basin has been documented and monitored by Woo and his associates for years (Woo & Steer 1983; Woo & Marsh 1990). According to Woo (1983), up to 80% of the annual precipitation at RB occurs as snowfall, and about 70% of the annual precipitation total leaves the McMaster River basin as runoff. Snow melt is responsible for 90% of the annual surface runoff.

iv. Climate

a. Clyde River

Clyde River lies within Maxwell's (1981) subregion IVd and its climate approximates that of a polar semidesert with a mean annual temperature of -12°C and summer precipitation of ≥5.5 cm (sources in Mode 1980). Summer precipitation averaged 6.5 cm during the course of this study and matched that measured during the period 1948-1972 (Fletcher & Young 1976). Total annual snow accumulation was consistently >51 in for the period 1948-72 (Fletcher & Young 1976). The mean July temperature is said to be 4°C (Edlund 1987, 1990). Intensive studies in the area (Andrews et al. 1980) have put the estimate closer to 4.6°C. Screen temperatures measured during July 1988-90 for this study, taken on the northwest-facing slope described above, averaged closer to 4.9°C. This can be explained by the fact that the measurement site is much more vegetated with a lower albedo, greater slope and more westerly aspect than the AES station at the airport, which is located on exposed gravels.

In addition, two of the three summers (1988 and 1990) were 'above average' in terms of temperatures recorded over the last four decades (AES records).

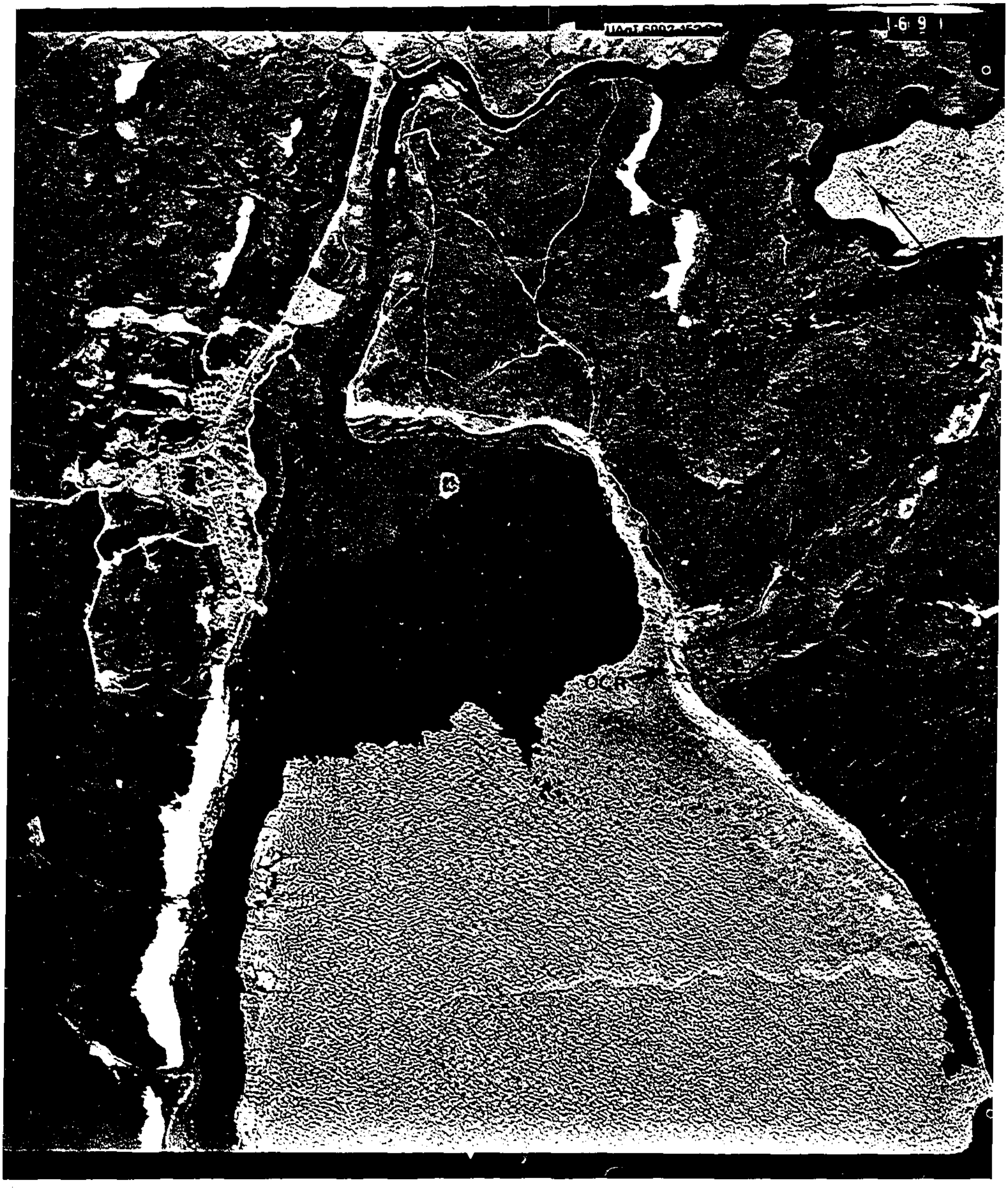
Mean annual wind speeds are 5.1-10 mph with both summer and winter winds primarily out of the northwest (Fletcher & Young 1976). Most of the annual precipitation falls as snow during the eight-month winter when no melting occurs and winds cause the snow to drift and compact in the same areas each year. These patterns of accumulation can be seen in **Plate 2.7**, with west-facing slopes having maximum exposure. Plants on these sites annually experience growth earliest.

b. Truelove Lowland

TL lies within Maxwell's subregion IVa, which possesses a relatively maritime character, more akin to the southerly and eastern Baffin Island coasts than the rest of the arctic archipelago at the same latitude (Maxwell 1981). No long-term weather records exist for Devon Island, but numerous short-term (mostly summer) surface and subsurface records exist for several portions of the lowland during the IBP (Barrett 1972; Courtin & Labine 1977). Since that time, discontinuous records have been kept at a station on the beach ridge adjacent to the base camp. Edlund's (1987) map of mean July isotherms for the archipelago (**Fig. 1.3**) employs more recent and extensive (but still mostly coastal) data than Young (1971) and shows north Devon Island as lying within the 4°C zone. The mean screen temperature for July 1989 at the TL base camp was indeed 4.0°C, while precipitation for June, July and early August of the same year was ca. 100 mm (Trask 1989, pers. comm.).

Total annual snow accumulation is generally less than 40 in (sources in Barrett 1972). Patterns of snow accumulation, melt and associated

Plate 2.7 - Vertical aerial view of Patricia Bay and vicinity showing the proximity between the old (right-hand side - OCR) and new (left - NCR) settlements of Clyde River. Late-lying snow banks are all in the lee of east-facing slopes. Heavily-used tracks at top center lead from old settlement to Cape Christian and the new settlement. Arrows at top and left point to albedo shifts caused by dust and impeded drainage resulting from new gravel roads. Arrow at far right points to fluvioerosional plume from single-pass vehicle track seen in Plate 2.4. Scale = 1:20000. Photo date: 17 July 1983.


1-6 9 1
OCR

community-level plant phenology are detailed by Barrett. He found that the foreslopes of beach ridges remained snow covered up to 1.5 weeks longer than adjacent meadows and 1.5-3.0 weeks longer than the tops of the beach ridges. Microclimatological characteristics in similar communities show that the pattern of temperature for a given site changes greatly from year to year. However, beach ridges tend to exhibit a greater yearly amplitude of subsurface, surface and air temperatures than wet peats in adjacent meadows (Courtin & Labine 1977).

c. Resolute Bay

RB is frequented by fogs and low clouds during July and August, contributing to fairly low summer insolation values and air temperatures. Cook & Raiche (1962 in Cruickshank 1971) reported a mean July temperature of 4.5°C. Arkay (1972) reported means of 3.28 and 4.61 for July 1969 and 1970 respectively, and Edlund (1987) places RB within her 4°C bioclimatic zone. Mean annual precipitation for the periods 1949-1963 was 13.5 cm (Cruickshank 1971), not dissimilar from Woo's (1983) more recent total of 13.7 cm, only 5.9 cm of which was from rain. Mean wind speed for all four seasons is within the range of 5.1-10 mph, with summer winds predominantly out of the southeast.

2.2 Biological subsystems

i. Fauna

a. Muskoxen

Muskoxen are the largest of the terrestrial herbivores in the Canadian Arctic and currently range, often in limited numbers, over much of the arctic archipelago with the exception of Baffin Island (Urquhart 1982). The northern lowlands of Devon Island, including Truelove, comprise critical habitat for the species (Ovibos moschatus) and are considered biophysical 'oases' important to the region's terrestrial food web (Anonymous 1973; Nettleship & Smith 1975; Bliss 1977). Essential components of muskox habitat are difficult to characterize. However, coastal lowlands, lake margins and riparian habitats with wet meadows dominated by sedges and willows are preferred by muskoxen (Fischer & Duncan 1975). Their diet consists of sedges and willows in summer and principally sedges in winter. Geographic variations in diet reflect differences in plant communities and snow cover (Urquhart 1982).

Barr (1991) provides a summary of the history of muskox exploitation and conservation in the region, noting that the species has been legally protected since 1917. Limited hunting of the northeast Devon Island population has been practiced by the Inuit of Grise Fiord since 1969 (Kiewe 1977). The ability of the species to cope with anthropogenic alterations of habitat (roads, pipelines, mines, etc.) remains unclear (Urquhart 1982). Details on species habitat, productivity, behavior and general status in the Queen Elizabeth Islands are provided by Parker (1978), Gray (1987), and Pattie (1990).

b. Caribou

Caribou of the arctic archipelago (Rangifer tarandus and Rangifer tarandus pearyi) are smaller and generally more numerous than muskoxen. In terms of their general physiognomy and floristics, the habitats of these two species are quite similar and would appear to overlap considerably, although there is evidence of mutual exclusion in terms of geographic distribution and forage utilization (Kevan 1974; Parker & Ross 1976). Relative to the muskox, which is sedentary, caribou show a greater tendency for nomadism or migration to preferred habitats within and among the arctic islands (Freeman 1976; Miller 1990).

Archaeological evidence (sources in Riewe 1977) indicates that caribou were abundant and exploited by indigenous peoples several hundred years ago on the lowlands of north Devon Island, but declined following an increase in muskoxen and have now been missing there for several decades. Caribou continue to be an important resource to the Clyde Inuit of Baffin Island, where their distribution (as exploited by Inuit hunters) has been mapped in general by Wenzel (1991) and, in somewhat greater detail, by Riewe (1992). Habitat studies on other islands have shown that willow (Salix arctica) is the single most important food item for caribou, particularly in the summer, though the diet is supplemented with forbs, grasses and some sedges in the winter (Parker & Ross 1976; Parker 1978).

As with muskoxen, it is uncertain what the effects of various direct and indirect human impacts would be on arctic caribou populations, although there has been an often heated and continuing debate on this topic (Sage 1981; Murkowski 1991). Caribou feeding biology, productivity, conservation status, and distributions of populations and habitats are discussed further by Batzli et al. (1981), Gunn et al. (1981), White et al. (1981), and Bliss (1986).

c. Birds

Among arctic birds present at the study sites, greater snow geese (Chen caerulescens atlanticus) and rock ptarmigan (Lagopus mutus) are primary consumers and thus the most significant in terms of vegetation exploitation. Pattie (1977) noted that among the lowlands of north Devon Island, plant growth is more lush and bird densities are highest at Truelove. The Clyde Foreland has been noted as an 'arctic oasis', based primarily on its abundance of passerine birds, by Nettleship & Smith (1975). Both species are minimally exploited by Inuit for food (Riewe 1977). Salix arctica is the major food source of ptarmigan, which typically feed in rocky areas (Riewe 1977), while the seasonal geese prefer wet meadows where they selectively graze portions of the rhizomes of such species as Carex aquatilis var. stans, Arctagrostis latifolia, Dupontia fisheri (*sensu lato*) and Eriophorum spp. (Giroux et al. 1984). Evidence of feeding by ptarmigan was fairly strong on the Thule housepads at TL.

d. Others

Other regional grazers include hare (Lepus arcticus) and lemmings (Dicrostonyx groenlandicus). The former prefers Salix arctica as forage (Smith & Wang 1977), while the latter grazes a number of species including S. arctica, Saxifraga oppositifolia, Dryas integrifolia, Pedicularis spp. and various graminoids (Watson 1956; Fuller et al. 1977). As with geese and ptarmigan, hare and particularly lemmings can be locally important in terms of grazing effects on vegetation, soils and nutrient and animal population cycling (Batzli 1978; Miller 1978). Lemmings were found to graze selectively on housepads and adjacent trampled vegetation at CR. Hare grazed selectively on Thule housepads at TL, where lemmings grazed selectively not only on these same pads but in vehicle tracks as well. Arkay (1972) reported grazing within her study area at RB by hare, caterpillars (Byrdia groenlandica), and especially lemmings.

ii. Flora and vegetation

a. Clyde River

The vascular flora of CR (including cryptogams), as reported by Polunin (1948) and Porsild & Cody (1980), comprises a total of 59 taxa, of which 34 occur in the meadow and beach ridge stands sampled for this study. Totals for more inland sites are given by Hainault (1966; 61 taxa) for the south end of Inugsuin Fiord, Webber (1971; 78 taxa) for the Lewis Valley at the northwest end of the Barnes Ice Cap, and Dansereau (in Baird 1950; ≥100 taxa) for the head of Clyde Inlet. Dansereau notes that the flora at the latter site is relatively rich for this latitude and considers it to be largely the result of a strong climatic gradient existing between the more maritime coast and the more continental interior and that his collection area in particular was "a kind of oasis" (see Baird 1952: 274).

According to more formal regional syntheses, even slight differences in 'summer warmth' are apparently crucial in terms of delimiting gross distributions of certain plants and growth forms (Young 1971; Edlund 1990).

The Clyde area is variously classified biogeographically by several different authors and, in floristic terms, is probably best considered a transition zone between the rich low arctic zone found on portions of south Baffin Island and the high arctic zone of the northeastern archipelago (Young 1971).

Among coastal sites on eastern Baffin Island, the Clyde foreland is relatively cool. This may possibly be attributed to the ice in Patricia Bay, which breaks up several weeks later than that in the main fiord, and to the frequent fogs that occur along the foreland and inland only as far as the contemporary settlement and the study site at 'akiani' (the other side). Ice breaks up much earlier around Pond Inlet and Bylot Island to the north and Broughton Island to the south and the more maritime influence would appear to be reflected in the sizes of their floras, these being ca. 100, 101 and 93 taxa respectively (Polunin 1948; Drury 1962; Porsild & Cody 1980; Hines & Moore 1988).

A total of 51 bryophytes (including 5 hepatics) and 12 lichens occurred in the sampled stands at CR. As with vascular plants, these figures do not reflect the total flora of the study area for either life form. A coastal-interior gradient of species richness among lichens, similar to that discussed above for the regional vascular flora, is reported by Hale (in Baird 1952). A more complete bryophyte flora for the general region is detailed and discussed by Steere (1948).

The vegetation of the area around CR have been described by Polunin (1948). Of interest are his observations (p. 104-105) that "phanerogamic vegetation is noticeably poorer on most north- and east- (toward the sea) facing slopes than on those having a southerly or westerly aspect, at least when other habitat conditions are similar . . . when the incline is slight and water plentiful, what is probably the most luxuriant vegetation of the immediate vicinity tends to be developed. Thus the vegetation is closed and often quite luxuriant".

The meadow communities surveyed, generally poor in species, are representative of those found along coastal lowlands of northeast Baffin Island where surface moisture is available throughout most or all of the growing season. These lowlands all lie within the 'High Arctic Wetland Region' designated by the National Wetlands Working Group (Tarnocai & Zoltai 1988). Zonation of vegetation is evident within the predominant hummock-hollow complex, where hummock tops are dominated, in terms of cover, by Salix arctica, with lesser amounts of Dryas integrifolia, Cassiope tetragona, Luzula spp. and Potentilla fruticosa. A small cluster or mat of common fruticose and crustose lichens (Alectoria, Thamnolia, and Cladonia spp., etc.) typically adorns the drier hummocks. The hummocks themselves are largely comprised of the peat mosses Sphagnum squarrosum and S. capillifolium var. tenellum, with significant but lesser amounts of Aulacomnium turgidum, Pogonatum and Polytrichum spp.

Hollows are characterized by the rhizomatous graminoids Carex aquatilis var. stans and Eriophorum angustifolium, with lesser amounts of Juncus biglumis. Mosses abundant in the hollows are typically Calliergon sarmentosum, Drepanocladus revolvens and Meesia uliginosa, with some Aulacomnium palustre and Bryum pseudotriquetrum. The foliose lichen Peltigera aphthosa is common on the sides of hummocks and in the more mesic hollows. One of the stands sampled occurs on and around a beach ridge which serves to impound surface moisture in the adjacent wet meadow behind. Hummocks are generally lacking here and the undisturbed sward is comprised of Dupontia fisheri ssp. psilosantha and C. aquatilis var. stans. Mosses are similar to the 'hollow' species, while lichens are lacking.

b. Truelove Lowland and Resolute Bay

The total vascular flora of Truelove Inlet is reported by Barrett & Teeri (1973) to be 98 taxa, of which 40 occur in the stands among meadows and beach ridges sampled for this study. The flora is quite rich for its latitude and in comparison to other lowlands in the Queen Elizabeth Islands (Muc 1977; Henry 1987). The floras of the sedge-meadows at TL and CR are quite similar, differing in the presence of a few minor forbs, such as Saxifraga hirculus and Pedicularis sudetica, both lacking at CR. Of greater significance is the presence of Calliergon giganteum and Meesia triquetra within the bryoflora of TL, indicating that its soils are more alkaline than those around CR, where Calliergon sarmentosum and Sphagnum spp. are present in abundance. Of the 134 taxa listed for the byroflora of TL by Vitt (1977), 52 occur in the sampled stands in addition to 8 hepatics and 14 lichens, only one of which (Peltigera aphthosa) is present within the meadow stands. The beach ridge flora sampled at RB is essentially a depauperate version of the TL beach ridge flora, containing only 10 vascular taxa, 7 mosses and 6 lichens. A key difference between the study sites at TL and RB is the generally calcareous nature of the substrate resulting in surface waters and mineral soils with a pH that ranges from circumneutral to mildy alkaline. Indeed, much of the bryoflora is comprised of species which are indicative of minerotrophic fens.

As with CR, the study site at TL lies within the High Arctic Wetland Region (Tarnocai & Zoltai 1988). The tundra stands sampled are within the hummocky and wet meadows described and mapped by Muc (1977) (**see Map enclosure B**). As mentioned earlier, these meadows have mostly gentle (<2°) slopes, remain wetter longer into the growing season, and have smaller hummocks than those at CR. The latter may be attributed to both the lack of slope and the effects of moderate grazing by muskoxen (Henry 1992). As a result, the degree of coverage and biomass by deciduous and evergreen shrubs, such as Dryas, Cassiope, and Salix spp., is greatly reduced relative to CR. At the same time, the amount of aquatic sedges (Carex aquatilis var. stans, Eriophorum angustifolium), grasses (Dupontia fisheri ssp. psilosantha) and mosses (Meesia, Drepanocladus, Calliergon spp.) is increased. Other stands at RB and TL occur in polar desert and semi-desert vegetation types on dry, cobbly beach ridges of the kind described respectively by Arkay (1972) and Svoboda (1977). Vegetation has been mapped at large scale at TL (**Map enclosure B**) and at RB (by Arkay 1972). The sampled stands at TL were similar to Svoboda's semi-desert, but with lesser amounts of Dryas integrifolia. Vascular cover was ca. 20% and included mainly Salix arctica, Saxifraga oppositifolia, and Carex spp., with scattered forbs. Lichen cover was generally extensive, with Lecanora epibryon and Rhizocarpon geographicum providing the greatest cover. Common moss genera included Bryum, Distichium, Ditrichum, Encalypta, Mnium, and Myurella (Steere 1951; Vitt & Pakarinen 1977).

2.3 FIELD WORK SCHEDULE

Preliminary site reconnaissance and consultation with the Hamlet Council took place in Clyde River in early August 1987. Field work took place in Clyde River from: 27 May to 1 September 1988; 26 May to 14 July and 7 to 31 August 1989; 7 June to 21 July and 14 to 28 August 1990. Field work took place at Truelove Lowland from 21 July to 2 August 1989 and 24 July to 10 August 1990. Sampling of flora and vegetation in Resolute Bay took place 11 August 1990.

2.4 MATERIALS AND METHODS - Clyde River (CR), Truelove Lowland (TL), and Resolute Bay (RB)

i. Phenology

Observations were made for each species at CR on the date of first flowering, peak flowering, last flower observed, first fruiting, and seed release (if any was observed). These observations were made through the entire growing season in 1988 and as time allowed in '89 and '90.

ii. Temperature/precipitation

A small Stevenson's screen was used to house a Taylor min/max thermometer mounted at 4' (1.2 m) above the ground and to record ambient diurnal temperature at the study site. A Taylor rain gauge was mounted nearby in the same place each year and checked regularly. Comparative data were obtained from the Atmospheric Environment Service Station at the Clyde River airport. Seasonal climate records for TL were obtained from the Arctic Institute of North America, except for maximum air temperature in 1990, which was unavailable. Climate data for RB was obtained from AES and the literature.

iii. Vegetation survey.

During the 1989 and 1990 field seasons 20 x 20 m stands (**see Map enclosure A**) were subjectively placed in areas representing: (1) the predominant vegetation cover types; and (2) an array of distinct disturbance

TABLE 2.1

Disturbance and site characteristics*, Clyde River, Baffin Island, Truelove Lowland, Devon Island, and Resolute Bay, Cornwallis Island.

Stand No.	Stand label	Study Site	Activity ceased	Vehicle(s) utilized	Local slope	Orientation of tracks to slope
1	SPM 1	CR	ca. 1969	Case	5.0°	Diagonal
2	SPI 1	CR	ca. 1969	Case	4.5°	Diagonal
3	SPI 2	CR	ca. 1972	Case	1.0°	Parallel
4	SPI 3	CR	ca. 1972	Case	0.5°	Parallel
7	HP 'B' 1	CR	ca. 1969	na	2.0°	na
9	MPM 1	CR	ca. 1969	Case	4.0°	Parallel
10	MPM 2	CR	ca. 1969	Case	3.0°	Parallel
11	MP WC	CR	ca. 1972	Case	4.0°	Perpendicular
12	MP Interfluve	CR	ca. 1972	Case	3.0°	Perpendicular
13	SPM 2	CR	ca. 1969	Case	4.5°	Perpendicular
14	HP 'B' 2	CR	ca. 1969	na	2.0°	na
15	SP Interfluve	CR	ca. 1969	Case	3.0°	Perpendicular
16	SP WC	CR	ca. 1969	Case	3.0°	Diagonal
17	ChemDump	CR	ca. 1969	na	4.0°	na
18	HP 'A'	CR	ca. 1969	na	3.0°	na
19	HP 'C'	CR	ca. 1969	na	1.0°	na
1	MP Imp	TL	≤ 1971	MF/BW	0	na
2	FP Imp	TL	≤ 1971	MF/BW	0	na
3	SP Imp	TL	≤ 1971	MF/BW	1.0°	Parallel
4	MPM 1	TL	≤ 1971	MF/BW	1.0°	Parallel
5	MPM 2	TL	≤ 1971	MF/BW	1.0°	Perpendicular
6	MPM 3	TL	≤ 1971	MF/BW	0.5°	Perpendicular
7	MP Imp	TL	≤ 1971	MF/BW	0	na
8	MPM '86	TL	1986	AR	1.0°	Parallel
9	MPI '86	TL	1986	AR	0	na
10	FP Imp	TL	≤ 1971	MF/BW	2.0	Parellel
11	MPW Restore	TL	1972	MF/BW	0	na
12	MPW Restore	TL	1972	MF/BW	0	na
13	MP Wet	TL	≤ 1971	MF/BW	0	na
14	Thule Restore	TL	1986	na	3.0	na
15	Thule pad 1	TL	ca.1200	na	3.0	na
16	Thule pad 2	TL	ca.1200	na	1.0	na
1	Thule pad 3	RB	ca.1000	na	0.5	na

*Label abbreviations are: SP=Single-pass; FP=Few passes; MP= Multi-pass; each is followed by a habitat characterization: WC=Water channel; M=Mesic; Imp or I=Imperfectly drained. W=Wet. Some 'wet' and 'interfluve' sites at are labelled in full. HP=Contemporary housepad and adjacent trampled terrain followed by type designation (A, B, C). Trampling intensities are indicated in Chap. III. Study sites are abbreviated 'CR' for Clyde River, 'TL' for Truelove Lowland, and 'RB' for Resolute Bay. Vehicles are abbreviated as: MF=Massey-Ferguson '65' tractor; BW= Bombardier 'Weasel'; AR=Arnold 'Ranger'; Case=J.I. Case 1000D excavator. Most vehicle use at TL occurred during the summer. Single-pass tracks at CR were initiated during the summer, while multi-pass tracks were used on a year round basis. Drained peatlands occur downslope from many tracks which run perpendicular to local slope.

Table 2.2a. Original cover scale of Braun-Blanquet (1932), extended to a combined cover/abundance scale by Barkman et al. (1964) and then recoded by van der Maarel (1979).

Braun-Blanquet		Barkman		van der Maarel's scale
Symbol	Cover (%)	Symbol or Abundance	Cover (%)	
		r	rare	1
		+	few	2
1	<5%	1	many	3
		2m	abundant	4
2	5-25%	2a	5-12.5%	5
		2b	12.5-25%	6
3	25-50%	3		7
4	50-75%	4		8
5	>75%	5		9

Table 2.2b. Sociability classes (from Braun-Blanquet 1932)

Sociability	1 - growing once in a place, singly
"	2 - grouped or tufted
"	3 - in troops, small patches or cushions
"	4 - in small colonies, in extensive patches or forming carpets
"	5 - in great crowds or pure populations

regimes. Except for one beach ridge stand, the former are all variants on the oligotrophic and mildy acidic peat-dominated meadows which characterize the 'well-developed' vegetation described for the area by Polunin (1948). The latter include housepads (3 types) in five sites, single-pass vehicle tracks in five sites, and multiple-pass vehicle tracks in four sites (**Table 2.1**).

The general locations of stands to be sampled were carefully chosen according to two main criteria: (1) the nature and level of disturbance; and (2) the relative 'homogeneity' (*sensu* Braun-Blanquet 1932: 39) of the adjacent undisturbed vegetation. The large size (20 x 20 m) of the undisturbed stands exceeds that employed by other tundra classification schemes (Komárková & McKendrick 1988), but was chosen to allow for sampling a minimal area (*sensu* Barkman 1989a) of disturbed vegetation within the tracks. Vegetation sampling methods followed Westhoff & van der Maarel (1978) with the following modifications: (1) vascular vegetation cover was estimated in the field to the nearest 1% and later transformed according to van der Maarel (1979) prior to multivariate analyses (**Table 2.2a**); (2) non-vascular taxa were ranked in the field according to sociability (**Table 2.2b, Appendices 5-8**). Visible surface disturbance was mapped at large scale (1:200). The location of each sample stand was noted on an enlarged B/W aerial photograph of the entire study site. Some sites still had snow cover over portions of them at the start of the field season, in which case depth was measured, the general aspect photographed and date of final emergence noted. Additional photos recorded the general aspect of each site, the nature of disturbance and soil profiles.

Four to eight quadrats were sampled in each disturbed and undisturbed or 'natural' stand portion in 1989 at CR and TL, for a total of eight to sixteen quadrats per stand. At first a number of 'complete, permanent' samples - including all phytosociological data - were taken, after which the frame was flipped over and an equal number of 'temporary' quadrats were double-sampled for vascular composition and cover prior to clipping vascular biomass. In 1990 the number of quadrats was kept at 10 per stand (five disturbed and five natural) based on analysis of the 1989 data. In general, the results of this method are strongly influenced by the species richness of the spot where the smallest plot or quadrat is located, as well as within strata (i.e. vascular vs. non-vascular), which is more variable in hummocky than wet sedge meadows.

Although the quadrats were of a size which invariably included a portion of a given hummock and its adjacent hollow, where these were present, notes were kept on whether the majority of the sample (>50%) was classified as hummock or hollow. In the end, the split at CR was about even with only slightly more hollow-dominated samples being included (ca. 52.0%), the effects of which on the overall vegetation analysis are not considered significant. At TL, the floristic and microtopographic variation between hummocks and hollows in the stands surveyed was much less pronounced by comparison with CR. In more hydric stands at both study sites, and under most disturbance regimes, this variation was lacking.

Vascular species cover and composition were determined using 25 x 50 cm quadrats divided into fifty 5 x 5 cm portions. This size was recommended for these purposes, as well as standing crop measurement, by Wein & Rencz (1976) and proved adequate under a nested sample test (Mueller-Dombois & Ellenberg 1974). Within each of these a smaller (10 x 10 cm) quadrat was used to determine presence/absence and 'sociability' (Table 2.2b) of bryophytes within the non-vascular stratum. If no hummock/hollow designation was appropriate, bryophytes were sampled randomly within the entire larger quadrat. Presence/absence of saxicolous lichens was recorded in beach ridge quadrats and stands but not within meadows. Epigeic lichens were uncommon in most meadow stands, but presence/absence was recorded wherever they occurred according to the criteria discussed below for rare species.

The quadrats were placed, according to random grid numbers, in undisturbed vegetation adjacent to vehicle tracks. Individual random numbers were used for placement of quadrats along a single tape within the tracks. This procedure was modified slightly where peatland drainage was a factor to allow for the random placement of transects perpendicular to local slope. Quadrats were then placed at random distances (in cm) perpendicular to the tape at distances of 2 and 10 m above and below the tracks and, in one case, on the berm between two single-pass tracks. For housepads (**see Map enclosure A**), a compass was laid in the apparent center of each pad and used as the datum from which to extend five 30 m transects (tapes). This distance was chosen so that the transects would extend into what was judged to be relatively undisturbed terrain, based on interpretation of enlarged airphotos and interviews. A table of random numbers was used to orient (among a possible 360°) each transect and then again at 5 m intervals to position the quadrats at random distances (in cm) perpendicular to the tape. For the chemical dump site, a similar datum was placed at the edge of the old weather station (**see Map enclosure A**) and perpendicular transects were randomly located within five 20 m intervals extending downslope toward the shore. The ends of these transects were considered to be in similarly assessed relatively undisturbed vegetation and the actual quadrats placed at random distances (in cm) perpendicular to the transect.

Height measurements were taken systematically at 15 points within each quadrat and notes were made on the presence/absence of above and/or below ground runners (stolons and/or rhizomes). Inflorescence counts were made within each quadrat for dominant graminoids. Rare species which were present within a stand but not within a quadrat were recorded in the manner of Barkman et al. (1964) such that 'r' (rare) signified one or a few individuals and '+' signified occasionals with less than 5% visual cover-abundance (**Table 2.2a**). Taxa occuring only outside the quadrat (but within the stand) were noted in parentheses. In addition to cover, estimates of sociability were made based on the the degree of gregariousness of each vascular species (**Table 2.2b**). According to Braun-Blanquet (1932:37), this 5-ranked measure is an important indicator during the course of succession, and is especially desirable where species occur in groups or colonies, as many plants do in both disturbed and undisturbed tundra meadows. Bryophytes were similarly ranked and total bryophyte cover was recorded (in addition to litter, standing water and bare ground or rock). In this manner, 250 quadrats comprising 19 stands were surveyed and mapped at CR (**see Map enclosure A**), 132 quadrats comprising 16 stands at TL (**see Map enclosure B**), and 10 quadrats comprising one stand at RB.

Two corners of each quadrat were marked using 18" x 3/8" wooden stakes, unpainted except for orange flashes at the tip and labelled with embossed plastic 'Dymo' tape appended with heavy duty staples. These were almost completely embedded at the end of the study and are intended to serve as 'permanent' markers for the quadrats. While heaving may occur over time in some places, this was not observed during the course of the study. A small problem in 1988 had been removal of a few obviously protruding stakes by young children, but this had virtually ceased by 1989. Other than this brief and inconsequential disruption, most surface disturbance by Inuit within the study site was limited to camping along the unvegetated beach and occasional harvesting of Cassiope tetragona, both activities occurring well away from the sample stands. Children occasionally catch lemmings within the study area, but with little apparent impact.

iv. Disturbance survey

The nature, degree and frequency of animal activity (including humans) was estimated for each quadrat. Animal activity was gauged according to type (i.e. lemming or ptarmigan) and relative ground cover of feces or nesting materials, and whether this pattern was repeated in successive years. At CR, a chronology of past human activity for each of the disturbance types listed above was assembled based upon: (1) interpretation of a series of archival vertical and oblique airphotos (range 1:5000 to 1:10000) covering the period from 1960 to 1989 **(Plates 2.7 to 2.14; Appendix 9)**, from all of which enlargements were made; (2) a local land use map (1:1200; **Map enclosure A**) from the period 1960-69 detailing the locations of major footpaths as well dates and locations of housing construction during the peak years of human settlement. The 1969 airphoto, depicting the absolute peak of settlement, was enlarged to match the scale of this land use map; (3) interviews with Inuit residents; and (4) *in situ* investigations.

For impacts other than single-pass vehicle tracks, levels of disturbance were estimated and ranked (e.g. light, moderate, and heavy trampling) based on a synthesis of information derived from these sources **(Table 2.1 and Chap. III)**. Hydrological changes from both single- and and multi-pass vehicles, as well as surface disturbances such as trampling and chemical dumping, have apparently affected local surface albedo. To estimate these effects, tonal variation within enlarged B/W airphotos was analyzed with a Macbeth™

Plate 2.8 - Vertical aerial view of old settlement at CR showing the original Hudson's Bay Post with associated government buildings. Note white toxic plumes extending downslope from the hydrogen generator and weather station buildings. There is also a black plume from leaking drums containing used oil, indicated by arrow at left. Arrow at center points to beginnings of foundation for DNA teacher's residence. Arrow at top points to dump, to which trash was hauled by hand or on sleds. Note the relative lack of vehicle tracks (a few are seen along the shore to the left of the settlement), and the undisturbed nature of the terrain and hydrology to the right of the settlement. Scale = 1:5000. Photo date: 21 July 1960.

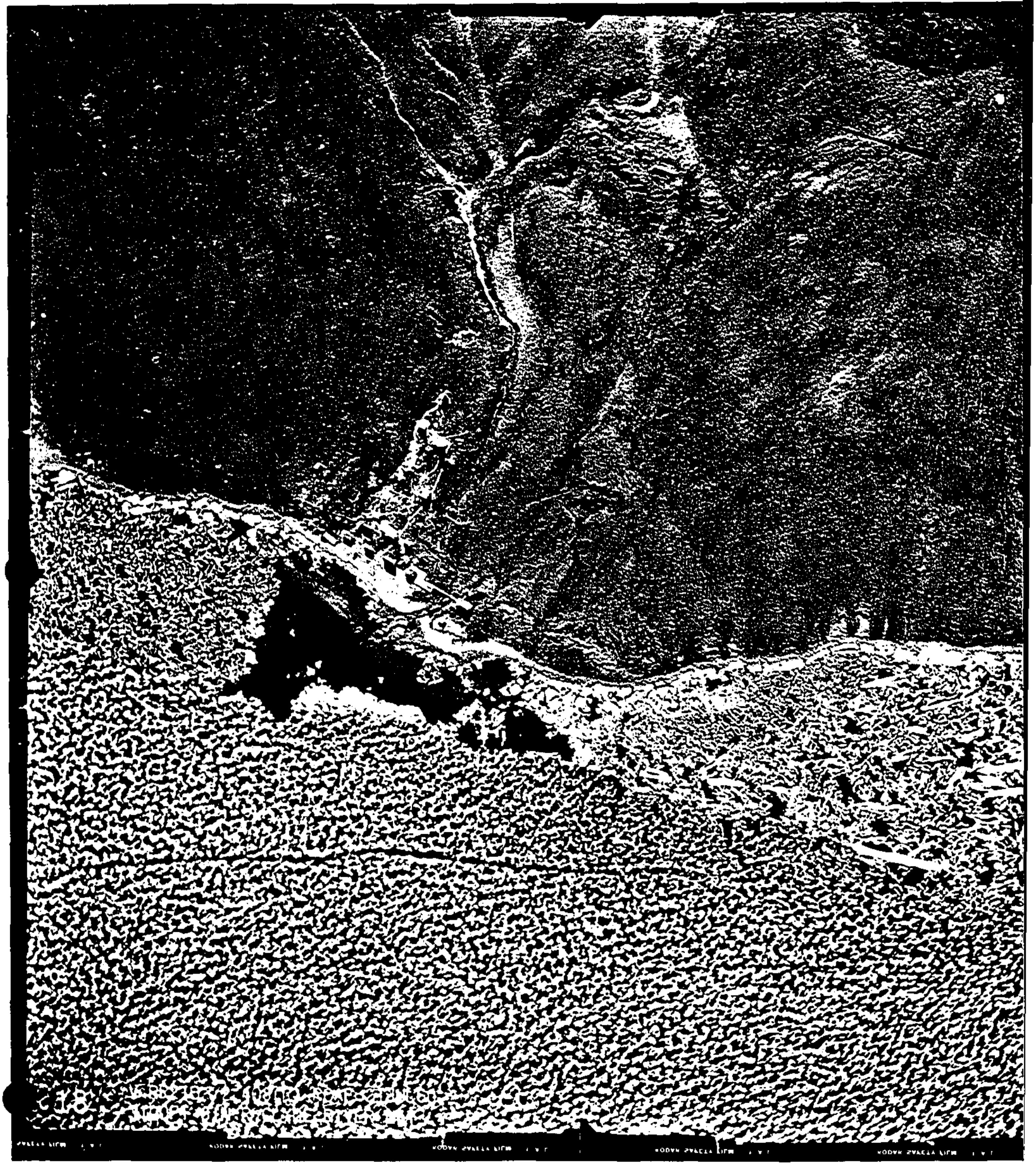


Plate 2.9 - Vertical aerial view of old settlement at CR during the peak of settlement and just prior to the dismantling of Inuit residences, most of which were built between 1962 and 1966 (**see Map enclosure A**). Note the expansion of the settlement into the previously undisturbed area seen in the previous plate, mostly Inuit housing and governnment buildings, plus an Anglican mission house. There are numerous changes in hydrology and surface albedo evident and the toxic plume from the weather station has expanded considerably. Trash had been hauled to the dump by tracked vehicle since 1965 and its tracks are visible over much of the terrain. Bare mineral soils are exposed due to trampling, increasing reflectance in the immediate vicinity of many of the Inuit houses. A bit further away the organic layer is trampled, but intact, and its albedo has decreased considerably relative to to undisturbed terrain nearby. Water channels are clearly visible to the left of the settlement. Arrows indicate where multi- (left) and single-pass tracks (right) have diverted runoff from snowmelt and increased surface albedo downslope. The generally wet tundra led to the construction of raised boardwalks, seen running between Inuit residences and government buildings. It was the lack of additional dry building sites that ultimately led to the relocation of the settlement to a drier area on the other side of the bay. Scale = 1:6000. Photo date: 9 August 1969.

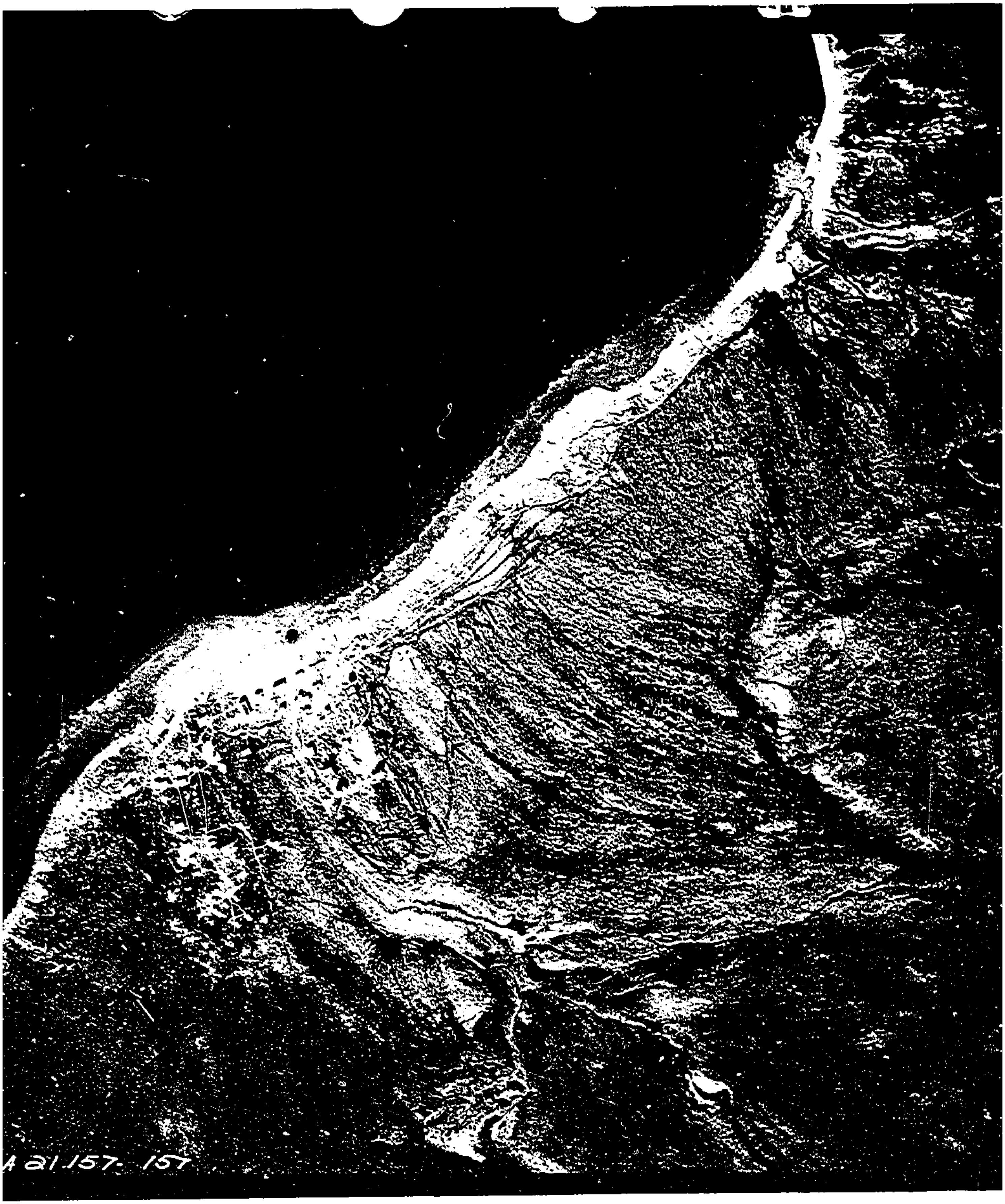

A a1.157- 157

Plate 2.10 - Vertical aerial view of old settlement at CR after the relocation of the Inuit residences and most of the HBC and government buildings. Vegetation regrowth has begun to mask some of the original scars, but many bare spots remain on and around abandoned housepads. Large arrow points to a single-pass vehicle track which ran diagonal to local slope in an area which drains a number of late-lying snowbeds (see **Plates 2.4, 3.4 and 3.8**) and resulted in serious fluvial erosion. Subsidence from thermal erosion, however, was minimal. All stands are labelled, with the exception of Stands 6 and 8, which were superseded by Stands 18 and 19, respectively. Scale = 1:6000. Photo date: 8 July 1973.

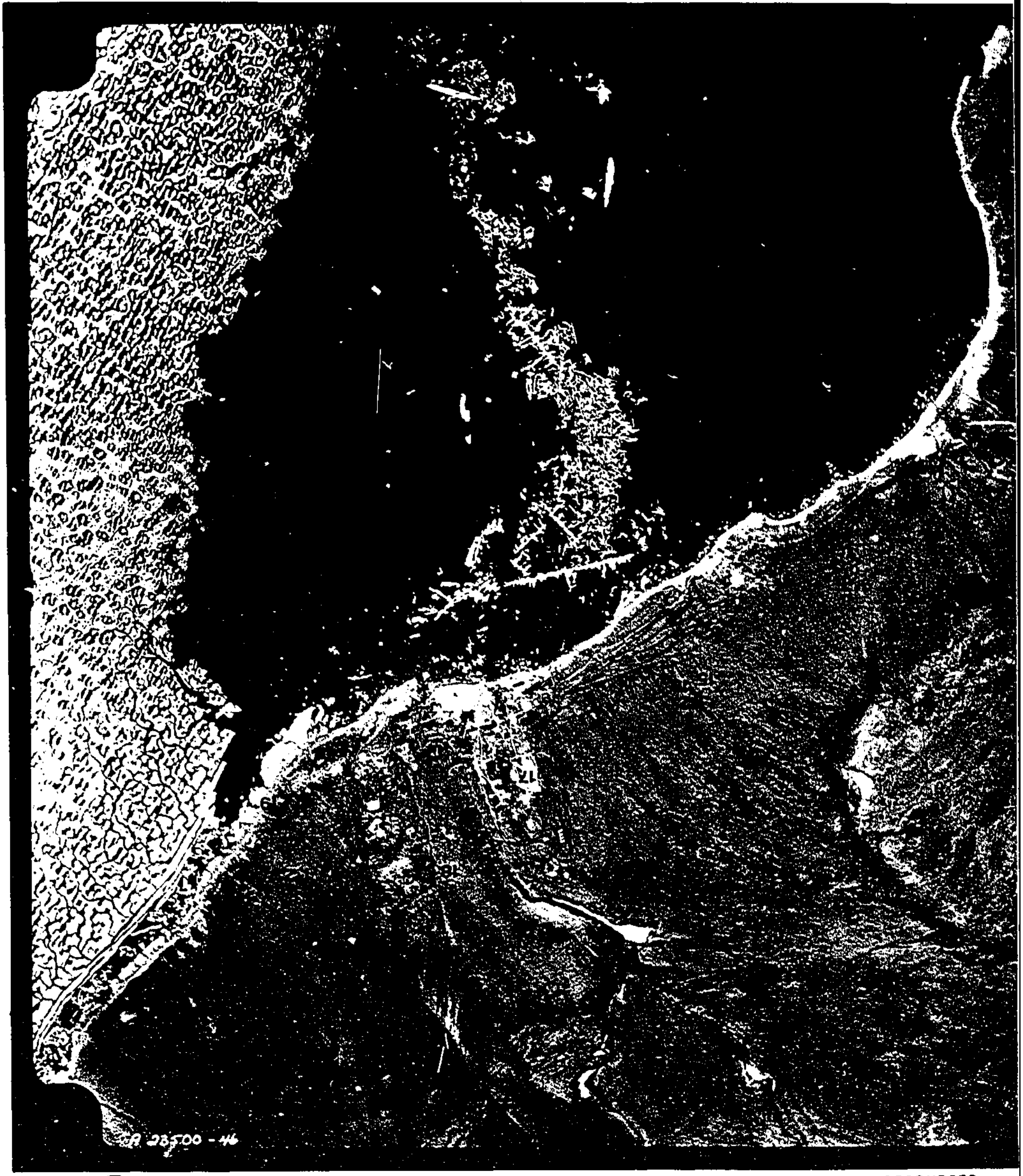

A 23500 - 46

Plate 2.11 - Oblique aerial view of northern portion of study area at CR showing single- and multi-pass tracks which once comprised the 'road' to Cape Christian and, later, the new settlement. Natural hydrological patterns can be seen upslope from the uppermost set of tracks, where vegetation has a greener hue. Large gully at lower right has formed from the channelling of surface runoff and is a sizable stream during snowmelt. Houseframe at center was abandoned during relocation. During summer some Inuit still camp along the beach and occasionally use trucks and ATC's along the the track closest to the shore. The uppermost multi-pass track was last used summer 1973 and vertical airphotos show many of the single-pass tracks to be older. Photo date: 23 August 1989.

Plate 2.12 - Oblique aerial view of abandoned HBC/Government compound at CR showing plumes of used oil from leaky drums and aluminum oxides from the weather station. Fuel tanks and the old dump are at rear. The main set of tracks leading to dump follows the gulch at right, which is a river during snowmelt but runs virtually dry by late August. Photo date: 23 August 1989.

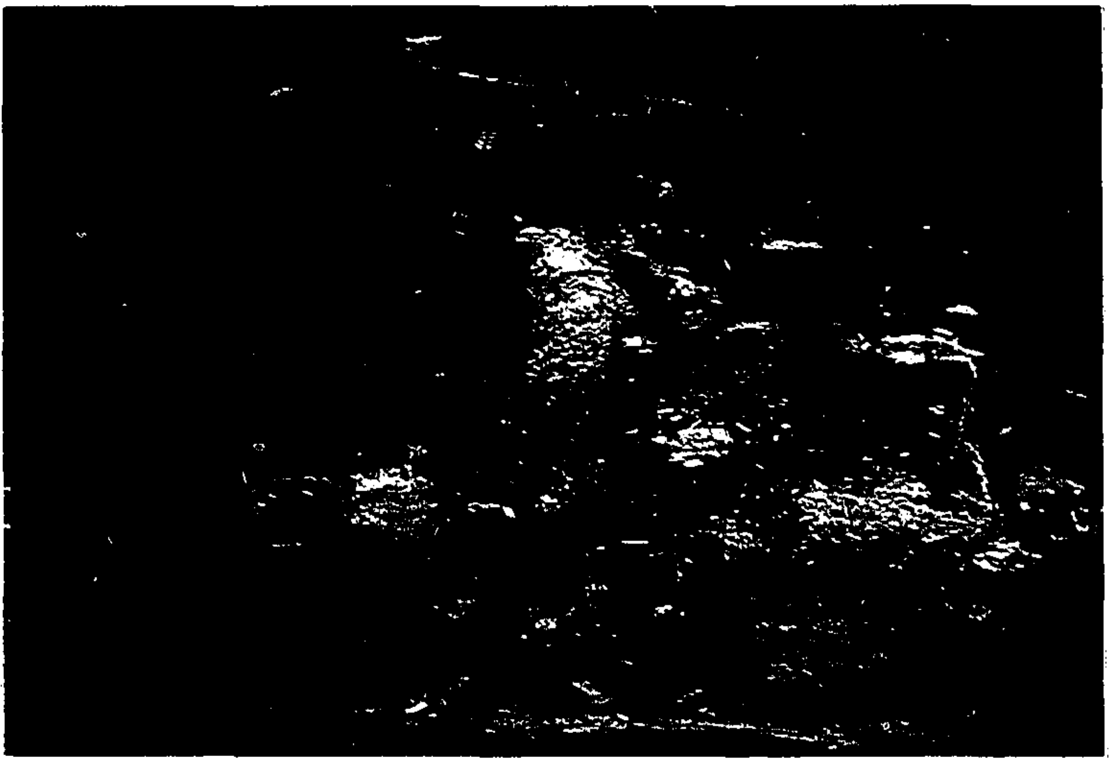
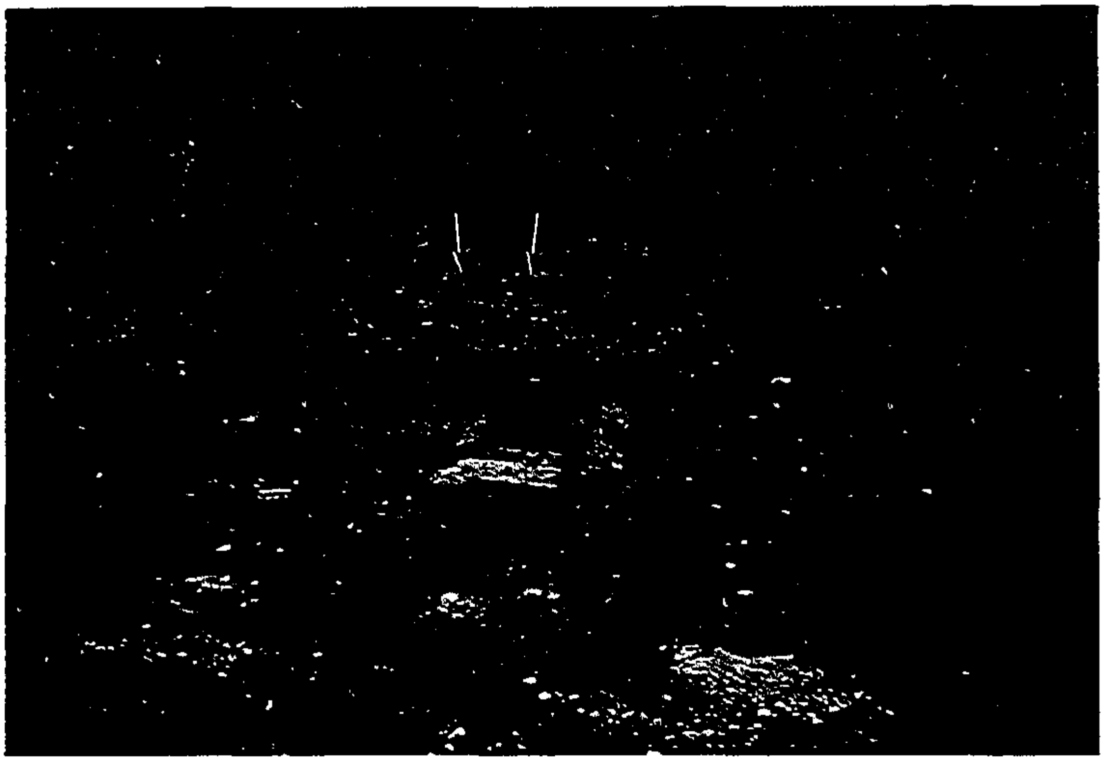


Plate 2.13 - Oblique aerial view of central portion of the study area at CR showing former foundations from Government buildings (foreground) and Inuit residences (background). Vegetation in this section is turfy and of a different hue than adjacent untrampled areas. Alopecurus alpinus and Poa arctica are abundant in the vascular canopy and the amount of dead standing tissue is fairly high, despite evidence of moderate to intense grazing by lemmings. The grasses and dead tissue contribute to the lighter hue of the vegetation, visible also in the 1983 photo (**Plate 2.7**). Cryptogamic layer is dominated by Aulacomnium spp. and Bryum spp., which have replaces much of the former cover of Sphagnum spp. Arrows point to the greenest patches (**see also Plate 1.13**), which comprise housepads for which no materials (i.e. sand/gravel) were added and, especially, adjacent heavily trampled ground. These patches are where lemming activity is most intense, as gauged by evidence of nesting and grazing, and have the lowest amounts of dead standing crop and litter. A preliminary clean-up effort targeting old fuel drum was completed just prior to this photo and drums that were previously scattered about are seen here in neat stacks. Immediately after the photo was taken the drums were moved to the new dump on the other side of the bay. Note single-pass track and erosional plume at rear. Photo date: 23 August 1989.

Plate 2.14 - Oblique aerial view of southern portion of the study area at CR showing former dumping site for Inuit, where trash was hauled by hand and by tracked vehicle. Dark areas at center indicate where fuel drums were scattered until the clean-up. Relatively few multi-pass tracks exist in this area, which is instead a maze of single-pass tracks as seen in the 1969 airphoto (**Plate 2.9**). Many of the deeper ruts are still visible here. Photo date: 23 August 1989.



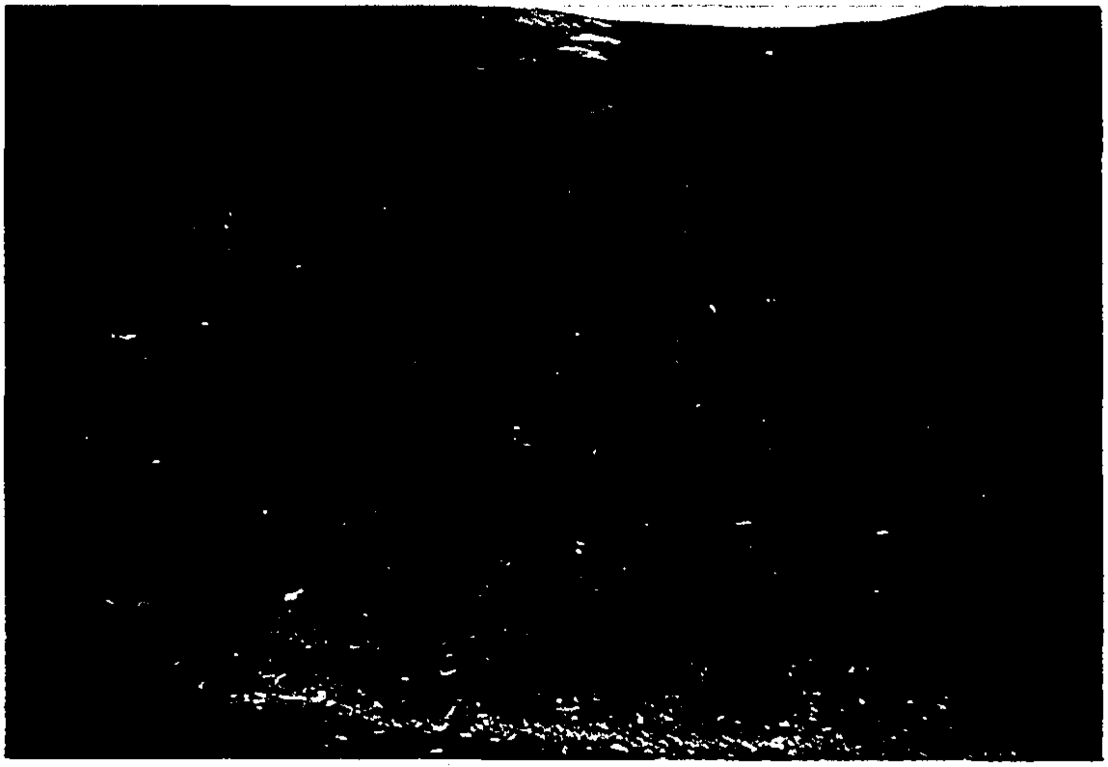
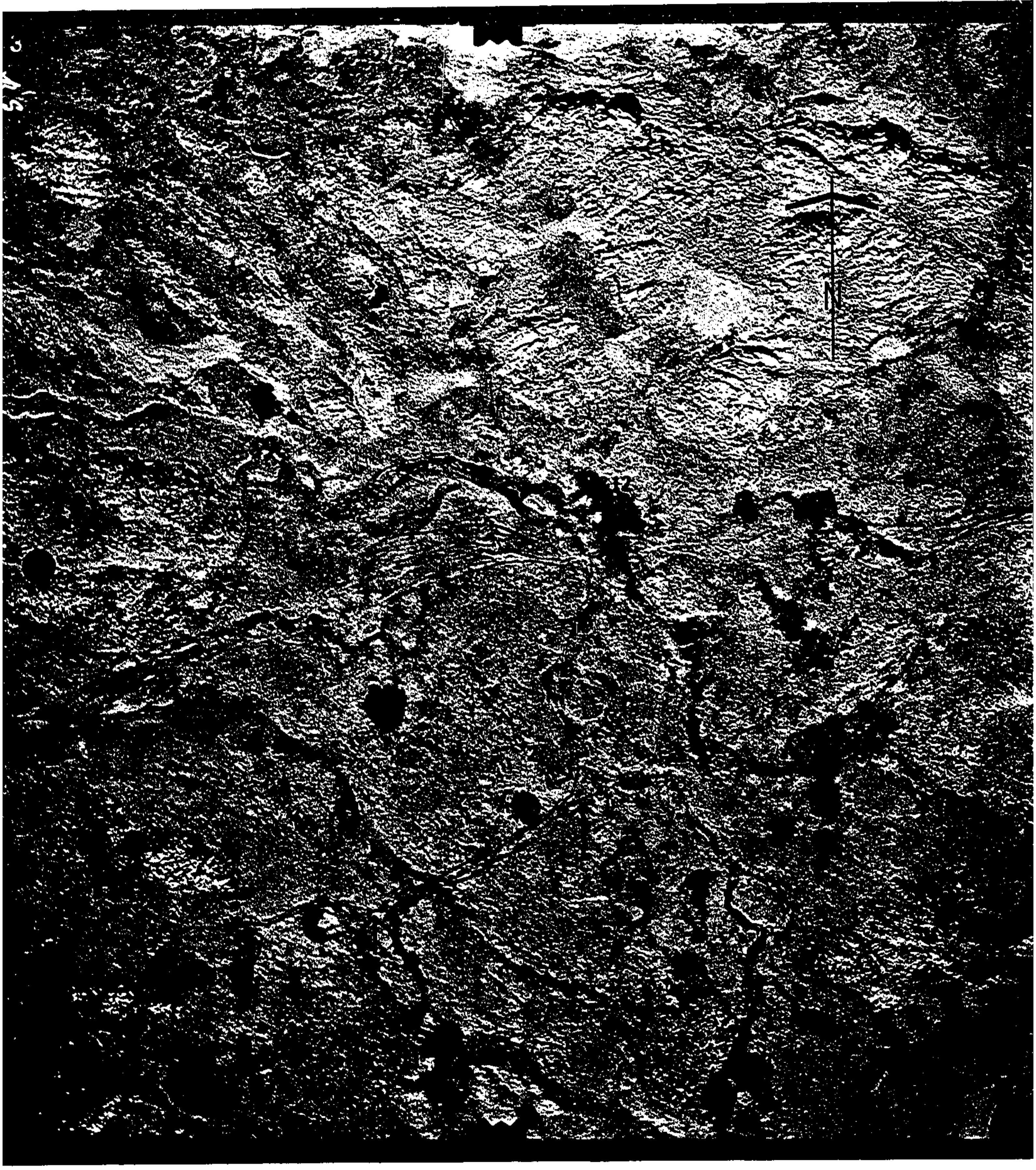


Plate 2.15 - Vertical aerial view of portion of the study area at TL showing vehicle tracks and locations of Stands 1, 2, 7, 11 and 12 (**see also Map enclosure B**). Stands 11 and 12 comprise sites of attempted restoration using sod plugs by Barrett (1975). Photo date: 18 August 1971.



N

Plate 2.16 - Vertical aerial view of portion of the study area at TL showing vehicle tracks and locations of Stands 3, 4, 5 and 6 near the north shore of Swamp Lake. Photo date: 18 August 1971.

Plate 2.17 - Vertical aerial view of portion of the study area at TL showing vehicle tracks and locations of Stands 8, 9 and 13. Photo date: 18 August 1971.

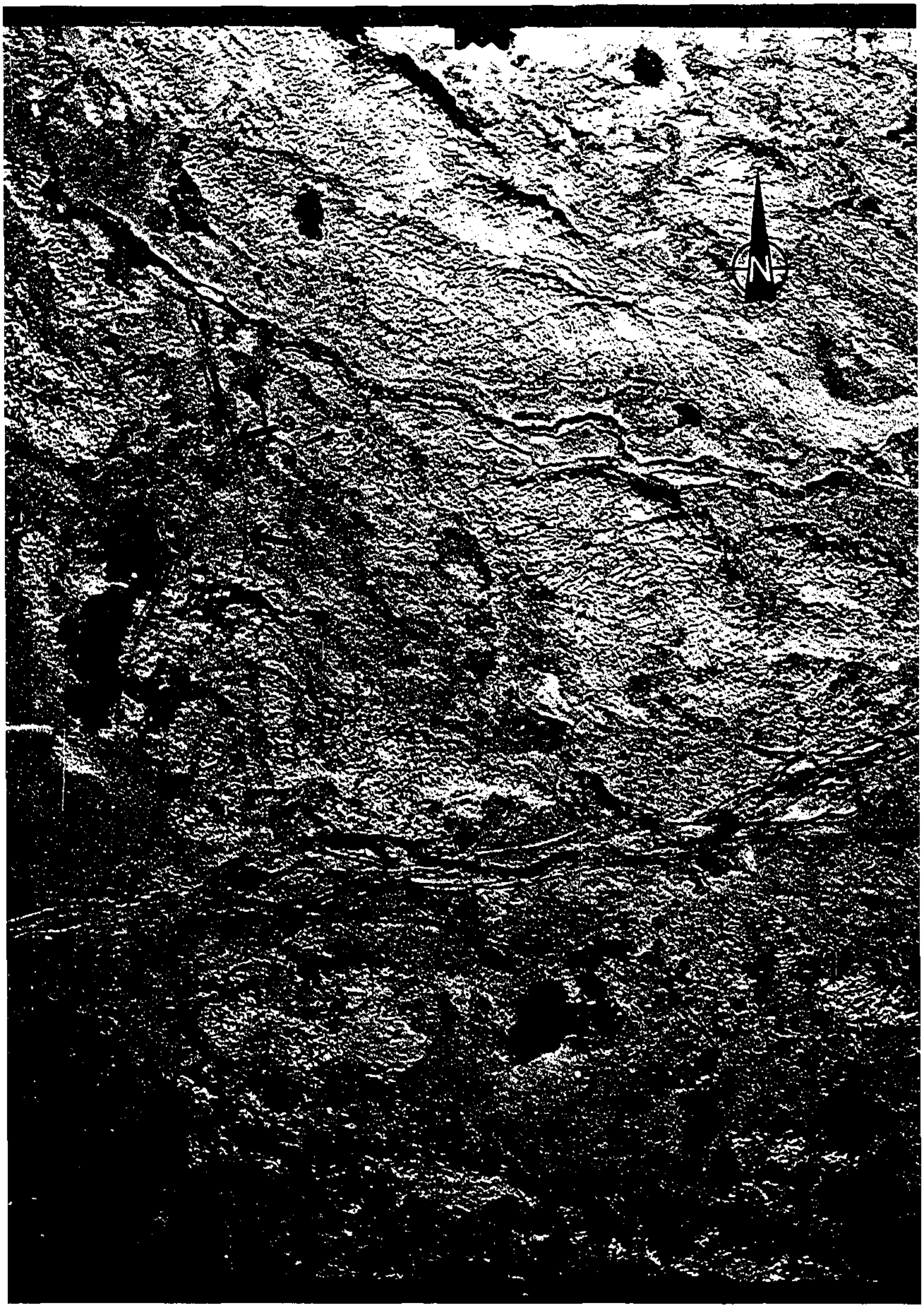

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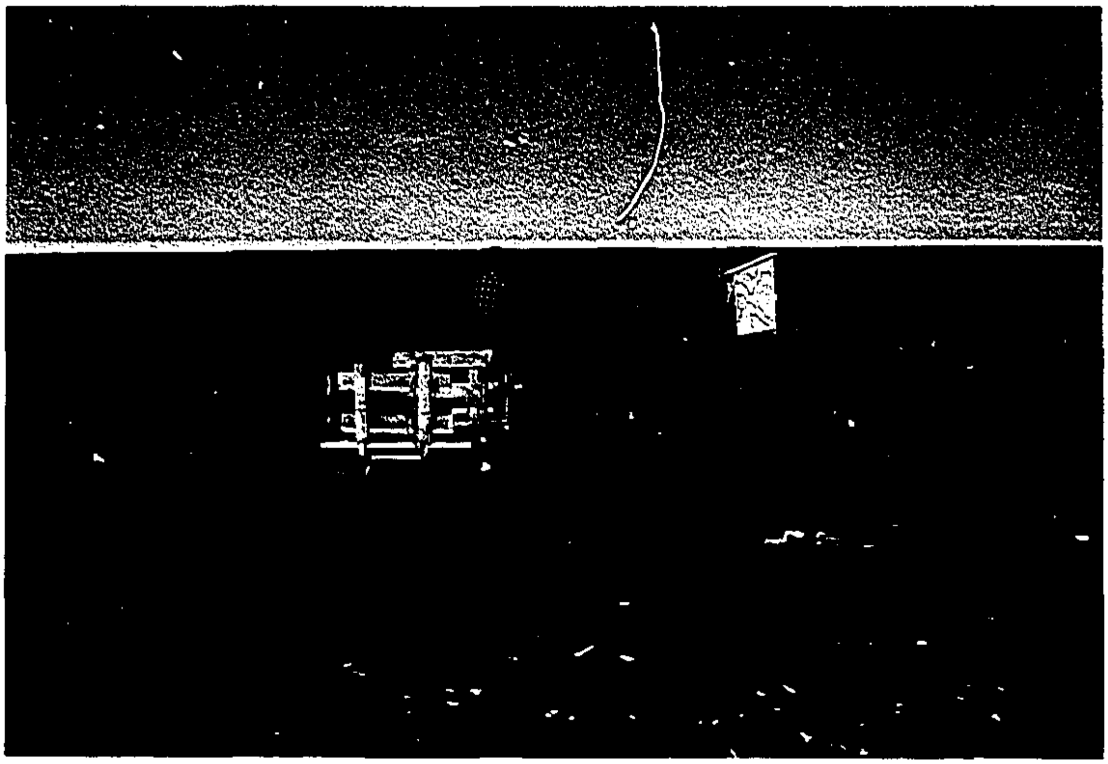
Plate 2.18 - Vertical aerial view of portion of the study area at TL showing vehicle tracks and location of Stand 10. Photo date: 18 August 1971.

Plate 2.19 - Vertical aerial view of portion of the study area at TL showing Thule winter dwellings on the north shore (Bear Bay) and locations of Stands 14, 15 and 16. Photo date: 18 August 1971.


N
16

Plate 2.20 - Lightweight tracked vehicle (Arnold 'Ranger') in use on beach ridge near base camp at TL. A trailer capable of carrying six fuel drums was used with this vehicle during clean-up of the northern beaches, most recently in summer 1986. Photo date: 24 July 1989.



'QuantaLog' RD-400 Reflection Densitometer, which provides a measure of diffuse density on a scale from -0.5 (white body) to 0.5 (black body).

All vehicle tracks surveyed at CR were created by one J.I. Case™ 1000D excavator which arrived ca. 1965. The Case excavator weighed 17000 lbs (7727.3 kg) and had twin 16" (41 cm) wide tracks with 2336 in^2 (15067 cm^2) potential surface contact for both tracks combined. The vehicle was thus capable of exerting ca. 7.3 lbs per in^2 (0.51 kg per cm^2).

Most vehicle tracks surveyed at TL were among those initially documented by Barrett (1975), who investigated the early stages of vegetation response at several sites, in addition to making some attempts at sod restoration. These sites were marked by Barrett on the original 1971 airphotos, as are the stands sampled for this study on the copies included here (**Plates 2.15 to 2.19**). The tracked vehicles used include an Arnold 'Ranger' (**Plate 2.20**), two Massey-Ferguson model 65 trackers, and a Bombardier 'Weasel'. The latter two are heavier than the Ranger and were in use during the period 1960-67 across many parts of the lowland (Barrett 1975). The Ranger arrived in 1967 and is still in use (occasionally with one or two small trailers), mostly for hauling freight and refuse around the research camp and the adjacent airstrips. For comparison with the older disturbances, a set of multi-pass tracks from summer 1986 were surveyed in 1989. Sites of earlier fertilization studies (e.g. Babb 1972) were avoided.

In addition, three archaeological (Thule era) dwellings were sampled in 1990 on the north shore of TL (Federal Government site designation nos. QkHn-10, QkHn-11, QkHn-12) and an additional site near RB (QeJu-2). All but one of these sites were unexcavated. All appear to have been winter dwellings of the structural type described by Schledermann (1976) and are discussed from an archaeological perspective by Helmer (1991) and Schledermann &

Nash (1977). The dates of occupation are ambiguous for the TL sites, according to Helmer (1991), but the most recent estimated date for human usage is 800 ybp (Helmer 1992, pers. comm.). One of the TL dwellings (QkHn-12) was recently excavated, after which its stone foundation was reconstructed (Park 1986). This dwelling was sampled for comparative purposes. The archaeological sites were sampled in a manner similar to the contemporary housepads at CR with the following exceptions: (i) only five quadrats each were situated on the dwelling (with quadrats restricted to the floors of the unexcavated dwellings and to the back wall of the reconstructed dwelling) and on the adjacent (1-2 m distant), relatively undisturbed beach ridge; (ii) active layer depth was not probed; and (iii) soil compaction was not gauged by cone penetrometer. The latter two precautions were taken to avoid damage to artefacts.

v. Environmental parameters

a. Active layer

Development of the active layer at CR was measured using a 1 cm x 1 m steel probe calibrated with 10 cm etched increments. Readings were taken once daily during 1988 by probing randomly just outside a chosen edge of each quadrat. In 1989 these readings were made from 10 June to 15 July. After 15 July, sampling frequency was reduced to twice weekly and continued until 30 August. In 1990, readings were made 2-3 times weekly until 21 July and once weekly thereafter. At TL in 1990, active layer depths in all meadow stands and at the excavated Thule dwelling were measured on 28 July.

For multivariate analyses, total depth of thaw was used as a baseline index of the potential environment for annual root development. This value is perhaps of less relevance to some species, such as <u>Eriophorum angustifolium</u>, whose roots tend to grow to moderate depths apace with the thawing front in spring, and more relevant to deep rooting plants, such <u>Alopecurus alpinus</u> (Bell & Bliss 1978; Callaghan et al. 1991).

b. Soil temperature

In 1989, six sites were randomly chosen, according to the same grid/transect methods used for quadrat placement, to measure soil temperature in areas with multiple-pass vehicle tracks, and in adjacent undisturbed ground. Fenwall model GB-32 thermistors were taped to wooden stakes and placed at depths of 5, 10 and 15 cm below the surface in undisturbed tundra and at the same depths below the soil surface in tracks where no organic mat remained. These were installed as soon as the active layer had developed to a depth of 15 cm. Measurements accurate to ±0.1°C were made at least once (often twice) daily until 14 July and 2-3 times weekly thereafter. Diurnal measurements were made by sampling every few hours for periods of 26-36 hr. These measurements were made several times during the growing season under a variety of weather conditions. In 1990, temperature in every quadrat was measured at the same depths using YSI Series 4000 thermistors mounted with epoxy on fiberglass rods inserted into pre-formed holes. Measurements accurate to ±0.1°C were made upon apparent equilibration. Readings were taken for most stands at CR on several different days chosen to represent variable conditions of radiation and ambient temperature (e.g. completely overcast vs. cloudless, cool vs. warm, and 'night' vs. day). At TL, soil temperatures were measured over one 24 hr period with overcast skies from 29-30 July 1990. For multivariate analyses, summary figures for soil temperature were taken from a single cloud-free day at mid-growing season at each study site, to better illuminate potential variation among habitats.

c. Soil compaction

A cone penetrometer (19" staff with 0.5" cone) was use to measure soil strength within each vegetation type during mid-late July of both 1989 and 1990. Resistance readings were taken as the cone base reached depths of 1", 2", 3", 5" and 7" during five random probes outside the edges of each quadrat. These readings were averaged by depth for each site. For multivariate analyses, only 3" (7.6 cm) measurements were used since this depth tended be well within the rooting layer and usually corresponded to the median depths sampled for soil temperature and soil moisture/bulk density.

d. Relative soil moisture/bulk density

Soil cores 5 cm in diameter (volume 100 cc) were extracted once from just outside each permanent quadrat over a precipitation-free 48 hr period from 7-9 July 1989 at CR. Several stands were resampled 5-7 July 1990 for comparative purposes. In each case sampling took place ca. three weeks after most of the study site was snow-free. These were taken between 5-10 cm (rooting depth) below the mineral soil/organic layer interface, the depth of which was noted in each case and photographed in many, or 5 cm below the surface in the event the organic mat had been removed. At this time, if needed, additional soil profiles were made along disturbance borders to note the nature and depth of rhizomatous invasion.

Care was taken during insertion of each core to exert even pressure to provide samples suitable for measuring both gravimetric water and bulk density. A core was aborted if a stone or other obstruction was noted during insertion. Two additional cores, for a total of 300 cc, were taken for nutrient analyses from a subset of 30 quadrats - 3 from on and off each of the following: multiple pass vehicle tracks; single pass vehicle tracks, and; housepad Type A and adjacent trampled areas and controls. After an initial 'wet' weighing, cores were air dried at room temperature for 4 weeks, then oven dried at 105°C for 24 hours and weighed again in the field with a triple-beam balance to nearest 0.10±0.10 g. Cores were then sieved and stone content was considered the fraction >2 mm in diameter, thereby allowing correction for the weight of the stones for gravimetric water determination.

At TL, soil moisture and bulk densities for meadow stands were sampled over a precipitation-free 24 hr period from 26-27 July 1989. Archaeological sites were similarly sampled on 4 August 1990. The same procedures employed at CR were used for measurement of these parameters except that, after weighing 'wet' samples in the field, they were stored in airtight bags in a cooler at ca. 4°C for 1 week until my return to CR. At that time the samples were air dried for 2 weeks prior to oven drying and weighing.

e. Physical/chemical analyses

In 1989, a subset of 300 cc samples from CR were submitted to Dr. Charles Tarnocai of the Land Resources Directorate at Agriculture Canada in

Ottawa for determinations of total nitrogen, and extractable phosphorous, potassium and carbon in each, expressed as percent dry mass, as well pH. The proportions of sand, silt and clay in the <2 mm fraction were also determined during this analysis (methods for P, K, pH and particle size follow Sheldrick (1984); N and C are by the LECO CHN-600 determinator (see Sheldrick 1986). In 1990, an additional 30 samples were submitted to Dr. Gus Mackenzie of Macdonald College and tested for percent organic matter content and percent carbon (Walkley-Black), extractable phosphorus and potassium (Mehlich III) and corrected conductivity (Richards 1969).

In 1990 the pH of mineral (and occasionally highly organic) soils and surface waters (if any) was measured in the field for each quadrat, using a Cole Parmer model 5985-80 Digi-Sense™ meter accurate to ±0.05 using methods given in Sheldrick (1984). Surface waters were measured in disposable 50 ml paper cups. Mineral soils were thoroughly mixed several times over a period of 30 min at a ratio of 1:1 with distilled water. The ratio was adjusted to 1:4 for high organic content samples. These slurries were then allowed to stand for 30 min at room temperature (approx. 15°C), after which time readings were taken with the glass electrode in the supernatant water. Similar measurements were made for all sites at CR in late June, late July, and late August for 10 of the 16 sites (at least one from each disturbance type). At TL all readings were made on 6 August 1990.

For multivariate analyses, only mid-season mineral layer measurements were used, since surface waters (a) were not universally present, even during snowmelt, and (b) were temporally much more variable than mineral soils. While, surface pH may have much to do with establishment of propagules, such as bryophyte fragments, in miniscule safe sites, mineral soils were assumed to better define overall conditions within the patch. The only exceptions to this were the Thule dwellings, in which the 'soils' were virtually all peat and other organic materials.

A subset of 18 of the 1989 meadow soil samples from TL were submitted for analysis to Earl Gagnon of the Department of Land Resource Science at the Ontario Agricultural College, Guelph. Determinations were made for total nitrogen, as well as phosphorous, potassium, magnesium and calcium, in addition to pH. The nitrogen is reported as percent dry mass, and includes the mineral and organic fraction. The other elements are an extractable portion only and are reported in mg/kg. Methods for nitrogen follow Keeney & Nelson (1982). All other methods are as per Ontario Soil Management Committee (1989). An additional eight meadow soil samples were gathered for comparative purposes in 1990 and analyzed at Macdonald College, according to the methods discussed above for CR. A subset of 18 soil samples from the archaeological sites surveyed in 1990 at TL were similarly analyzed at Macdonald College.

vi. Sampling/temporary quadrats

a. Standing crop

The majority of biomass sampling at CR was conducted in early August 1989. Some additional sampling (Stands 15-19) took place in mid-late July 1990. At TL, sampling of the meadow stands took place 28-31 July 1989. Archaeological sites and a few additional meadow stands (stands 10-13) were sampled between 28 July and 1 August 1990. During the IBP, Muc (1977) noted that, in 'warmer' summers, early August was considered to be the time of peak aboveground vascular biomass for sedge-moss meadows at TL. He also noted, however, that in cooler summers development of peak above-ground standing crop was delayed until mid-August. Unfortunately, daily maximum temperature was not recorded for the 1990 growing season, but 1989 had a greater proportion of overcast days with a greater amount of precipitation. Overall, flowering appeared to be reduced in 1989 relative to 1990 (Trask 1992, pers. comm.).

There are no comparable data on productivity for CR. However, my own air temperature records from this study site show that 1990 was noticeably warmer than 1989. Phenological records were also kept and show that peak flowering for most species occurred about a week earlier in 1990 than in 1989. Assuming that the relationships evident between annual variation in climate and peak biomass are similar to those reported for TL, peak biomass in 1990 (the warmer summer) would have been slightly earlier than in 1989. Thus, the sampling dates at CR are assumed to have approximated peak aboveground standing crop for each of the years sampled.

A 25 x 50 cm quadrat was temporarily placed immediately adjacent to each permanent quadrat and frequency values recorded as described above for permanent quadrats. To provide samples for aboveground standing crop, live and dead material of all vascular species were then clipped at the point where the stems/shoots emerged from the surface (either moss or soil). At CR, these were separated by species in the field, transported in paper lunch bags and air dried at room temperature for 10 days prior to returning from the field. At TL, vascular plants were similarly sampled except that these were not sorted in the field according to species. Air dried samples were separated by species into living and dead material back at McGill.

Upon returning to the laboratory, herbaceous species were sorted into living (current year) and dead (all previous years) tissue and separated. It should be noted that leaf tissue of Cyperaceae dead for >1 yr. had a distinctly different hue of brown than those leaves which were recently dead or dying. This 'rust' appears first at the tip of a leaf and recedes down towards the shoot. Regrowth of these tips has been observed and thus only leaves dead >1 yr were separated. For woody (e.g. Salix spp.) species, most current-year leaves remained attached to twigs, as they had been in the field. It was rare to observe last year's leaves on both Salix arctica and S. reticulata, so that all detached leaves of these species which remained in the bag were counted as 'living'. S. herbacea, however, grows virtually within thick moss mats and is thus able to sometimes retain a few dead leaves, which were readily apparent and easily separated. In this manner living and dead foliar and woody tissues for each species were separated, oven dried at 85°C for 24 hrs. and weighed.

b. Plant tissue element analysis

After drying and weighing for aboveground standing crop, live leaf tissues from species representing the two dominant growth forms (rhizomatous graminoids, deciduous shrubs) were ground in a Wiley mill through a 40-mesh screen and then analyzed for concentrations of the macronutrients N, P, K, Mg and Ca. All digestions and analyses were performed by the Department of Land Resource Science at the Ontario Agricultural College, Guelph according to the methods of Thomas et al. (1967). The concentrations of N and P in the digestion solutions were measured by a Technicon Auto Analyzer, and Ca, Mg and K by an atomic absorption spectrophotometer. The results are presented as a percentage. The species analyzed were Alopecurus alpinus, Carex aquatilis var. stans, Eriophorum angustifolium, and Salix arctica. Samples analyzed from TL were obtained 28 July-1 August 1990 and those from CR 10-11 July 1990.

vii. Sampling/voucher specimens

a. Vascular plants

In addition to 46 vascular collections made at CR in 1988, 49 collections (of 45 species, 3 sheets of each) were made between CR and TL over the course of the 1989 growing season and another 49 collections from all three study sites in 1990. Final verifications of preliminary identifications were made at the National Herbarium in Ottawa by Dr. William J. Cody, except for Draba spp., which were determined by Dr. Gerald A. Mulligan. Vouchers of most taxa are retained by the National Herbarium and a complete list appears in **Appendix 1.**

b. Bryophytes

In 1989, specimens of what were apparently the most common bryophytes at several sampled sites were gathered at CR and identified by Dr. Marian Kuc. More extensive surveys of the bryofloras of all three study sites, using presence-absence as discussed above, were made in 1990. The majority of these specimens were verified by Dr. Dale H. Vitt and a complete list appears in **Appendix 2.** Vouchers of most of the Baffin Island taxa are retained by the herbarium at University of Alberta, Edmonton. Dr. Howard A. Crum verified a small collection made from the spoil heap at the archaeological excavation site at TL.

c. Lichens

Specimens of macrolichens were gathered at all three study sites in 1990. Final verifications were made in Ottawa at the Canadian Museum of Nature by Dr. Irwin M. Brodo and Pak Yau Wong. These taxa are listed in **Appendix** 3.Vouchers are in my possession.

d. Algae

Algal specimens were gathered at CR and TL in 1990. These were verified by Dr. Paul Hamilton of the Canadian Museum of Nature and the taxa are listed in **Appendix 4.** Vouchers are retained in Ottawa by the Museum.

2.5 UNIVARIATE DATA ANALYSES

Both biotic and abiotic variables were tested for normality by using moments reports and standardized skewness and kurtosis measures (Zar 1984; SAS Institute, Inc. 1989). Few data of either type were normally distributed outside of the wettest meadows and were subject to statistical analysis (i.e. correspondence analysis) after making appropriate data transformations. Some data, such as seasonal active layer development and soil nutrient data, were not entirely suited for multivariate analyses, either because of their highly temporal variation or because of the number of samples was too small. In such cases independent samples were subject to the Mann-Whitney test (Zar 1984; BrainPower, Inc. 1985), considered one of the most powerful and useful of the nonparametric tests for differences between samples (Zar 1984; Siegel & Castellan 1988).

2.6 MULTIVARIATE ANALYSES

i. Classification

a. Background and rationale

The description and classification of vegetation continues to be of importance in ecology and biogeography in some ecoregions, and the history, advantages and disadvantages of the many methods in use have been summarized extensively by Shimwell (1971) and Whittaker (1978), and more recently by Causton (1988) and Økland (1990c). The special problems and aims of vegetation classification in the Arctic were recently addressed at The International Circumpolar Arctic Vegetation Classification Workshop and are summarized by Walker (1992). The workshop participants agreed that a unified floristic classification system, similar in approach to that devised by Braun-Blanquet (1932; see also Westhoff & van der Maarel 1978), is appropriate for the Arctic because of its common flora. But the ultimate justification for a floristic-based system, as opposed to systems based on physiognomy, structure, climate, or combinations of these and other variables, is that species can be viewed as the ultimate integrators of the ecosystem. Species composition represents the sum of evolutionary/environmental interactions and thus can reveal a great deal about the characteristics of landscapes and the biophysical processes occurring within them (Walker 1992). All patches within a landscape are different and unique, yet some are more similar than others such that vegetation can be classified into different types, which are of great practical utility (Miles 1979). In the context of anthropogenic disturbance, floristic classification can serve as both a means of identifying and comparing existing local and regional patterns, as well as monitoring long-term recovery by tracking floristic changes in disturbed patches.

In discussing Braun-Blanquet-style classification, Westhoff & van der Maarel (1978) contend that the vegetation of a region with a uniform climate and a uniform geological history usually shows great uniformity in the ecological amplitudes and therefore in the sociological positions of its species. Theoretically, higher level syntaxa could occur over wide geographic areas in the circumpolar north and there is some evidence to support this (Daniëls 1985; Dierßen & Dierßen 1985; Elvebakk 1985). At the association level, Beschel (1970) felt that tundra plant communities intergrade so readily as to make classification difficult at best. This contention is supported by the recent use of multivariate analysis in a high arctic lowland, which revealed considerable floristic overlap among the most widespread plant communities (Muc et al. 1989). The authors also noted the wide ecological amplitudes of the most prominent vascular plant species.

For this study, two-way indicator species analysis (TWINSPAN™, Hill 1979b) was used to classify natural and anthropogenic vegetation from all three islands. Being polythetic and divisive, TWINSPAN is recommended for hierarchical classification because of its robustness (Gauch 1982). TWINSPAN has been deemed an effective tool for computer-assisted phytosociological clustering and table sorting and is considered a more objective way of constructing a Braun-Blanquet-style hierarchy of vegetation types (Gauch & Whittaker 1981; Mucina & van der Maarel 1989). The resulting divisions are referred to as 'noda'. Each 'nodum' is a vegetational entity expressing concentrated species-in-sites coincidence, which is not necessarily discretely separated from other noda (Noy-Meir 1971). TWINSPAN is designed to arrange the two clusters at each node in the way that results in placing the most similar samples together in the dendrogram's sampled sequence. This makes the information in the dendrograms more lucid (Gauch 1982). In TWINSPAN the qualitative concept of a differential species is transferred to quantitative data by use of 'pseudospecies'. A pseudospecies is defined by a minimum abundance of a species. This minimum is called the cut level (Økland 1990c).

Because TWINSPAN is based on correspondence analysis (CA), Groenewoud (1992) warns that the realiability and usefulness of a TWINSPAN analysis depends on how well CA extracts axes that have an ecological meaning, how well the CA axes are divided into meaningful segments, and how faithful certain species are to to certain segments of the multivariate coenoplane. He notes that the first split is usually reliable, but that subsequent divisions should be interpreted with caution in more complex data sets and that these should be broken into subsets to focus on major gradients. This is concordant with the likelihood of samples in large data sets exhibiting reticular rather than simple hierarchical structure. To date there have been few applications of such computer-assisted classification in the High Arctic (Bergeron 1988; Muc et al. 1989). Only one researcher (LaFarge-England 1989) has numerically classified a full survey of the non-vascular cryptogamic flora, although she did not include vascular vegetation.

b. Analysis

TWINSPAN's default options were used with the following exceptions: (1) minimum group size for division was set at four; (2) cut levels were set at 0, 1, 2, 3, 4, 5, 6, 7 to better reflect the range of vascular species' abundances after transformation of the species data. Few individual species exhibited cover/abundance >50%, which is equivalent to cut level 7 after transformation (van der Maarel 1979). For non-vascular species, comparison of the original field classes (few, abundant, dominant) with presence/absence for data input showed that the presence/absence classification was fully the equivalent of the more subjective ranking. Apparently the floristic data contain the great majority of the variation in the vegetational data (Forbes 1992d). Thus the more objective presence/absence transformation was retained for non-vascular species; (3) rare taxa were considered those occurring in ≤2 samples in a given stand and were removed prior to analysis. Most rare taxa were erect solitary forbs, equisetoids, and lichens.

ii. Ordination

a. Background and rationale - Unconstrained ordination

The result of ordination in two dimensions (two axes) is a diagram (biplot) in which sites are represented by points in two-dimensional space. The aims of ordination are: (1) to arrange the points such that points that are close together correspond to sites that are similar in species composition, and points that are far apart correspond to sites that are dissimilar in species composition; and (2) to suggest new combined variables for further study (ter

Braak 1987b; James & McCulloch 1990). An important criterion for selecting an ordination technique is that it effectively summarize community variation relative to underlying gradients (Gauch 1982). One of the most effective and popular methods of ordination is the non-linear detrended correspondence analysis (DECORANA™, Hill 1979a, a.k.a. DCA), a method of indirect gradient analysis based on weighted averaging which was designed to correct the faults of correspondance analysis or CA (Gauch 1982; Jongman et al. 1987; van der Maarel 1989). The detrending step in DCA is designed to remove the information already accounted for by the first axis, which would otherwise contribute to the so-called 'arch effect'; thus, any additional information can be seen more clearly and interpreted more readily (Gauch 1982; Peet et al. 1988).

All ordination methods deal with multidimensional matrices, and all involve scaling (Økland 1990c). In terms of scaling, DCA units are consistent and have extrinsic meaning. They are called "s.d." units (for average standard deviation of species turnover, Gauch 1982), and one s.d. represents approximately a 50% change in sample composition. Arguments for and against the scaling of ecological gradients in units of compositional turnover are presented by Wilson & Mohler (1983), Økland (1990c) and others. For example, Wartenburg et al. (1987) and Minchin (1987) have cautioned that there may be a problem with the definition of s.d. units in concrete terms, because the method used to rescale the axes is essentially an arbitrary mathematical model not necessarily related to reality. Other disadvantages are the inaccuracy of DCA for gradient length estimation when beta (ß) diversity is low (Oksanen 1983), the potential for problems posed by deviations from the unimodal response model and, like all other ordinations, its vulnerability to extreme outliers (Økland 1990c). Advantages of the s.d. unit are the simple interpretation, and the relative robustness of DCA as a method for rescaling single gradients.

In effect, s.d. units provide a useful measure of floristic distance, and DCA axes represent changes in floristic composition of samples (Jongman et al. 1987; Walker 1990). The more the scale favors the quantitative aspect (abundance) of the vegetation over the qualitative aspect (presence), the longer the DCA axes. The gradient length estimate decreases when infrequent species are deleted (Eilertson et al. 1990). Peet et al. (1988: 925) have pointed out that "the real value of DCA is in the analysis of multidimensional gradients . . . or to gradients of unknown dimensionality". They also noted that DCA is better at ordering long gradients than short ones. In a recent critique of DCA, based on various real data sets of varying complexity, Groenewoud (1992) cautions against the temptation to pack too much into the analysis and that often only the first gradient can be interpreted with confidence. His recommendation then, as with TWINSPAN, is to restrict the sampling mainly to one gradient at a time.

Another method popular with community ecologists is the linear principal components analysis (PCA) (ter Braak 1987b). The choice between linear and non-linear methods is not a matter of personal preference. Where gradients are short, there are sound statistical reasons to use linear methods. As gradient lengths increase, linear methods become ineffective so that ecological data collected over a broad range of habitat variation may require non-linear models. The range of 1.5-3.0 s.d. for the first axis represents a 'window' over which both PCA and DCA, or both redundancy analysis and canonical correspondance analysis (CCA), can be used to good effect (ter Braak & Prentice 1988). An average species turns up, reaches it optimum (mode) and disappears within 4 s.d. along the gradient (6 s.d. according to Minchin

1987) (Økland 1990c). Thus, samples that are 1 s.d. apart are about 50% similar. Preliminary analyses showed that the first axes of all ordination biplots were longer than 2.0 s.d., with most being longer than 2.6 s.d. and many longer than 3.0 s.d. Based on these results, I decided to use only DCA for species ordination so that the results from all data sets and subsets would be readily comparable.

b. Constrained ordination

Canonical or constrained ordination techniques are designed to detect the patterns of variation in the species data that can be explained 'best' by a set of measured environmental variables. Whereas ordination is the tool for exploratory analysis of community data with no prior information about the environment (indirect gradient analysis), constrained ordination is the equivalent tool for the analysis of community variation in relation to the environment (direct gradient analysis) (ter Braak & Prentice 1988). Canonical correspondance analysis (CCA) is a multivariate extension of weighted averaging ordination. CCA constructs those linear combinations of environmental variables along which the distributions of the species are maximally separated; eigenvalues produced by CCA provide a measure of this separation (ter Braak 1987a). Only the fraction of variation in the vegetation which can be attributed to variation in the supplied environmental variables is expressed (ter Braak 1987b; Økland 1990c).

In CCA the data on species composition are explained through a Gaussian response model in which, again, the axes are linear combinations of the environmental variables. Thus the vital assumption in CCA is that the response model is unimodal (ter Braak 1987b). Violations of this assumption are likely to increase where overall species turnover among stands is minimal within a given data set, reinforcing the importance of estimating gradient lengths prior to analysis, as discussed above. In effect, where gradients are relatively long, CCA allows a quick and reasonably robust appraisal of how community composition varies with the environment (ter Braak 1986; Økland 1990c). As with unconstrained ordination, for very short gradients the choice of model (i.e. CCA vs. redundancy analysis or RDA) may not be easily settled, but for data with the longest coenoclines greater than 2.0-2.5 s.d., CCA is likely to be superior (ter Braak 1987b).

Constrained ordination has become available rather recently and, compared to DCA and PCA, relatively few applications have yet been published (see, however, Borgegård 1990; Økland 1990c; Allen et al. 1991; Heikkinen 1991; Hill 1991), none of which are from arctic sites or treat tundra vegetation. As the method includes environmental variables as well as species frequency and abundance data, evaluation is far more complicated than is the case for ordination (Økland 1990c). In general, constrained methods such as CCA and detrended or DCCA are most powerful if the number of environmental variables is small compared to the number of sites (ter Braak & Prentice 1988). The technical details of constrained ordination are complex and discussed here mainly from the perspective of output interpretation. Computational details are provided by ter Braak (1986; 1987a, b).

iii. Analysis

a. Vegetation (unconstrained ordination)

Detrended correspondance analysis was applied to species data using the program package CANOCO™ (ter Braak 1991), which includes Hill's (1979a) DECORANA™ program. In indirect gradient analysis (DCA) attention is first focussed on the major pattern of variation in community composition (ter Braak & Prentice 1988), but can also be used in the geographic analysis of community data, as has been done here (see also Allen et al. 1991; Hill 1991). Økland (1990c) and others (Vitt et al. 1986; Heikkinen 1991) note that if a classification of the sample plots is available, it can be used as an informal aid to interpretation of the ordination diagrams. Thus the sample stands are labelled in the ordination diagrams (biplots) according to their TWINSPAN-derived nodal designations. Additional notations indicate the few cases where such noda are comprised of more than one sample stand.

Key components of DCA output include eigenvalues for each of the four axes, estimated gradient lengths, and separate biplots for species and samples. Throughout the analyses the option for detrending by segments was used, as recommended by Økland (1990c). The emphasis in interpretation of the results was on sample ordinations. Hill & Gauch (1980) note that species ordinations are not as good as sample ordinations and that species modes which lie outside of the sampled region may be estimated poorly. Also, the widths of large gaps in the data can be poorly estimated although short gaps are handled well. To understand the effect of anthropogenic disturbance on the vegetation, the data set was ordinated in several ways. First, as in TWINSPAN, the maximum data set of 256 samples was analyzed, which resulted in extremely crowded biplots. A division made on the basis of the TWINSPAN analysis guided separation of disturbed and undisturbed samples, which were ordinated again. Later, several random splits of the main data set were made to determine the veracity of the splits based on the TWINSPAN analyses. These were in essential agreement in all cases. Both processes were repeated several times to create more readily interpretable data subsets, after which disturbed and undisturbed sites were ordinated together once again. Among species, only a few extreme outliers appeared. These were removed during this combination of procedures, in keeping with the recent cautions of Eilertson et al. (1990) against using the standard downweighting option. Sites of chemical dumping were comprised of species more or less confined to those samples so that they consistently skewed both the ordinations and classifications and were eventually removed from the analyses.

b. Vegetation and environmental variables (constrained ordination)

Data sets and subsets were subject to constrained ordination (CCA) in a succession of prodecures similar to that for DCA described above. Key components of the output from CCA are given in a summary table. When covariables are lacking in the analysis, as was the case in each of the analyses conducted, output components include the following: eigenvalues for each axis; sums of unconstrained and canonical eigenvalues (total intertia); percentage variance for species data and species-environment relation; and species-environment correlations. Elsewhere in the output appear canonical coefficients, intra-set correlations of environmental parameters, and two correlation matrices; one for the correlations between environmental variables, displayed before the calculation of the ordination axes, and one displayed thereafter for the correlations between ordination axes (ter Braak 1988, 1990).

The species-environment correlation measures the strength of the relationship between species and environment for a particular axis. It is the correlation between the sample scores for an axis derived from the species data and the sample scores that are linear combinations of the variables. However, a high correlation does not mean that an appreciable amount of the species data is explained by the environmental variables. The amount explained is given by the eigenvalue in constrained analysis (ter Braak 1990). Compared to species-environment correlation, a better measure of the relative importance of an axis is the eigenvalue, with values between 0 and 1 (Økland 1990c). The eigenvalues in CCA are usually smaller than those in DCA because of the restrictions imposed on the site scores in the former (ter Braak 1987b). The total inertia is the total variance in the species data as measured by the chi-square of the sample-by-species table divided by table total (Greenacre 1984 in ter Braak 1990) and, accordingly, is greater in data sets with high turnover of species composition. This value is equivalent to the sum of all unconstrained eigenvalues in ordinations such as these without covariables in the analysis.

The percentage of variance of the species data explained by the axis is given cumulatively and is derived from the eigenvalues and the sum of all unconstrained eigenvalues. For abundance data or presence-absence data these percentages are typically quite low in CCA, given that species data are often very 'noisy' (ter Braak 1990; Økland 1990c). Yet, an ordination diagram that explains only a low percentage may be quite informative. With environmental variables in the analysis, CANOCO uses these to explain the species data, yielding fitted values for the species. In CCA this is a weighted regression and the total variance of the fitted values is precisely the sum of all constrained eigenvalues, with each axis explaining a part of this variance. This information is also given cumulatively, as the percentage variance for species-environment relation.

Canonical coefficients indicate the degree of vegetational change occurring per unit of change in the centered and standardized environmental variable *k* along axis *h*, given that all other variables are constant. The correlation between the fitted sample scores (x_{hj}) and environmental variable (z_{kj}) is the intra-set correlation (Økland 1990c). In CCA, CANOCO also includes an option for testing the significance of axis-environment relationships with a Monte Carlo permutation test. In this test, CANOCO uses permutations of the residuals of the species after fitting environmental variables. After a normal run, this option can be applied to test both the first axis and the overall results (for technical details see ter Braak 1990). Another option is forward selection, which allows permutation testing of individual environmental variables. Each data set and subset was run through CCA a number of times for application of the Monte Carlo test to the first axis, the overall results, and the individual environmental variables.

Sample-species biplots require considerations of scaling, which affects the amount of scatter among axes of an ordination diagram. Choices of abundance scale and ordination method do not depend on each other (Økland 1990c). In CCA the default scaling is scaling 2 (also known as Hill's scaling). As in DCA with detrending-by-segments, samples are weighted averages of species in scaling 2. In running CCA, I usually tried separate runs with scaling 1 and 2. Scaling 1 is more appropriate when the focus is on the configuration of samples in the ordination; with scaling 1, inter-sample distance approximates their chi-square distance. Scaling 2 is more appropriate if the emphasis is on the species configuration; with scaling scaling 2, inter-species distances approximate their chi-square distance (ter Braak 1990).

After running both the classification (TWINSPAN) and ordination (DCA, CCA) analyses, the entire data set was randomly split to see if the results were similar to what had previously been obtained. The samples were then stratified into disturbance classes aimed at restricting the analysis to one major gradient at a time (Groenewoud 1992). In most cases the patterns present reflected those discerned in the earlier analysis, a fact I contributed largely to the high frequencies and great fidelities of many individual and groups of cryptogamic species (Forbes 1992d). As in the previous analyses, the patterns of variation within large data sets were invariably evident in the ordination diagrams, but tended to be so crowded that differentiating among different samples and disturbance regimes was often difficult, even along the first 'most reliable' axis.

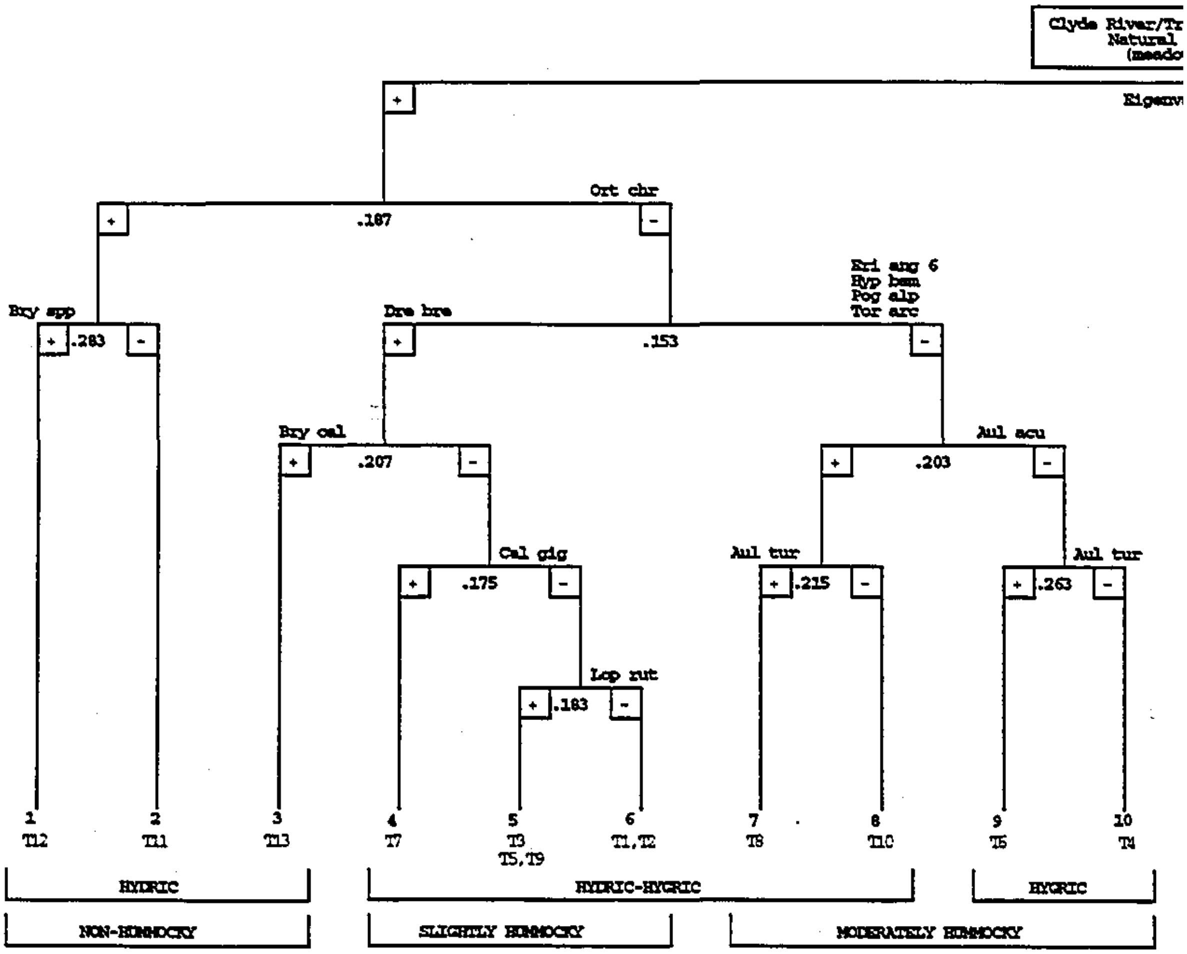
CHAPTER III. DATA ANALYSIS

3. 1 Classification of natural vegetation

Meadows at Clyde River and Truelove Lowland

Table 3.1 (see enclosure) is derived from vegetation data (126 samples x 99 species) from the combined natural meadow stands from CR and TL. Given the limited dimensions of the program (256 samples), the data had to be broken into subsets. As discussed earlier, this was done randomly at first to test the strength of the patterns. Eventually, separate runs were made with combined undisturbed and natural vegetation data from CR and TL/RB. These subsets were analyzed with vascular vegetation only and with combined vascular and non-vascular vegetation data (Forbes 1992d). The combined data sets proved greatly superior for differentiating both within and among natural and disturbed vegetation cover types and the following discussion is restricted to analyses of this sort. In the combined natural/undisturbed vegetation analyses, almost all vegetation types classified *a priori* into either subset were quickly and easily differentiated in the TWINSPAN-derived dendrogram. The few exceptions were either extremely wet or minimally disturbed stands.

Beach ridge stands at TL and RB were found to be lightly trampled and were analyzed with the disturbed vegetation. Stand 17 at CR was determined as an outlier in earlier runs and was removed prior to analysis. This stand is immediately adjacent to the chemical dump site and is apparently lightly disturbed, seemingly by local tracking of chemicals and some light trampling effects. No species were downweighted during the analysis. Seven cut levels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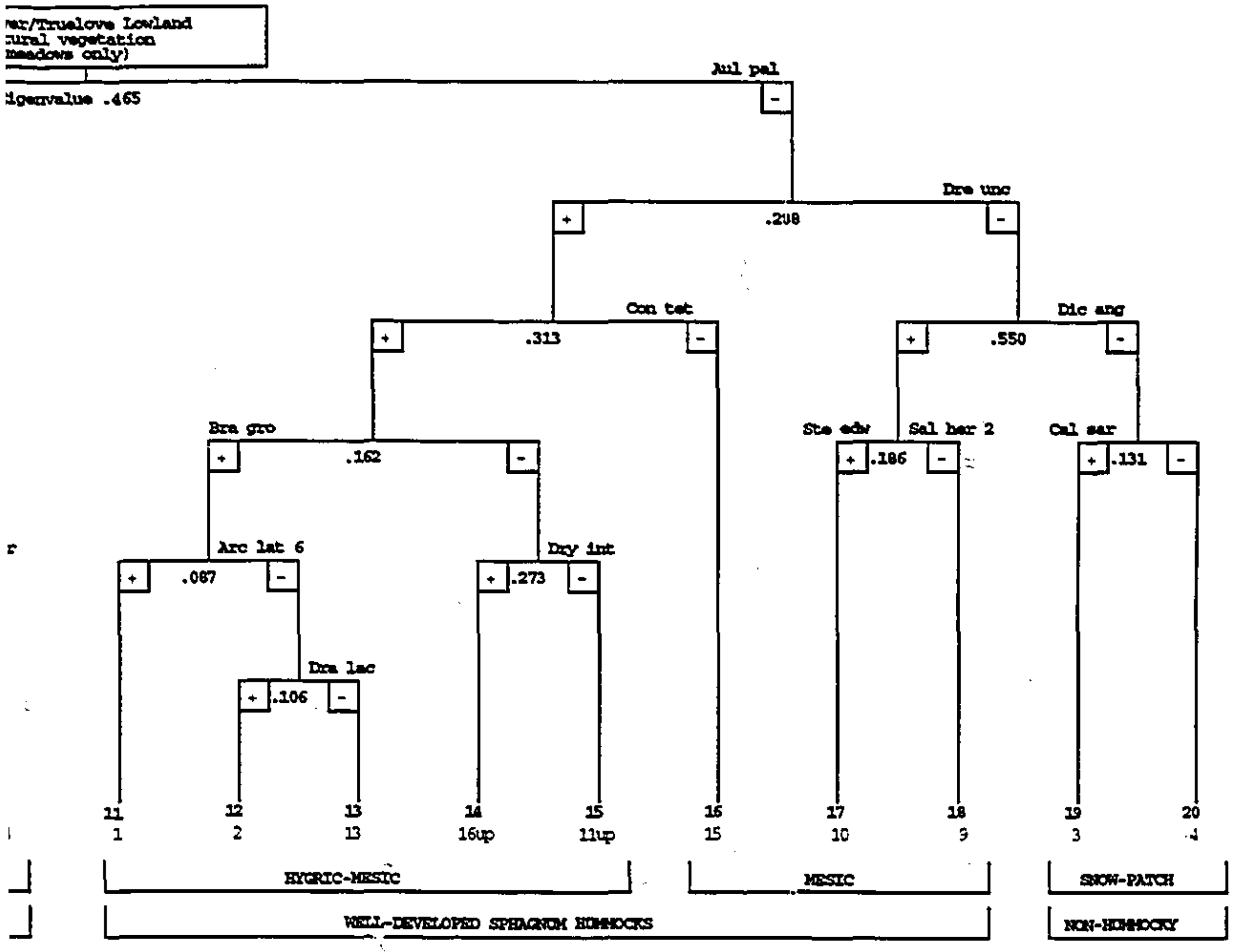
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were specified as 0, 1, 2, 3, 4, 5, and 6 corresponding to transformed cover/abundance values ranging up to 25%. It is rare that one vascular plant comprises more than 25% cover in any quadrat and indeed only one pseudospecies from cut level 6 appears in the dendrogram. Previous TWINSPAN analyses using only vascular species (pseudospecies) yielded tables of limited utility since there was considerable floristic overlap between stands and many samples were misclassified (Forbes 1992d). Results presented here are based on analyses which included both vascular and non-vascular taxa.

The TWINSPAN classification was run to six levels of division which are illustrated here and provide a total of 20 noda in which all but two noda, both from TL, are comprised of one stand each. The dendrogram illustrates the hierarchical relationships of 6 relative moisture classes subordinate to 5 major physiognomic groups pertaining to the presence and stature of hummocks. From left to right the noda exhibit an approximate gradient of decreasing moisture and soil pH, with some exceptions. The 'indicator' value of several of the taxa is discussed below in relation to each other and to the findings of others.

The first split in the hierarchy separates the meadows of each island based on the occurrence of the moss Aulacomnium palustre, which was present in all natural and many disturbed meadow stands at CR but entirely lacking in the sampled meadow vegetation at TL. Vitt (1975) dicussed the apparent rarity of A. palustre on the lowlands of northern Devon and noted this situation constrasts sharply with its abundance on lowlands south of the Queen Elizabeth Islands. Given its high frequency within the meadows of CR the simple presence of this species appears to be of little diagnostic value in differentiating vegetation types at local scales, although actual cover/abundance values may be of greater utility in this respect. Another interesting difference involves the hydrophile Saxifraga hirculus (*sensu lato*), which is a common meadow species at TL, but occurs nowhere in the somewhat drier meadows of CR, although the latter is well within its range (Porsild & Cody 1980). Although present in most of the sampled meadow stands at TL, it did not occur at high enough frequencies to be a useful as a local indicator.

The two major vegetation groups at CR are those with and without Sphagnum hummocks. Relative to CR, microrelief is considerably reduced in the hummocky meadows of TL, though there is still a clear floristic distinction between the wet meadows and those characterized by the comparatively small hummocks, the latter being generally richer in species. In the following vegetation subsection headings, I have indicated the three or four most characteristic taxa based subjectively on their various contributions to cover and structure (first two taxa) and geobotanical indicator value (third and fourth taxa). In addition, numerous annotations are made for individual species in the text. The discussion is organized according to the gradients appearing in the dendrograms and proceeds, roughly, from wet to dry (left to right) in each case.

i. Clyde River

Of the 19 stands sampled at CR, 10 are included in this analysis. Three stands encompassing housepads (5, 6, 8) that were originally sampled in 1989 were resampled in greater detail in 1990 and became Stands 18 and 19. These and other stands which include even lightly trampled or chemically altered ground (7, 14, 17) have been excluded from this analysis. Previous runs of both TWINSPAN and DECORANA had distinguished these stands from natural vegetation. As well, Stand 12 is in fact the lower portion of a series of transects which comprise Stand 16 and thus exists entirely downslope from a set of single-pass vehicle tracks. On the basis of the apparent hydrological impact associated with this location as determined in earlier runs (see also **Plates 3.1, 3.2**), I considered it to be disturbed and excluded it from this analysis.

a. Hummocky meadows - Carex aquatilis var. stans - Salix arctica - Sphagnum spp. - Calliergon sarmentosum

Most of the landscape on the lowland is moderately sloping (3-5°) and the natural vegetation is characterized by a complex of Sphagnum hummocks, comprised primarily of S. squarrosum and S. capillifolium var. tenellum with lesser amounts of generally acidophilic associates such as Anastrophyllum minutum, Dicranum angustum, Hylocomium splendens and Polytrichum spp. As can be seen in the airphotos (i.e., **Plate 2.9**), the hummocky meadows exhibit a pattern of variation subparallel to local slope resulting from water tracks. Similar features are described from the North Slope of Alaska as being "shallow channels that conduct snow meltwater and subsurface water during the thaw season . . . giving the topography a ribbed appearance" (Walker et al. 1989:253). Water tracks at CR are 'hillslope water tracks', which differ from lowland 'water-tracks' described from temperate mires in North America and Europe. The latter refers to minerotrophic drainage tracks in lowlands through generally flat peatlands (Walker et al. 1989). The hillslope water tracks at CR are typically spaced 10-20 meters apart. These will be referred to hereafter a water channels to avoid confusion with

Plate 3.1a - General aspect within a water track zone (**Stand 11**) showing diversion of runoff from snowmelt by multi-pass vehicle tracks at CR. Note that virtually no moisture is reaching the meadows downslope from the tracks, a situation which has persisted for at least 21 yr. Once it reaches the tracks, water flows to the left out of view into a large gully which has formed over the years (see **Plate 2.9**). Photo date: 12 June 1990.

Plate 3.1b - General aspect within a water track zone (**Stand 11**) showing diversion of runoff from snowmelt by multi-pass vehicle tracks seen in **Plate 3.1a**. Photo was taken one week after all snow had disappeared from the meadows upslope (right), but surface and subsurface percolation kept water running into the tracks for another two weeks or more. Water is running gently but constantly toward the camera, removing fines from the ruts and leaving wet, inorganic stony sands. Center berm ranges from organic muds, with <u>Alopecurus</u> <u>alpinus</u> and <u>Dupontia</u> <u>fisheri</u> ssp. <u>psilosantha</u>, to remnant turfs with <u>Carex</u> <u>aquatilis</u> var. <u>stans</u> and <u>Eriophorum</u> <u>angustifolium</u>. Downslope meadows (left) are dry within a day or two of snowmelt (**see Plate 3.6**), receiving additional moisture during the growing season only from fogs and the minimal amount of precipitation which falls. Photo date 21 June 1989.

Plate 3.2 - Close-up of single-pass track channelling runoff from snowmelt at CR. Track is within Stand 16, located on the edge of water zone, which is not quite as hydric as a water channel, nor as mesic as an interfluve. Dominant mosses here, providing structure for the hummocks, are Sphagnum spp. Note the healthy, bright green hue of S. squarrosum seen in the running water just behind the quadrat frame, compared to its yellowish-brown appearance on the berm downslope. Quadrat frame measures 25 x 50 cm. Photo date: 18 June 1990.

vehicle tracks. Vehicle tracks running perpendicular or diagonal to local slope tend to divert runoff away from downslope areas, especially within water channel zones (**Plates 3.1 and 3.2**), but also in interfluves.

Given the westerly aspect of the study site, and the early melting of large snowbanks relative to easterly slopes (see **Plate 2.7**), there are relatively few well-developed water channels at CR. Still, those present range in the amount of moisture channelled, the wettest examples being represented by Stands 11up and 16up (Noda 14, 15) in which Eriophorum angustifolium was the dominant vascular plant but wet Salix arctica was also present. Macrolichens are virtually lacking. Here there was minimal differentiation between the vegetation on the tops of the hummocks and the interhummock areas due to the overall wetness. Slightly less wet were the water channels represented by Stands 1, 2, and 13 (Noda 12, 13), in which cover of E. angustifolium was slighty reduced while the dwarf shrubs S. reticulata and Dryas integrifolia increased in frequency and cover. Stands 1, 2 and 13 are differentiated from Stands 11 and 16 in the dendrogram by the presence of Brachythecium groenlandicum. This moss occurs at low frequencies in Dryas-heath communities of quite similar floristic and physiognomic description in northeast Greenland (Elkington 1965). Vitt et al. (1988) report it from alpine and subalpine areas of northwest North America, where it is often an associate of heath plants like Tortula norvegica and Cassiope. The weakness of the nodal separation is indicated by the low eigenvalue (.162). Peltigera aphthosa was the only lichen present in Stands 11 and 16.

Interfluves between hillslope water channels are relatively mesic by comparison with more pronounced vegetation differences between hummocks and hollows. An example is Stand 15 (Nodum 16), referred to as mesic in the dendrogram and characterized by the presence of Conostomum tetragonum, an acidophile (Steere 1978) which was absent in the water channels. Nearly half of the quadrats included hummocks dry enough to be capped by a variety of common fruticose lichens such as Alectoria spp., Cetraria nivalis, Cladonia spp. and Thamnolia subuliformis. The pleurocarpic mosses Drepanocladus revolvens and Calliergon sarmentosum, abundant interhummock species in the water channels, remained frequent but were truly abundant only in the wettest hollows. The latter seems to be a reliable indicator of acidic localities (Vitt 1975; Vitt 1990, pers. comm.).

Stands 9 and 10 (Noda 17, 18) are also mesic and structurally quite similar to Stand 15, being isolated from the larger snowbanks east and upslope of the settlement by the stream which runs just upslope and south of the knoll on which they are located (see **Plate 2.10**). TWINSPAN differentiates these stands, along with Stands 3 and 4 (Noda 19, 20), based on the presence of the mesic moss D. uncinatus, which was lacking in both the water channels and the interfluves. In Stands 9 and 10 lichens occupied approximately 50% of all hummock tops, including a crustose Ochrolechia sp. The grass Hierochlöe alpina was an occasional, an indicator of dry conditions (Porsild & Cody 1980). Cover of Carex aquatilis var. stans and E. angustifolium was reduced and the mosses D. revolvens and C. sarmentosum were not present, indicating the relative lack of moisture.

b. Non-hummocky meadows - Carex membranacea - Eriophorum angustifolium - Marsupella arctica - Dactylina arctica

Stands 3 and 4 are radically different from the Sphagnum meadows in terms of vegetation composition and structure. This is a Sphagnum-free area of late melting snow which has minimal slope (≤ 1°) and is in the lee of the former settlement. Although excessively wet when the late-lying snow melts, the complete lack of peat and an open vegetation cover contribute to excessive drying later in the growing season. The organic mat is extremely thin and dark in color here. E. angustifolium, Carex membranacea, Luzula nivalis and Salix spp. were the most abundant vascular species.

In the TWINSPAN dendrogram, it is the presence of Dicranum angustum, rather than the absence of Sphagnum spp., which differentiates these stands from Stands 9 and 10. Other bryophytes characteristic of Stands 3 and 4 included Drepanocladus revolvens, D. uncinatus, Ptilidium ciliare and Marsupella arctica. The latter is "always in acidic areas" according to Schuster (1988: 157), while P. ciliare (pp. 29-30) is "strongly drought-tolerant" and is found "chiefly under relatively exposed conditions, where dessication is frequent". This describes well the habitat of Stands 3 and 4 after the snow melts. These are also the only stands where the lichen Dactylina arctica was found, an acknowledged and reliable indicator of late-snow habitats along with Cassiope tetragona (Thomson 1984), a common associate in these stands. A sterile Ochrolechia sp. also occurred in scattered patches. This genus was otherwise found on only the driest hummocks in Stands 9 and 10 and in Stand 11dn, a drained hummocky peat meadow.

ii. Truelove Lowland

a. Hummocky meadows - Carex aquatilis var. stans - Salix arctica - Hypnum bambergeri - Orthothecium chryseum

Relative to CR, the meadow vegetation of TL is wetter and more homogenous, as indicated by the generally lower eigenvalues which separate the major groups. Local slope is minimal and water channels are lacking in the sampled stands. The first split is attributed to the presence/absence of Orthothecium chryseum, a common species characteristic of hummocks in the hummocky sedge-moss meadows (Vitt 1975). These stands are further divided into moderately hummocky and slightly hummocky meadows. The former were characterized here by Hypnum bambergeri and Tortella arctica, species of seepage zones in drier meadows and Ca-rich, moist sites respectively (Kuc 1973; Vitt 1975). They also exhibited a greater cover of Eriophorum angustifolium, a species almost always present but markedly reduced in the wettest meadows.

The further split within moderately hummocky meadows continues to make good ecological sense as A. acuminatum (along with Tomenthypnum nitens, not appearing in dendrogram) consistently occupied the sides and tops of hummocks and is thus an indicator of raised microrelief and moist (hygric) but not wet (hydric) conditions. A. turgidum is another good indicator here, as it was often found growing intermixed with A. acuminatum on the larger, drier hummocks in the sedge meadows (Vitt 1975). Among vascular species the presence of Carex membranacea (not appearing in dendrogram) is also indicative of the more mesic conditions of the hummocks. In fact, these stands correspond well to the subassociation 'caricetosum membranacei' described by Barrett (1972) for the lowland. Both hummocky and hydric meadows described here correspond to his 'Caricetum stantis' association.

b. Hydric meadows - Carex aquatilis var. stans - Drepanocladus revolvens - Meesia triquetra - Calliergon giganteum

As in the hummocky meadows, the species appearing as indicators of hydric stands are wholly appropriate. Drepanocladus brevifolius, for example, is commonly associated with wet, Ca-rich fens, as are Bryum calophyllum, Calliergon giganteum and the hepatic Lophozia rutheana (Kuc 1973; Schuster & Damsholt 1974; Vitt 1975; Steere 1978; Vitt 1991, pers. comm.). Shrubs were virtually lacking in the hydric meadows (Stands T11, T12, T13).

These meadows are extremely impoverished floristically and were comprised almost exclusively of Carex aquatilis var. stans, with small amounts of Dupontia fisheri ssp. psilosantha, Eriophorum angustifolium and Juncus biglumis among vascular plants. Among bryophytes, 78% of the cover is provided by only three species: Calliergon giganteum, Drepanocladus revolvens and Meesia triquetra (Vitt & Pakarinen 1977). As with the others mentioned above, M. triquetra is a rich fen indicator of high fidelity (Montagnes 1990). Other bryophytes occurring frequently in the sampled stands included Campylium arcticum, Catoscopium nigritum and Cinclidium latifolium, also species of Ca-rich habitats (Holmen et al. 1974; Vitt 1975; Steere 1978). The hydric and hydric-mesic meadows correspond well to Barrett's (1972) 'caricetosum stantis' subassociation.

3.2 Classification of anthropogenically disturbed vegetation

Clyde River, Truelove Lowland and Resolute Bay

Table 3.2 (see enclosure) represents vegetation data (246 samples x 154 species) from anthropogenically disturbed stands from all three islands including both meadow and beach ridge stands. As with natural vegetation, the outlier Stand 17 was removed prior to analysis. Being the site of intensive chemical dumping its vegetation was not continuous with the rest of the stands at CR (nor TL or RB) and it consistently skewed ordination and classification results. Again, no species were downweighted during the analysis and the same cut levels (0-6) were used as above. The TWINSPAN classification was run to seven levels of division, at which point all but six of the 41 noda were comprised of one stand each.

i. Truelove Lowland

a. Multi-pass vehicle tracks

As in the natural meadows, Aulacomnium palustre factors into the first split on the right-hand side, being present at high frequencies in many disturbed situations at CR, as well as on the two unexacavated Thule pads (T15on, T16on) at TL. However, additional discrimination is provided by Drepanocladus revolvens and high cover/abundance of Carex aquatilis var. stans, which indicate the relative moisture of stands on the left-hand side of the dendrogram. From left to right the noda exhibit an *approximate* gradient of decreasing moisture, with some exceptions. Many of the indicators leading through the hierarchy to the first eleven noda are aquatics, such as Ranunculus hyperboreus, or pronounced hydropiles, such as Bryum cryophilum, Calliergon giganteum, Drepanocladus brevifolius and Meesia triquetra.

Porsild (1932: 30) reports both R. hyperboreus and R. pygmaeus to be "strongly nitrophilous". Interestingly, the former was present at relatively low cover values but with remarkable regularity in vehicle tracks through many meadow types, even in the wettest meadows where it might be expected to occur naturally. In this instance (T4), it occurred abundantly in the open, pooled water of a severely disturbed track through a mesic, hummocky transition zone from rock outcrops to wet meadows. Although R. pygmaeus did not occur in any of my sample plots, I made collections from small populations which were flowering profusely in a few scattered places around the old housepads at CR and it exists in great abundance in the effluent path below the dump at the new settlement there (**Plate 3.3**). Relative to the multi-pass tracks at CR (Noda 14-17), the eigenvalues are lower and number of indicators used to make divisions is often higher at TL. This was also the case for the undisturbed major meadow formations in **Table 3.1**.

b. Few-passes vehicle tracks

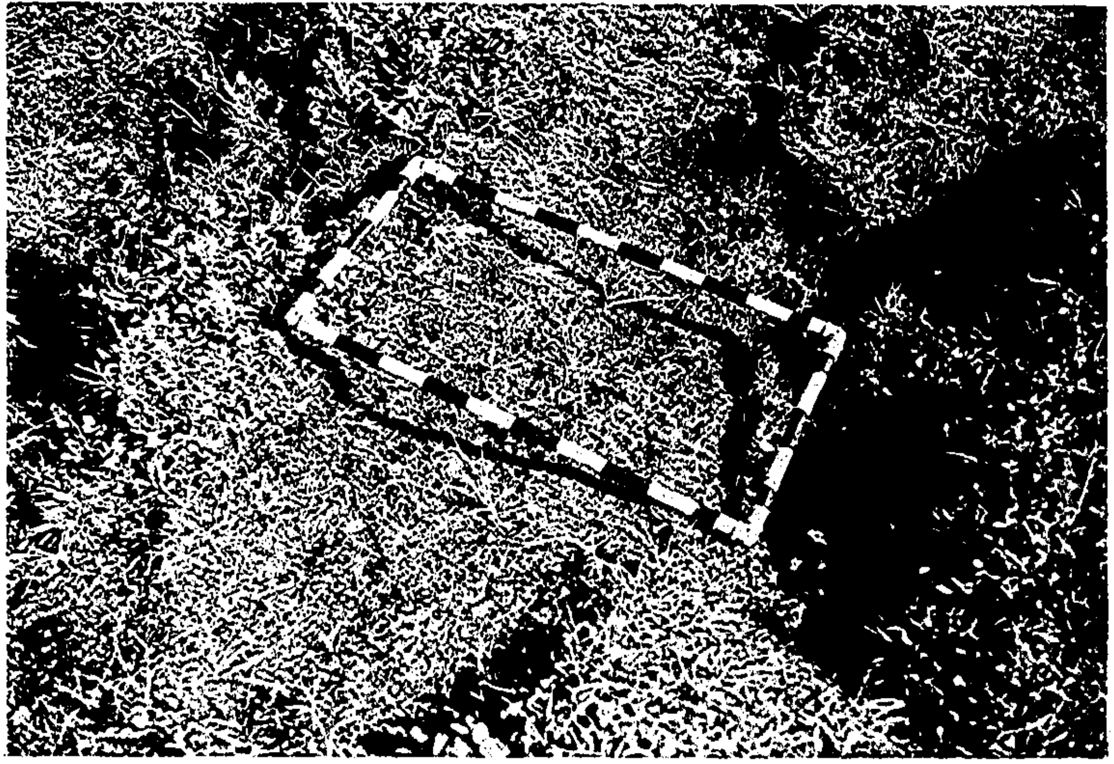
Stands T2 and T10 are differentiated here based on the presence of Pogonatum alpinum, a common species of meadow hummocks at TL (Vitt 1975). Both sets of tracks are through moderately hummocky meadows and although they remain slightly rutted and moist relative to the adjacent terrain, the high frequency of P. alpinum would appear to indicate that these stands were still more hummocky than the multi-pass tracks. Other mosses present at high

Plate 3.3 - View of effluent path below dump at the new settlement at CR. This area was not sampled but clearly demonstrates the colonizing potential of Alopecurus alpinus (green), in particular, and Oxyria digyna (red). Purple hue on high ground is from panicles of Arctagrostis latifolia ssp. latifolia. Abundant understory plants include Saxifraga cernua and Ranunculus pygmaeus. Although A. alpinus is reputed to rarely produce viable seed in the High Arctic (Bliss & Grulke 1988), it seems unlikely that an area this size could have been colonized to this extent solely by clonal growth of a species which is not found in the adjacent undisturbed vegetation and may not have existed on the site, or was at least rare, at the time of initial dumping 20 yr ago. One possibility is that the elevated nutrition and warmth provided by the southerly aspect led the initial colonizers to produce viable seed in one or more years, which contributed to rapid colonization of the site. The density and vigor of the sward is not unlike that seen on some abandoned housepads and adjacent heavily trampled terrain at the study site (**see Plate 4.13**). Photo date: 19 July 1990.

Plate 3.4 - Downslope portion of tracks seen in **Plate 2.4**. Water is moving slightly faster here and gully erosion is more evident, though not nearly as severe as further downslope where slope increases just slightly. Photo date: 21 June 1990.

Plate 3.5 - Multi-pass tracks perpendicular to local slope at CR (see **Plate 3.1**). Portions of tracks which remain under standing water long after snowmelt are dominated by Eriophorum angustifolium. Raised patch at mid-rear is well-drained and nearly devoid of vegetation with little evidence of active invasion. Large gully from concentrated runoff is at far-rear. Photo date: 19 July 1988.

Plate 3.6 - Close-up of drained peatlands 10 m below multi-pass tracks seen in **Plate 3.1** showing hollows with dead and shrunken Sphagnum spp., which used to dominate understory of vegetation, as it still does 20 m upslope (**Plate 2.5**). Populations of Carex aquatilis var. stans and Eriophorum angustifolium are nearly extinct and nutritionally impoverised relative to undisturbed populations. These plants are being replaced by expanding individuals of Salix arctica, and colonizing lichens and Luzula nivalis. Photo date: 19 August 1990.



frequencies, but not indicated in the dendrogram, included Bryum pseudotriquetrum, Catoscopium nigritum, Cinclidium latifolium and Orthothecium chryseum. Beyond that, the tracks exhibited an open vascular cover characterized by the same few graminoids which comprised many of the meadows: mostly Eriophorum angustifolium, Carex aquatilis var. stans and Juncus biglumis. A few seedlings of Salix arctica were observed, in contrast to both adjacent natural vegetation, where Salix populations were extensive, and other, wetter and/or more disturbed tracks, where Salix was lacking entirely.

ii. Clyde River

a. Multi-pass tracks

These tracks fall into two basic categories at CR - those that run perpendicular to local slope (11on, 12on), and those that run parallel to local slope (9, 10). Both are characterized by a complete lack of Sphagnum spp. and have been colonized by vascular and non-vascular taxa lacking in the adjacent undisturbed formation, such as Phippsia algida, Alopecurus alpinus and, to a lesser extent, Juncus biglumis. The tracks parallel to slope are least diverse floristically and are readily differentiated from the closest perpendicular tracks in Stand 11on (eigenvalue = 0.432), but poorly differentiated from each other (eigenvalue = 0.222). Some frequent colonizers not appearing in the dendrogram include Psilopilum cavifolium, Bryum cryophilum, B. pseudotriquetrum and Hypnum bambergeri, mostly species of disturbed and/or wet soils (Vitt 1975; Crum 1983).

Among graminoids, Dupontia fisheri ssp. psilosantha has extensively colonized the wettest portions of the track through Stand 11, which is well within a water channel zone. It was mixed in places with Eriophorum angustifolium, both here and in Stand 12. E. angustifolium seemed more abundant on those portions of the track which were slightly raised but still submerged during spring runoff (**Plate 3.5**). Carex aquatilis var. stans was present in all tracks, and in the natural vegetation, but was most important in terms of cover in the track through Stand 9. Interestingly, E. angustifolium appeared as a colonist in Stand 10, where it formed a closed cover over much of the tracks, though it was absent in the more mesic natural vegetation.

b. Single-pass tracks

Single-pass tracks at CR are from both major vegetation cover types. Stands 3 and 4 (Noda 12, 13) occur in an area of minimal slope (0-1.0°) which is lacking Sphagnum hummocks. Stands 1, 2 and 13 (Noda 19, 20) occur among hygric Sphagnum hummocks where local slope is 4.5-5.0°. The tracks in Stands 1 and 2 are diagonally oriented to local slope and those in Stand 13 are perpendicular to the slope. Stands 16on and 15 (Noda 18, 21) are tracks among Sphagnum hummocks and cross a water channel and its adjacent interfluve respectively. The latter is perpendicular to the local slope of 4.0°, while the former runs diagonal to it.

Despite the relative lack of slope in Stands 3 and 4, their positions within and below late-lying snow areas mean that water runs gently in the tracks during the early part of the growing season. This hydrology is important because even though gully erosion in this portion of the tracks is not significant (see, however, downslope area in **Plate 3.4**). What little organic mat existed has long since been removed (see **Plate 2.10**), as have a significant amount of fines (see Section 3.10.vii), and the specialist moss Blindia acuta has colonized most of the loose, small stones in the track. A similar situation has occurred at TL, where Seligeria polaris has colonized exposed calcareous pebbles and stones in tracks through Stand T5 (Nodum 7). Both are species of extremely distinct habitats (Vitt 1975; Steere 1978). Another colonist in the tracks in Stands 3 and 4 was Eriophorum scheuchzeri, which is adapted to fertile soils according to McGraw & Chapin (1989). It had a patchy occurrence in and around small, ephemeral puddles where organics have collected. Additional cover was provided by discrete clones of Carex membranacea and E. angustifolium and small tufts of Juncus bigumis but, in general, cover was more open than closed.

Stands 1, 2, and 13 have no colonists in the tracks and are weakly differentiated (eigenvalue = 0.173) based on their remant floras, in particular the lack of Salix reticulata and Sphagnum squarrosum in Stands 2 and 13. These three stands are, in turn, weakly differentiated (eigenvalue = 0.157) from the interfluve track through Stand 15. The split is based on two taxa. Aulacomnium acuminatum, as discussed earlier, is a species of drier hummocks, while Plagiomnium medium ssp. curvatulum is a plant of wet, peaty soils and along streams (Steere 1978). Together these taxa help to indicate the relative moisture of Stands 1, 2 and 13 compared to the interfluve. P. medium ssp. curvatulum was also frequent in the water channel Stand 16on, which is indicated here by the hepatic Ptilidium ciliare, an acidophile of good fidelity described above. It is interesting to note that S. squarrosum was completely lacking in the undisturbed interfluve zone, yet small patches had colonized the wetter portions of the vehicle tracks. Conversely, both Sphagna comprised much of the hummocky vegetation in the adjacent water channel, yet only S. squarrosum was missing in the vehicle track. The same situation was observed in Stands 1, 2 and 13.

c. Drained peat meadows

The channelling of surface and subsurface flow by both single- and multi-pass vehicle tracks during spring runoff has dessicated those portions of the meadows downslope from the tracks. The hydrological effect was apparently immediate (**Plate 2.9** and Section 3.10.2.a) and has had a cumulative impact on the vegetation composition which was easily detected by the numerical classification. The stands (Noda 22-25) straddle the transition from the left half of the dendrogram to the right half. This break is logical given the conspicuous lack of Aulacomnium palustre in Stand 12up, and the frequent presence of Meesia uliginosa. Stand 12up occurs immediately downslope from a single-pass track which traverses a water channel, as does Stand 16dn.

The geographic and local variation of A. palustre was discussed above. Given that the soil in Stand 12up has an average pH of 4.78, it would appear that M. uliginosa may have somewhat different habitat preferences in the High Arctic than in the Low Arctic. Steere (1978:302) describes this plant from wet fens, in streams and "always in frankly calcareous habitats" in northern Alaska. Vitt (1975), on the other hand, observed it as rare in the wet, calcareous meadows of TL, where it was found more often in the drier meadows and on hummocks in the wetter meadows. Polunin (1948) did not report this species from CR, but he decribed its habitat from Arctic Bay where it occurred in a 'bog' (he does not indicate its pH) with Sphagnum squarrosum, Calliergon giganteum and M. triquetra. The latter two were entirely lacking in the meadows sampled at CR. It occured in similar admixtures (mostly sphagnous, again no pH indicated) around northern Hudon's Bay (op. cit). Brassard (1971) noted M. uliginosa as nowhere abundant, but present in a variety of habitats including on Dryas and Cassiope hummocks, in mossy cracks and near pond margins. It would appear then that this species is increasingly tolerant of drier and more acidic habitats toward the eastern and northern margins of its North American range, but is still commonly found on wet, Ca-rich soils.

Stands 12up and 16dn occurred adjacent to one another in the water channel but have slightly differing hydrologies and this was reflected in the species present. Stand 12up is closer to the interfluve and, although it is apparently more mesic in the absence of vehicle tracks on this portion of the slope, is visibly wetter at mid-season than Stand 16dn. Stand 16dn is fairly in the center of the water channel, but the impression from the vehicle is more apparent here and continues to channel runoff more effectively than the vehicle track through Stand 12up. The resulting floristic and vegetational changes were more significant in Stand 16dn, but these are not entirely evident given the disjunct positions of these two stands in the dendrogram. Changes downslope from the track in Stand 16 include a complete lack of the more hydric mosses Calliergon sarmentosum, Drepanocladus revolvens and Plagiomnium medium ssp. curvatulum. However, populations of both Sphagnum spp. remained healthy and even dominant here and in Stand 12up. Among vascular plants there was a slight decrease in cover of Eriophorum angustifolium in both stands.

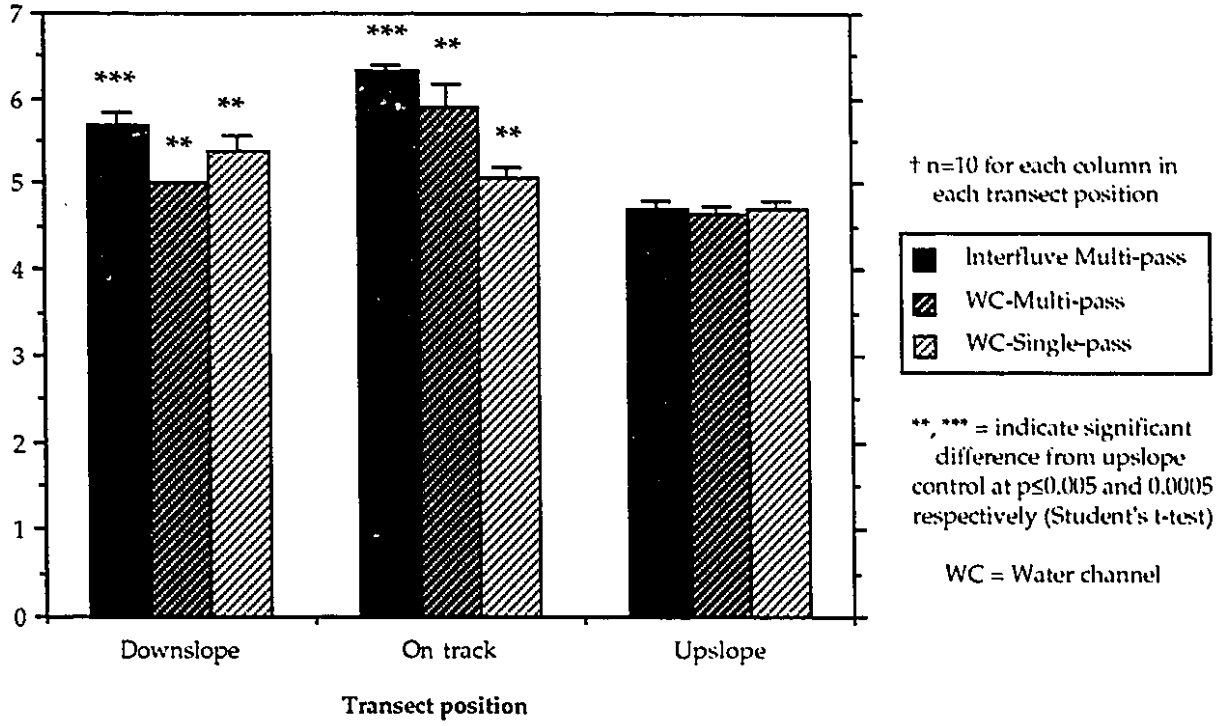
Stands 11dn, 12dn and 12(16)dn (Noda 23, 24) are all from 2 to 10 m downslope from multi-pass tracks (Stands 11on, 12on), 11dn being below the center of the water channel. Stands 12dn and 12(16)dn are in a line parallel to

12up and local slope and are thus closer to the interfluve. The two are separated in the dendrogram (eigenvalue 0.462) according to the increased frequency of Carex bigelowii, which has apparently colonized the dessicated hollows in Stand 11dn. There are several serious changes not evident from the dendrogram. Most importantly, populations of both Sphagnum spp. are now extinct (**Plate 3.6**). Some former Sphagnum associates (Steere 1978) have remained, such as Dicranum angustum in Stand 11dn and Drepanocladus badius in Stand 12dn.

One of the few colonists among bryophytes in the downslope vegetation was Isopterygium pulchellum, which was rare at this study site but is a common species of dry, calcareous meadows at TL (Vitt 1975). Interestingly, soil pH was slightly but significantly higher downslope (**Fig. 3.1**) and in Stand 17off, the only other stand where this species was collected during the study. Perhaps the best ecological indication of downslope dessication is the abundance of lichens which have colonized the sides and tops of many of the hummocks. These include several common and fertile fruticose forms, such as Alectoria spp., Cetraria nivalis, Cladonia spp. and Thamnolia subuliformis, and two sterile crustose forms (Collema sp. and Ochrolechia sp.). There were also significant changes in the cover, abundance and biomass of the rhizomatous graminoids Carex aquatilis var. stans and Eriophorum angustifolium, and similar increases in the caespitose graminoid Luzula nivalis, and the deciduous shrub Salix arctica (**Plate 3.6**).

Fig. 3.1 - Soil pH from vehicle tracks, drained peatlands and adjacent controls at CR. Note that pH is increased relative to controls in areas downslope from vehicle tracks and in tracks. These differences were significant during all three months comprising the growing season. This histogram depicts the approximate peak season.

Fig. 3.1 - Mineral soil pH - Vehicle tracks, drained peatlands and adjacent controls - Stands 11, 12 & 16 - Clyde River - 20 July 1990 †



† n=10 for each column in each transect position

, * = indicate significant difference from upslope control at p≤0.005 and 0.0005 respectively (Student's t-test)

WC = Water channel

iii. Clyde River and Truelove Lowland

Pedestrian trampled meadows and associated unexcavated Thule dwellings

Next to the drained meadows in the dendrogram, but differentiated by a near maximum number of indicator species and a moderately high eigenvalue (0.390), is a lightly trampled stand from CR (Stand 18lgt; Nodum 26). In one of the most revealing phytogeographic linkages to arise from this analysis, the vegetation of this stand was a mixed graminoid/shrub/forb turf with apparently close floristic affinities to the turf appearing on unexcavated Thule dwellings at TL (Stands T15on, T16on; Noda 27, 28). These stands have a long list of taxa in common with representatives from each life form. These include mosses, (Aulacomnium spp., Dicranum elongatum, Drepanocladus uncinatus, Pogonatum alpinum), hepatics (Anastrophyllum minutum, Tritomaria quinquedentata), vascular plants (Alopecurus alpinus, Poa arctica, Salix arctica, Saxifraga cernua) and a lichen (Peltigera aphthosa). In the TWINSPAN analysis, it is only the presence of a different species of Stellaria which distinguishes the palaeo dwellings at TL from the lightly trampled surroundings of the contemporary homesite at CR (S. longipes and S. edwardsii, respectively). Even this separation occurs only after seven levels of division.

The vegetation/floristic changes illustrated by four of the remaining five trampled stands (Noda 29-32) serve as an example for much of the analysis as whole, being organized from left to right along an apparent gradient of decreasing moisture and increasing degree of disturbance. In all, TWINSPAN differentiated three levels of treading intensity. The wetter, moderately trampled Stands 7mod and 19mod are indicated by the aquatic graminoid Dupontia fisheri ssp. psilosantha. Also abundant here, but not apparent from the dendrogram, were the hydrophiles Bryum cryophilum, B. pseudotriquetrum and Plagiomnium medium ssp. curvatulum. The frequent presence of Carex membranacea is consistent with the fact that Stand 7mod is somewhat less wet than Stand 19mod. Sphagnum ssp. were conspicuously lacking in all trampled areas. The more heavily trampled of the two, Stand 14mod, registers an increase in cover/abundance of A. alpinus. Interestingly, as with the lightly trampled meadow, these stands appear quite close to Thule dwellings at TL (and RB) in terms of their vegetation composition and cover.

iv. Truelove Lowland - Resolute Bay

Recently excavated and unexcavated Thule dwellings

Stands T14on and RBon (Noda 38, 39) represent recently excavated and unexcavated dwellings at TL and RB respectively. In the TWINSPAN analysis they are differentiated from the previous group of moderately trampled meadows only by the presence of Tortula ruralis. T. ruralis is characterized by Vitt (1975) as widespread at TL but most frequent in crevices and at the bases of calcareous rocks, but also common in drier meadows and often associated with D. flexicaule. Brassard (1971) reported T. ruralis to be one of the most conspicuous species around the ruins of Fort Conger on northern Ellesmere Island. Mogensen & Lewinsky (1982) found it to be common on Greelandic bird cliffs. Clearly more important in this instance is the large number of shared components from these sites, notably a moderately to very dense turf comprised of viviparous and rhizomatous graminoids, such as *Poa arctica* and *Alopecurus alpinus*.

The understory was comprised of mats of the mosses *Aulacomnium palustre* and *Drepanocladus uncinatus*, with abundant *Cirriphyllum cirrosum* and basal rosettes of *Saxifraga cernua*. Another notable aspect of the vegetation of these stands was the foliose lichen *Peltigera aphthosa*. This species was lacking on the beach ridges at TL and RB but has apparently colonized both the recently excavated dwelling (Stand T14on), where it was abundant between the flagstones of the central floor, and the moderately trampled portion of Stand 18 at CR (Nodum 31), where it was greatly increased in frequency and cover on the tops and sides of trampled hummocks relative to nearby undisturbed hummocks.

v. Clyde River

a. Pedestrian trampled stand

Stand 19hvy (Nodum 35) The drier, more heavily trampled vegetation of Stand 19hvy is indicated by and *Polytrichum commune* and *Cirriphyllum cirrosum*, both common species which occur in a wide range of natural habitats, including sand and rocks ranging from acidic to calcareous (Kuc 1973; Vitt 1975; Steere 1978). Also present but not shown here are the common dry ground and/or ruderal mosses *Ceratodon purpureus*, *Drepanocladus uncinatus* and *Pohlia nutans*. Vascular vegetation consisted of matted patches of profusely flowering *Alopecurus alpinus*, *Cerastium alpinum*, *Saxifraga rivularis* and *Stellaria edwardsii* and scattered clumps of the caespitose graminoids *Festuca brachyphylla*, *Puccinellia langeana* and *Phippsia algida*

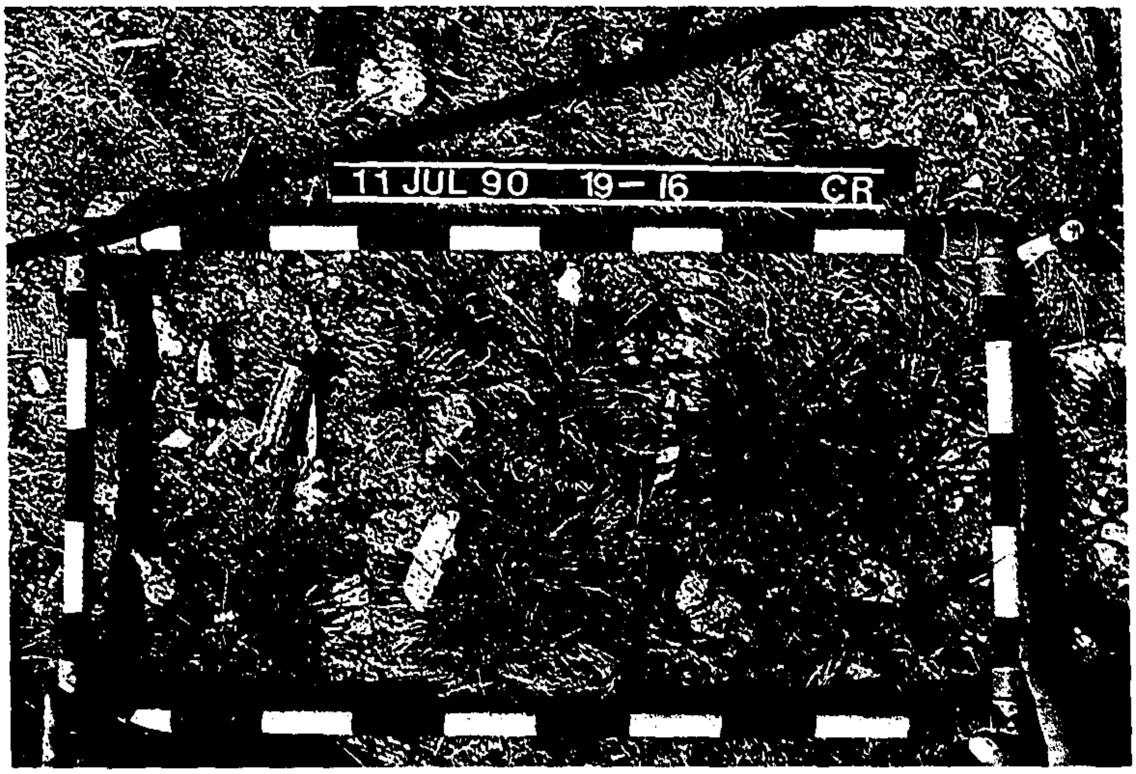
(**Plate 3.7**). Together these species indicate the dry, gravelly and heavily disturbed nature of the substrate.

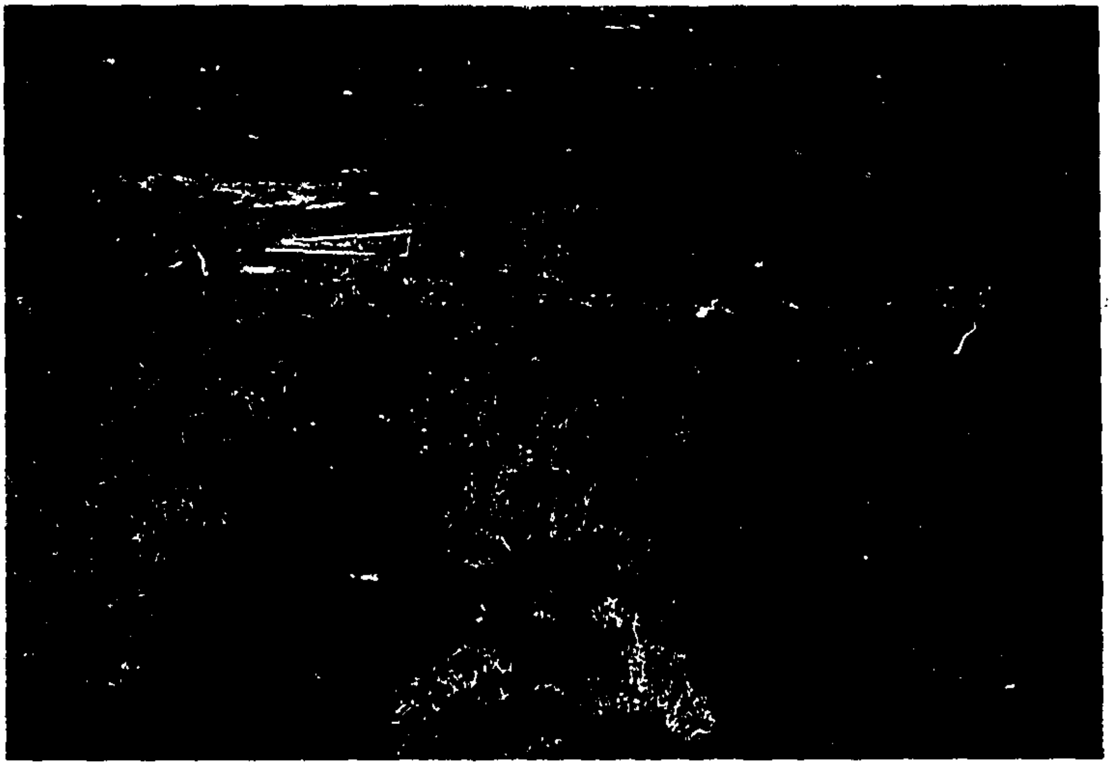
b. Contemporary housepads

The housepads are of three particular types, which can be considered as parts of two general groups. In the first (Stand 18on; Nodum 37), no materials were added and the house was placed more or less directly on the mesic tundra. In the second, (Stands 7on, 14on and 19on; Noda 35, 38) sand and/or gravel were used to fashion a dry, level foundation. Of the three, only 19on occurs on a beach ridge. Its separation from the others is pronounced (eigenvalue = 0.457), and its xeric status indicated by the ruderal colonist Byrum argenteum, the only stand in which this moss occurred, and the absence of B. pseudotriquetrum. The other three pads are situated in meadows and are more weakly differentiated (eigenvalue = 0.285), based on the presence of Polytrichum hyperboreum, which occurred only in Stands 7on and 14on and at high cover/abundance. Other colonizing taxa present were mostly graminoids, such as Puccinellia langeana and Festuca brachyphylla in the beach ridge stand, and Alopecurus alpinus, Luzula nivalis and Phippsia algida in the meadow stands. However, as in the above heavily trampled stand, a variety of upright and prostrate forbs were also common (e.g. Cerastium alpinum, Saxifraga cernua, S. rivularis and Stellaria edwardsii). Most occurred as patches or discrete clones and cover was generally open (see **Plate 3.7**).

Plate 3.7 - Quadrat from abandoned sand/gravel housepad (Type C) on a beach ridge at CR showing colonization pattern of caespitose grasses (mostly Puccinellia langeana, with lesser amounts of Phippsia algida and Festuca brachyphylla). Housepads of this nature range from nearly bare (marginal, extremely resistant environments *sensu* Svoboda & Henry 1987) to patches such as these in which the grass tufts begin to touch one another and coalesce (high resistance *sensu* Svoboda & Henry 1987). Note the seedlings of Alopecurus alpinus, emerging from the tufts at right, and the virtual absence of bryophytes and lichens between vascular plants.

Plate 3.8 - General aspect during late summer of snow patch area with single-pass track (Stand 4) seen in **Plate 2.4**. Vascular canopy of undisturbed vegetation is open and cryptogamic layer is mostly closed. With Sphagnum spp. absent there is little variation in microtopography. Despite the minimal local slope (0-1°), the low albedo of the undisturbed terrain contributes to high surface and subsurface temperatures after snowmelt and active development is enhanced relative to other stands. Note flowering culms of Eriophorum scheuchzeri in tracks, a species not present in the control area. Quadrat frame at rear is 1 x 1 m. Photo date: 7 August 1988.


11 JUL 90 19-16 CR



c. Beach ridges

The beach ridge stands are separated early in the analysis (eigenvalue = 0.508) and are indicated by a number taxa which are mostly indicative of dry conditions. Whereas the beach ridges of TL and RB are dissimilar from the adjacent Thule dwellings in terms of much of their vascular and lichen composition and cover, the bryofloras of both tended to include taxa indicative of calcareous substrates. Taxa appearing at higher frequencies on the xeric, rocky beach ridges included a Distichium sp. (probably D. capillaceum, Vitt 1991, pers. comm.), Ditrichum flexicaule, Drepanocladus uncinatus, Hypnum revolutum, Orthotrichum speciosum and Timmia austriaca. The most abundant vascular plants here were Salix arctica and Saxifraga oppositifolia with lesser amounts of Dryas integrifolia. The beach ridge at RB is only moderately dissimilar from those at TL (eigenvalue = 0.367), indicated by the absence of Encalypta rhaptocarpa. A long list of common lichens were frequent components of the vegetation here but were conspicuously lacking on the housepads. These included crustose (e.g. Rhizocarpon geographicum, Rinodina sp.), foliose (e.g. Caloplaca tornöensis, Parmelia omphalodes) and fruticose forms (e.g. Alectoria nigricans, Bryoria chalybeiformis, Cetraria spp. and Thamnolia subuliformis). The fruticose forms were often in poor condition, apparently being susceptible to even the lightest traffic from researchers and other visitors to the sites, although woody plants were in excellent condition and exhibited no breakage.

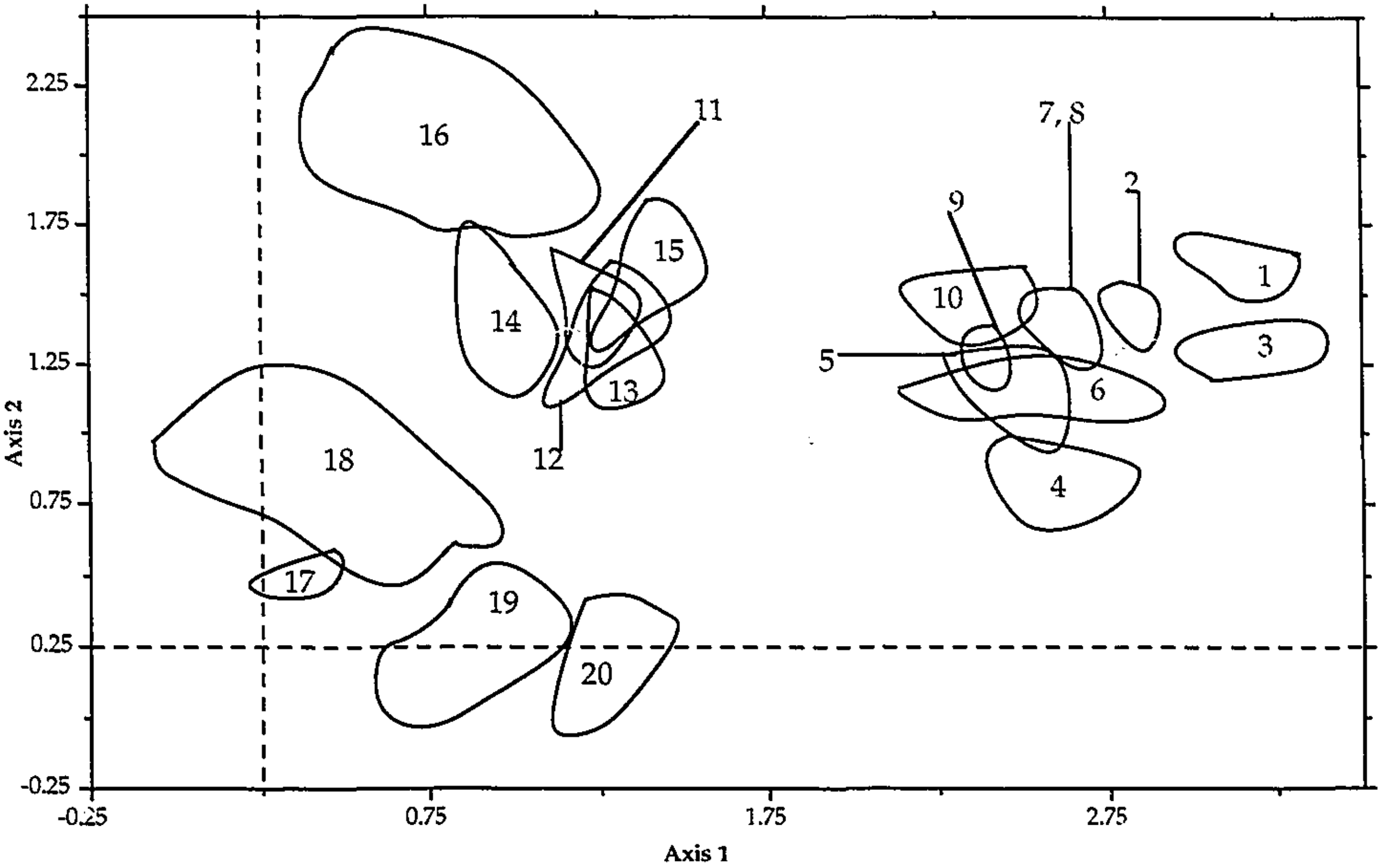
3.3 Sample ordinations of natural vegetation

Meadows at Clyde River and Truelove Lowland

Fig. 3.2 is a DCA ordination biplot, using detrending by segments, of the same species and samples as classified in **Table 3.1**. We see an abstraction of the phytogeographic relationship of the two study sites, as well as the general ecological relationships of the meadows within each landscape. The clusters have been delimited by hand and their numbers correspond to the noda assigned in the TWINSPAN analysis which appear in **Table 3.1**. Eigenvalues decline consistently over the first four axes (0.449, 0.242, 0.131, 0.100), suggesting that most of the variation in species composition is described by axes I and II, which are shown. The gradient of estimated species turnover (beta diversity) along the first axis is moderately high, 3.365 in terms of s.d. units (**Table 3.3a**). As gradients lengths approach 4.0 s.d., it is to be expected that stands at either end of the first axis will have few species in common (ter Braak 1987b). Noda 1-10 represent the stands from TL and Noda 11-20 represent those from CR. Although the vascular floras of the two meadow systems are nearly identical, there is clearly no overlap among samples from the two study sites when cryptogamic floristics are included as they are here (Forbes 1992d). This separation is due primarily to the degree to which the bryofloras of the two lowlands indicate the gross differences between a minerotrophic site (TL), on the right hand side, and an oligotrophic site (CR) on the left.

Within each lowland there are also differences in the degree of separation, despite the density of samples (*n* = 126). The gently sloped and relatively mesic oligotrophic fens of CR represent a wider local gradient

Fig. 3.2 - DCA biplot of natural meadow vegetation at CR and TL.



2.25
1.75
1.25
0.75
0.25
-0.25
-0.25
0.75
1.75
2.75
Axis 2
Axis 1
1
2
3
4
5
6
7, 8
9
10
11
12
13
14
15
16
17
18
19
20

Fig. 3.3a - DCA biplot of anthropogenically disturbed vegetation at CR, TL, and RB.

CRTLD(T)-17(DCA)

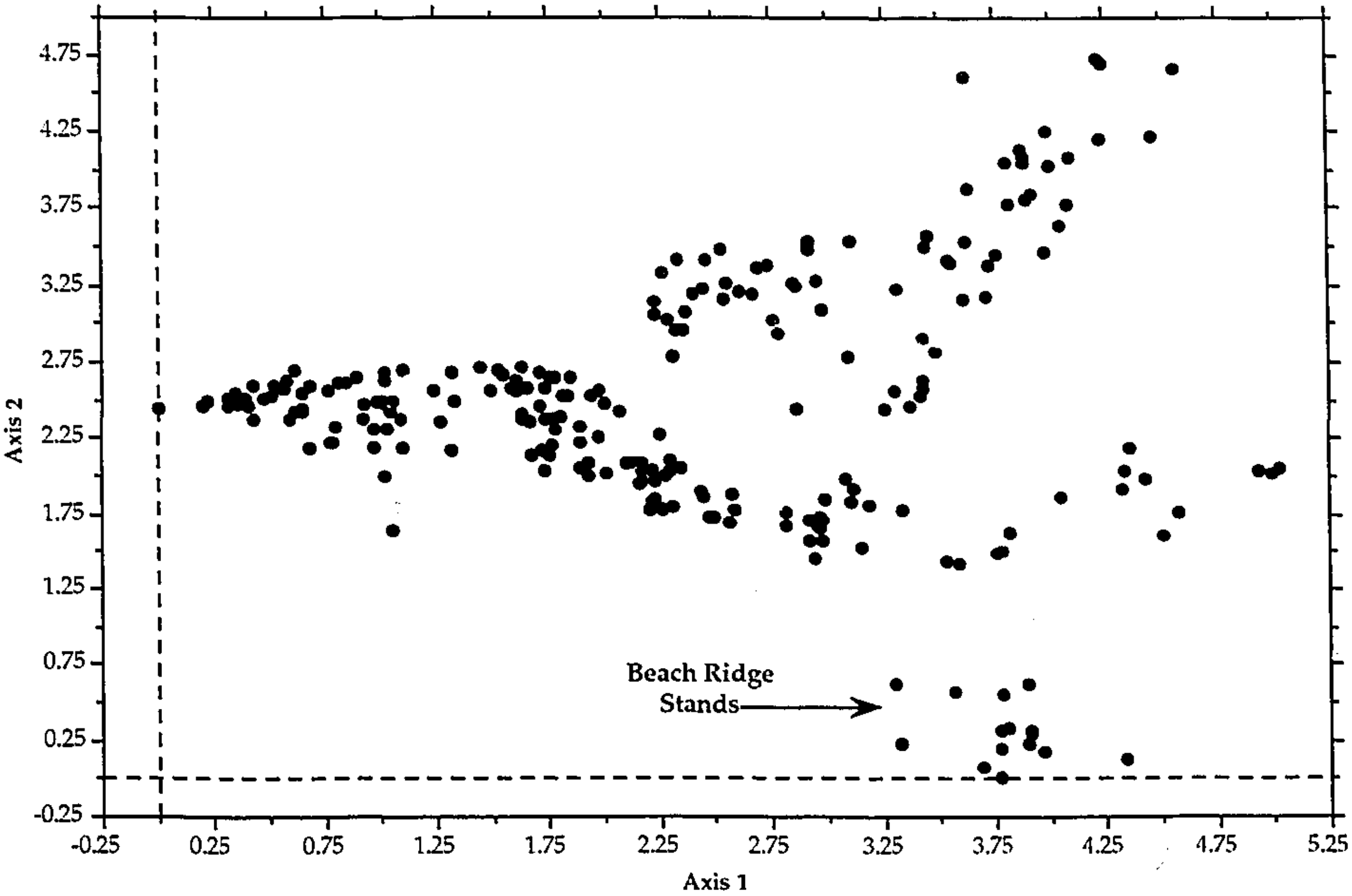


Fig. 3.3b - DCA biplot of anthropogenically disturbed vegetation at CR, TL, and RB.

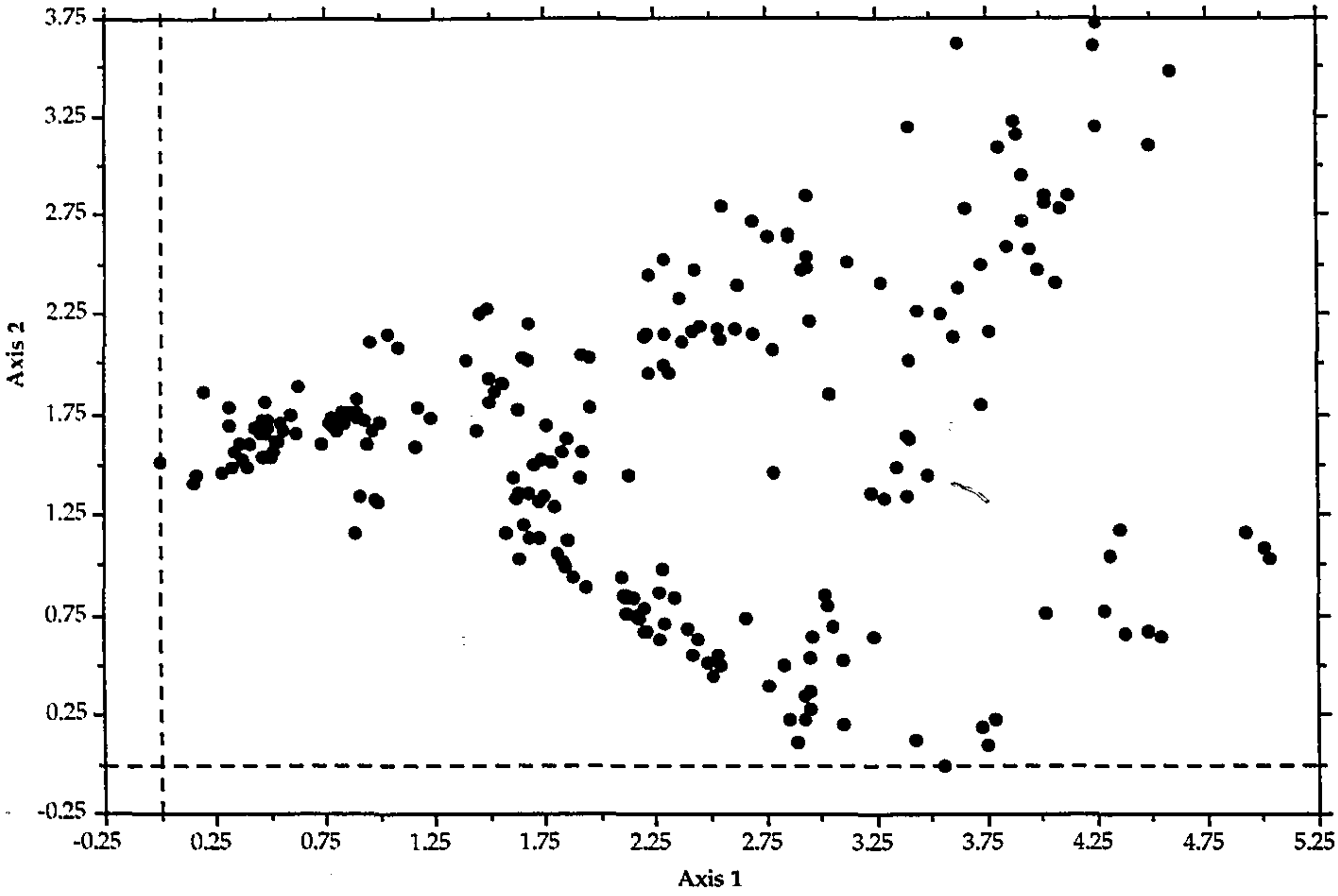

Axis 2
3.75
3.25
2.75
2.25
1.75
1.25
0.75
0.25
-0.25
Axis 1
-0.25
0.25
0.75
1.25
1.75
2.25
2.75
3.25
3.75
4.25
4.75
5.25

Fig. 3.4 - DCA biplot of natural meadow vegetation at CR.

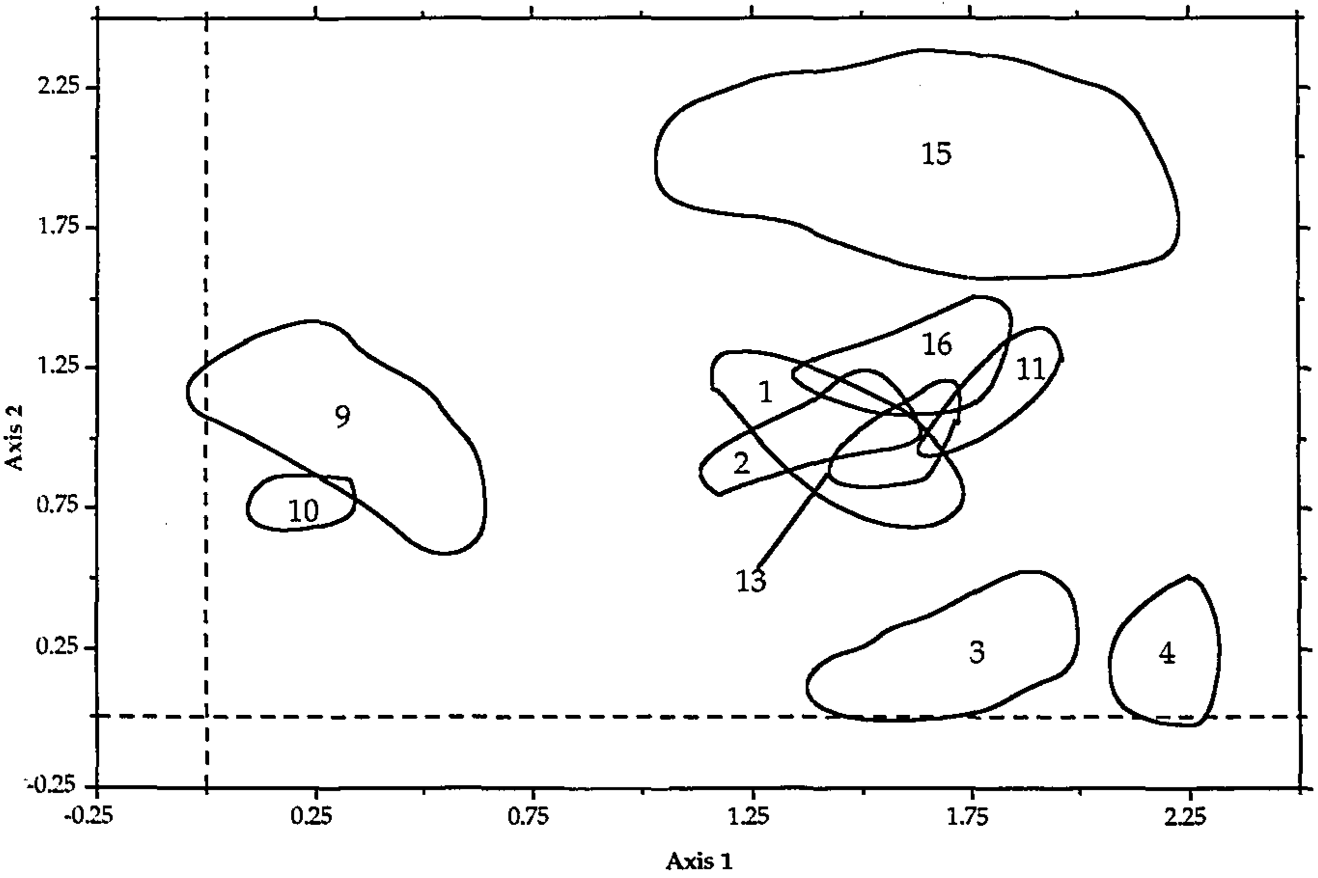

2.25
1.75
1.25
0.75
0.25
-0.25
-0.25
0.25
0.75
1.25
1.75
2.25
Axis 1
Axis 2
15
16
1
11
9
2
10
13
3
4

Fig. 3.5 - DCA biplot of natural meadow vegetation at TL.

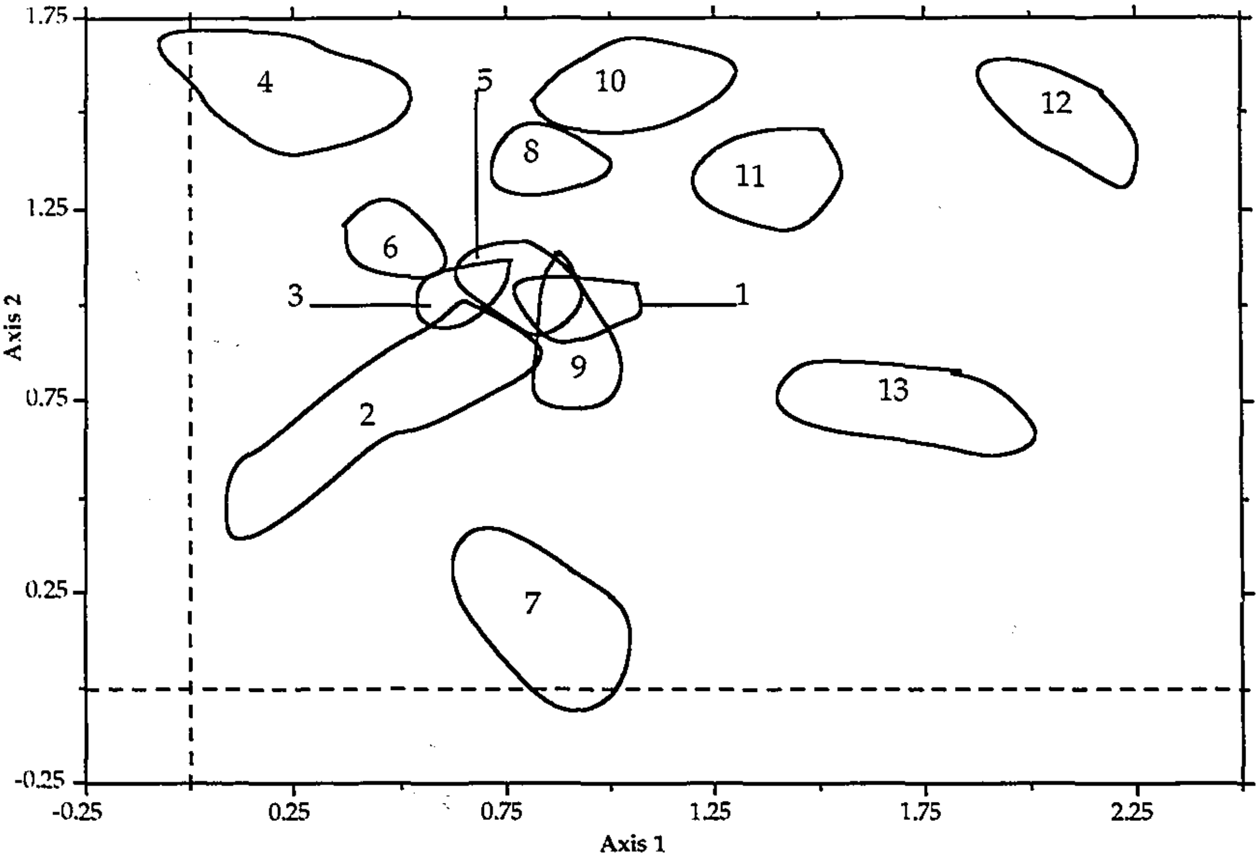

1.75
1.25
0.75
0.25
-0.25
Axis 2
-0.25
0.25
0.75
1.25
1.75
2.25
Axis 1
1
2
3
4
5
6
7
8
9
10
11
12
13

Table 3.3

Summary tables for detrended correspondence analyses

A. Natural meadow vegetation at CR and TL

	Axes				
	1	2	3	4	
Eigenvalues	0.449	0.242	0.131	0.100	
Lengths of gradient	3.963	2.416	1.847	1.983	
Cumulative percentage variance of species data	14.0	21.5	25.6	28.7	
Sum of all unconstrained eigenvalues					3.221

B. Anthropogenically disturbed vegetation at CR, TL and RB

	Axes				
	1	2	3	4	
Eigenvalues	0.614	0.457	0.271	0.216	
Lengths of gradient	5.032	4.731	2.829	3.912	
Cumulative percentage variance of species data	8.7	15.2	19.0	22.1	
Sum of all unconstrained eigenvalues					7.066

C. Natural meadow vegetation at CR

	Axes				
	1	2	3	4	
Eigenvalues	0.305	0.220	0.112	0.083	
Lengths of gradient	2.449	2.165	1.556	1.761	
Cumulative percentage variance of species data	13.4	23.1	28.0	31.7	
Sum of all unconstrained eigenvalues					2.271

D. Natural meadow vegetation at TL

	Axes				
	1	2	3	4	
Eigenvalues	0.212	0.143	0.081	0.049	
Lengths of gradient	2.216	1.680	1.383	1.096	
Cumulative percentage variance of species data	13.9	23.3	28.7	31.9	
Sum of all unconstrained eigenvalues					1.520

in terms of soil pH, drainage conditions, corrected conductivity, and species present and may be classified as 'poor' or 'transitional poor fens' according to these criteria (Sjörs 1952; Crum 1988). The wetter, minerotrophic or 'rich' fens of TL, by comparison, are clustered with little separation along either axis. In this respect, the results corroborate quite well those of the classification (**Table 3.1**), whereby the eigenvalues separating the major groups at TL are rather low. Similarly, the hydric-mesic stands from CR (Noda 11-15) are clustered with some overlap in the ordination space and have correspondingly low eigenvalues in the TWINSPAN dendrogram.

In an ordination the overall type of arrangement of stands seen here is called the "tongue effect", defined as a separation of sample plots near the end of the first axis, and can be caused by a number of factors (Minchin 1987). In this instance it appears that the tongue represents true structure in the data set, more or less distorted by the detrending procedure. It is well known that CA and DCA are vulnerable to large disjunctions (Vitt et al. 1986; Økland 1990a). However, the distortion is only a slight exaggeration of reality in this case. This is because the size of the quadrat used invariably meant that some samples were characterized by 'hummock' taxa (e.g. Carex misandra, Cladonia spp., Collema sp.), while others were more characterized by hollow taxa (e.g. Drepanocladus revolvens, Calliergon sarmentosum). The fact that both sets of these taxa occur in the same stand and occasionally in the same quadrat would lead one to expect the type of dispersion among samples seen here in Nodum 16 (Stand 15) from CR. In the species ordination, which are not shown, these taxa were mostly peripheral with moderately low weights and it appeared that their optima strongly affected the distribution of samples from Nodum 16 in the ordination space.

3.4 Sample ordination of anthropogenically disturbed vegetation

Clyde River, Truelove Lowland and Resolute Bay

The DCA ordination biplot in **Fig. 3.3a** was created with the same samples and species used in the TWINSPAN analysis (**Table 3.2**) and again detrended by segments. This simultaneous ordination of the 246 samples x 125 species resulted in the construction of two near continuous gradients with only one major break, this being caused by the beach ridges (lower right) which have sustained only minimal damage, such as breakage of some fruticose lichens, and have a rather distinct flora. The density of samples is twice that appearing in the analysis of natural vegetation and the potential for meaningful local interpretation based on the ordination space of the first two axes is limited given the apparent crowding of samples. Eigenvalues are higher than those from the natural vegetation (0.614, 0.457, 0.271, 0.216) and also decline consistently. However, the third and fourth axes register reasonably high values, indicating a potentially significant amount of information is not visible (**Table 3.3b**). The estimated lengths of the gradients along axes I and II are 5.032 and 4.731 s.d. respectively and considerably greater than those estimated for the natural vegetation. This indicates a much larger variation in species turnover between extreme samples along both axes and that terminal stands at opposite ends have no species in common.

Note that the gradient length of the fourth axis is higher than the third (**Table 3.3b**). Higher gradient length of a lower-ranked axis is often an indication that the latter is determined by outliers or random effects of high noise levels (Økland 1990c). Close inspection of the arrangement of the stands indicated that these were in virtual agreement with similarity estimates provided by the TWINSPAN analysis. For example, we are reminded of the early and pronounced separation of the beach ridge stands in the TWINSPAN analysis and that the unexcavated Thule dwellings from TL were quite similar to the lightly trampled meadow at CR (see Noda 26-28 in **Table 3.2**). Also apparent is the gradient of relative moisture along the first axis, with the wettest meadows of TL appearing at the far left of both the biplot and the dendrogram, and with gravel/sand housepads and beach ridges on the far right.

It is clear that the beach ridge stands are outliers with vegetation that is discontinuous with the rest of the data set and contribute to the tongue effect with great dispersion among samples on the right side of the first axis. These were removed from a subsequent analysis (**Fig. 3.3b**), which simultaneously improved both the dispersion and the continuity of the samples in the ordination space without changing its overall structure significantly. Eigenvalues and gradient lengths remained virtually unchanged on all but the second axis, which was expected. However, the biplot was deemed undesirable given the exceedingly crowded nature of the samples, the relatively high eigenvalues of the third and fourth axes and the limited potential for meaningful interpretation among sites, stands and, eventually, environmental variables. Instead, I decided to break the data into subsets for subsequent ordinations based on the vegetation units provided by the prior TWINSPAN analysis.

Both natural and disturbed data sets were subdivided and ordinated together and separately in the search for patterns. Such subdivision is common practice in multivariate analyses of large data sets. In particular, division of the material is useful when one gradient is relevant to a subset of the data-set only, and when poor performance is caused by outliers (Moen 1990; Økland 1990c; Walker 1990; Heikkinen 1991).

3.5 Sample ordinations of subsets of natural meadow vegetation

i. Clyde River

Ordinated separately from the meadows of TL, the biplot of natural meadow vegetation of CR (**Fig. 3.4**) appears quite similar to left portion of the biplot of the combined sites (**Fig. 3.2**). This implies that the relationship of the within-site stands in the latter are relatively independent of one another. Eigenvalues for the first four axes are 0.314. 0.213, 0.110 and 0.076 respectively (**Table 3.3c**). Shorter gradient lengths of the first two axes (2.287 and 2.329) reflect the reduction in species turnover between extreme stands. Once again, the stands with unusual combinations of species, due to either pronounced hummock-hollow microtopography (Stands 9, 10, 15) or late-lying snow (Stands 3, 4), appear at the periphery of the biplot. Stands with more moderate microrelief (Stands 1, 2, 13, 11up, 16up), generally lacking lichens and other plants characteristic of mesic-xeric conditions (e.g. Carex bigelowii, C. misandra, Lycopodium selago), are clustered at the center of the space with considerable overlap. Referring back to the TWINSPAN dendrogram (**Table 3.1**) we are reminded of their similarly poor differentiation.

ii. Truelove Lowland

A separate ordination of the meadows of TL (**Fig. 3.5**) displays greater dispersion than in the combined biplot of the first two axes (**Fig. 3.2**), but shows slightly lower species turnover than the meadows of CR, particularly along the second axis (**Table 3.3d**). Estimated gradient lengths for the first two axes are 2.216 and 1.680 respectively and eigenvalues for all four axes are reduced (0.212, 0.143, 0.081, 0.049) compared to CR. As in the biplot for CR, the first axis appears to be correlated to increasing moisture from left to right and the individual stands maintain their positions relative to one another.

3.6 Sample ordinations of subsets of anthropogenic vegetation

The large number of samples stands and disturbance regimes represented by the three study sites required that anthropogenic vegetation be analyzed in a series of subsets. The first subsets analyzed encompassed all stands within a given disturbance regime. Relative to the stands of trampled ground, the vehicle tracks and drained peatlands comprise gradient endpoints (at least conceptually). In an effort to better discern patterns of change within these different disturbance regimes, they were subsequently broken into additional subsets and ordinated together with their adjacent controls. Where the results were deemed superior (i.e. more interpretable) than the previous ordinations, these arrangements were retained for the constrained ordinations (section 3.9).

The DCA biplots, CCA triplots, and summary tables resulting from these analyses appear in **Appendices 10-28**. The overall results appear in the following sections and subsections. More detailed results are presented in the captions which accompany each appendix.

i. Clyde River

The first subset of anthropogenic vegetation combined all stands from CR representing tracked vehicle disturbance, as well as downslope stands affected by hydrological changes imposed by the tracks (**Appendices 10 and 14a**). A substantially greater amount of variance was accounted for by these axes compared to the biplot of natural vegetation (**Fig. 3.4**). Tracks through hummock-free snow-patches appeared at the left margin of the biplot had few species in common with the drained peatlands at the right margin. The primary gradient appeared to be one of organic mat depth. Tracked stands clustered at the center were characterized by a subset of the original plants on the various sites. This grouping represented a striking degree of floristic convergence. In the biplot of natural vegetation these stands had showed great intra- and inter-stand variation.

Ordination of abandoned 'contemporary' housepads and adjacent pedestrian trampled ground revealed a strong primary gradient which appeared to be correlated to the degree of initial disturbance (**Appendices 11 and 14b**). Disturbance intensity ranged from lightly trampled meadows on the left to heavily trampled ground and former housepads on the right. Species turnover was complete and the stands at either end of the gradient had virtually no species in common. A second axis, less clearly defined, appeared to be one of decreasing moisture from top to bottom.

ii. Truelove Lowland and Resolute Bay

Relative to the natural vegetation at TL, ordination of the tracked stands exhibited noticeable, if minor, change in that the stands were even more clustered than before (**Appendices 12 and 14c**). Estimated gradient lengths were slightly reduced, indicating a floristic convergence among stands. Similar to the ordination of natural vegetation, the primary axis represented an apparent gradient of increasing moisture from left to right. As in the classification analysis (**Table 3.2**), only a few tracks were characterized by colonists and most were characterized by remnants of the adjacent, natural vegetation.

Ordination of Thule dwellings and beach ridges (**Appendices 13 and 14d**) revealed a strong primary gradient and an almost complete differentiation in species composition between the stands at either end of the first axis. The beach ridges of TL and RB were relatively similar. There was far more variation among the Thule dwellings, even among unexcavated dwellings at TL which are only meters apart. The first axis corresponded roughly to intensity of disturbance. The number of active species in the analysis was twice that in the meadows, with many more ruderal plants figuring prominently on the housepads. Some vascular plants were near omnipresent and occurred at various frequencies in both meadows and on dwellings, contributing to the high species richness of the latter. The second axis was more poorly defined with lower species turnover and appeared to be based on variations in relative moisture.

3.7 Clyde River, Truelove Lowland, Resolute Bay

Ordination of the combined Thule dwellings, contemporary housepads, and trampled stands revealed strong local and geographic affinities among all of the vegetation types (**Appendices 15 and 19a**). The first axis appeared strongly linked with disturbance intensity, which increased from left to right. The second axis seemed to be one of decreasing moisture from top to bottom. Estimated gradient lengths for the first two axes were long and species turnover was high in both cases. There were noticeable parallels to the TWINSPAN analysis. Perhaps most importantly, the vegetation of the two unexcavated Thule dwellings from TL was again shown to be most similar to the lightly trampled meadow from CR.

3.8 Sample ordinations of combined natural and anthropogenic vegetation

i. Clyde River

When ordinated with their adjacent controls (**Appendices 16 and 19b**), most of the multi-pass tracks at CR exhibited an apparent increase in intra-patch compositional heterogeneity. Species turnover was high along the first axis and all the stands appeared as discontinuous from their controls. Some stands converged floristically, while others remained distinct. A key difference between untracked and tracked vegetation was the virtual lack of Sphagnum spp. and woody plants in the latter. By comparison with multi-pass tracks, species composition among stands was little changed between single-pass tracks and adjacent controls (**Appendix 17 and 19c**). The most significant change was due to the absence of lichens, particularly in tracks through the interfluve zone. Ordination of the drained peatlands with their controls (**Appendices 18 and 19d**) from upslope revealed only moderate species turnover between extreme ends of the gradients along the first two axes. Change was most pronounced in a former water channel drained by multi-pass tracks perpendicular to local slope.

ii. Truelove Lowland

The ordination of tracked stands and adjacent controls at TL (**not shown**) resulted in a biplot which was too crowded for meaningful interpretation. The main conclusion to be drawn was from the conspicuous absence of colonists to differentiate among the stands. This indicated the prevalence of remnant floras within these patches.

3.9 Sample analyses of community-environment relationships

i. Clyde River

a. Natural meadows

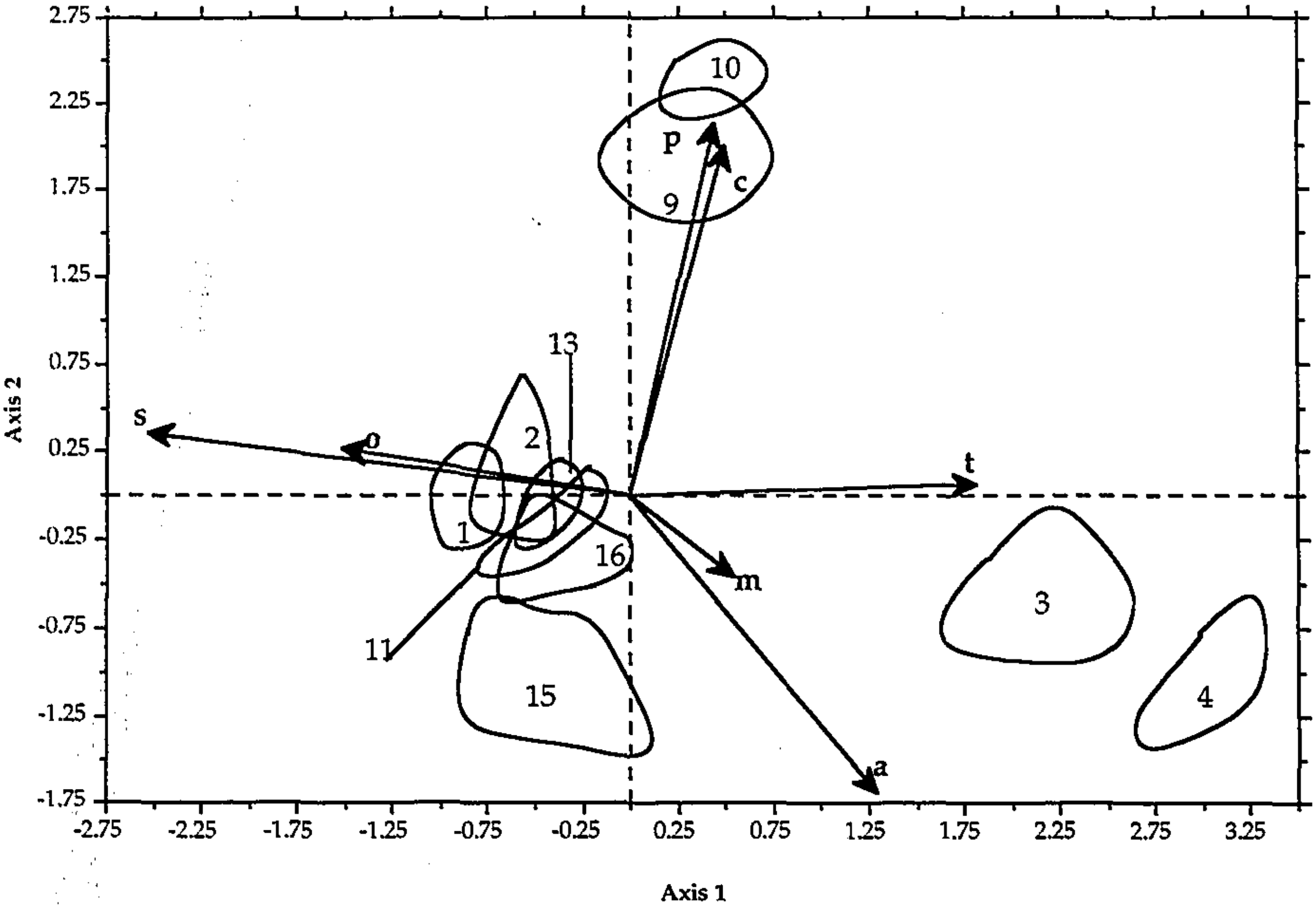
Fig. 3.6 is a canonical correspondance analysis (CCA)-derived triplot of the same samples x species matrix ordinated in **Fig. 3.4**, with the addition of eight environmental variables. In this case I used the default scaling (no. 2), in which the environmental triplot scores are correlations of environmental variables with the axes. Compared to most of the other scalings, ordination diagrams in scaling 2 allow easier, more intuitive, and more quantitative interpretations. As discussed in Chapter II, scaling 2 focusses on species configurations and inter-species distances approximate their chi-square distances (ter Braak 1990). Additional runs of this and other data sets were made using scaling 1, which focusses on the configuration of the samples and where inter-sample distances approximate their chi-square distances (ter Braak 1990). General results from both sets of analyses are presented briefly here, with the emphasis on scaling 2. More detailed results from these and the ordinations of disturbed communities are presented in **Appendices 20-28**.

Compared to the unconstrained (DCA) ordination, the eigenvalue for the first axis drops only slightly, from 0.318 to 0.284 (**Table 3.4**), while that for the second axis increases from 0.214 to 0.265. Apparently, the environmental variables measured are sufficient to predict the main variation in species composition extracted by DCA. The statistical significance of the CCA results was tested using the Monte Carlo permutation check included in CANOCO and found both the first axis and overall results to be significant ($p \leq 0.01$); it could therefore be concluded that there were significant differences in the vegetation with respect to the environmental variables correlated with the axis. The interpretation of both axes is unambiguous; the first axis is defined by slope and depth of organic mat, which are negatively correlated with soil temperature; the second axis is defined primarily by soil pH and compaction, which are negatively correlated with active layer depth (**Table 3.4**).

As in the DCA ordination, Stands 3 & 4 and 9 & 10 are grouped together as outliers, although this status is more pronounced in the CCA triplot and their positions are switched relative to the first two axes. The first axis shows that slope is minimal or lacking in Stands 3 and 4, that the organic mat is shallow and that soil temperatures are high compared to all other stands. The latter two conditions would appear to be indirectly related to the lack of slope (as well as distance from shore, not shown), which allows deep, late-melting snow to gather here. The reduced growing season results in an open, poorly developed community (**Plate 3.8**) with a thin, dark organic mat which, in turn, fosters high soil temperatures in the rooting zone. Although its development is delayed because of the snow cover, active layer depth is relatively great here from mid season onward (see Section 3.10.i). These

Figure 3.6

Canonical Correspondence Analysis (CCA) -derived triplot of undisturbed meadow vegetation at Clyde River



Environmental parameters in this and all other ordination triplots are as follows: **a**=active layer depth; **b**=soil bulk density; **c**=soil compaction; **m**=soil moisture; **o**=organic mat depth; **p**=soil pH; **s**=slope; **t**= soil temperature

Table 3.4

Parameter	Canonical Coefficients		Inter-set Correlations	
	Axis 1	Axis 2	Axis 1	Axis 2
Organic Mat Depth	-0.589	0.104	-0.568	0.097
Soil Moisture	-0.210	-0.172	0.202	-0.161
Soil pH	0.170	0.821	0.164	0.768
Bulk Density	-0.017	-0.116	-0.016	-0.109
Soil Compaction	0.118	0.774	0.181	0.723
Soil Temperature	0.704	0.022	0.679	0.021
Active Layer	0.498	-0.651	0.479	-0.609
Slope	-0.980	0.141	-0.943	0.132

	Axes			
	1	2	3	4
Eigenvalues	.284	.265	.141	.047
Species-environment correlations	.963	.935	.805	.595
Cumulative percentage variance				
of species data	13.2	25.6	32.1	34.3
of species-environment relation	35.0	67.6	84.9	90.6

stands are also dissimilar from the rest in terms their complete lack of Sphagnum spp. and the hummocky structure they impose upon the other meadows. As in DCA, they were removed from subsequent analyses.

In contrast to the above, Stands 9 & 10 are characterized by compact soils with high pH, a moderately deep organic mat and a shallow active layer. That soil compaction, as measured by a penetrometer, is not necessarily related to bulk density can be seen from both the triplot and in the the correlation coefficients (**Table 3.4**). The remainder of the stands are clustered near the center of the triplot and display considerable overlap, with the exception of Stand 15, an interfluve. This stand has the lowest pH with a fairly deep organic mat and a very shallow active layer. The water channels and wet stands (e.g. Stands 2, 11up, 13off, 16up) from both north and south of the abandoned settlement overlap the most and so represent the 'average' condition from among the sampled terrain units.

Using scaling 1 (not shown), the chi-square distances between samples were noticeably less than in scaling 2 but the outliers remained discrete and the overall structure of the triplot remained virtually identical. This indicates that the separation of these stands is justifiably a function of both their unique environments, as represented by the measured variables, as well as their unique species assemblages.

b. Vehicle tracks and adjacent controls

Appendices 20 and 22a are based on the same sample subset of the combined disturbed and adjacent control stands used in DCA with the addition of environmental variables. The eigenvalue of the primary axis decreased somewhat. The first axis was most closely tied to organic mat depth, active layer depth and soil temperature. Compaction also had a strong negative correlation with the first axis. The second axis was clearly one of soil pH. Many of these factors proved to be significant in the Monte Carlo permuation test. As in the DCA analysis, the tracked stands exhibited greater intra-patch heterogeneity than their adjacent controls. Much of the observed heterogeneity was due to species composition rather than environment. For single-pass tracks (**Appendices 21 and 22b**), the first axis and overall results were significant in the Monte Carlo test. The first axis was correlated primarily with slope and exhibited moderate correlation with soil temperature and pH. Soil pH increased in tracked areas. The second axis was negatively correlated with compaction, organic mat depth and active layer depth. It is notable that active layer depth, compaction and bulk density are reduced in the tracked stands, contrary to what was expected.

c. Drained peatlands and adjacent controls

In the triplot from CCA (**Appendices 23 and 25a**), the first axis was most strongly correlated with pH, negatively correlated with active layer depth, and was significant in the Monte Carlo test, as were the overall results. The second axis exhibited roughly equivalent correlation with three variables: soil temperature, pH and active layer depth. Organic mat depth had a moderate negative correlation with this axis. Soil pH was high in all drained peatlands relative to their controls and had a much stronger association with community variation than relative moisture. Changes in active layer depth were more variable.

d. Abandoned 'contemporary' housepads and adjacent pedestrian trampled meadows

The overall structure of the triplot from the CCA ordination (**Appendices 24 and 25b**) of the housepads and trampled stands was not unlike that from DCA. The extracted gradients explained a significant amount of the variation in composition among stands. This was indicated by the moderate change in eigenvalues from DCA. Also, in a second CCA triplot using scaling 1, the distances between samples changed only minimally. Much of the variation in the data set was explained by the first two axes.

Compared to the other disturbance regimes there was a much greater range in composition among stands. The first axis, defined primarily by slope, proved significant in the Monte Carlo permutation. The lack of slope on the housepads seemed to be a surrogate variable for disturbance intensity as represented by the other factors combined. Disturbance intensity increased from left to right. The second axis represented a gradient of organic mat depth and pH. At increasing levels of disturbance, both vegetation and environment tended to converge toward the center of the triplot, as in the DCA analysis.

ii. Truelove Lowland

a. Vehicle tracks

Eigenvalues in the CCA triplot were significantly reduced (**Appendices 26 and 28a**) compared to DCA on all four axes, indicating that the environmental variables measured did not account for a substantial proportion of the variation in species data. Still, the first axis and overall results were significant in the Monte Carlo test. The first axis was most closely tied to slope, and negatively correlated with organic mat depth. The second axis was negatively correlated with soil temperature and positively correlated with pH.

b. Thule dwellings and adjacent beach ridges

In the CCA analysis, the first axis was primarily one of soil moisture and pH, both of which were negatively correlated with organic mat depth (**Appendices 27 and 28b**). The second axis had a moderate negative correlation with organic mat depth. Both the first axis and overall results were significant in the Monte Carlo test. All of the stands maintained significant distances from one another in both scaling 1 and 2, indicating that both species and environment differed appreciably among stands.

3.10 Abiotic and biotic parameters not included in ordinations

i. Active layer development

a. Clyde River

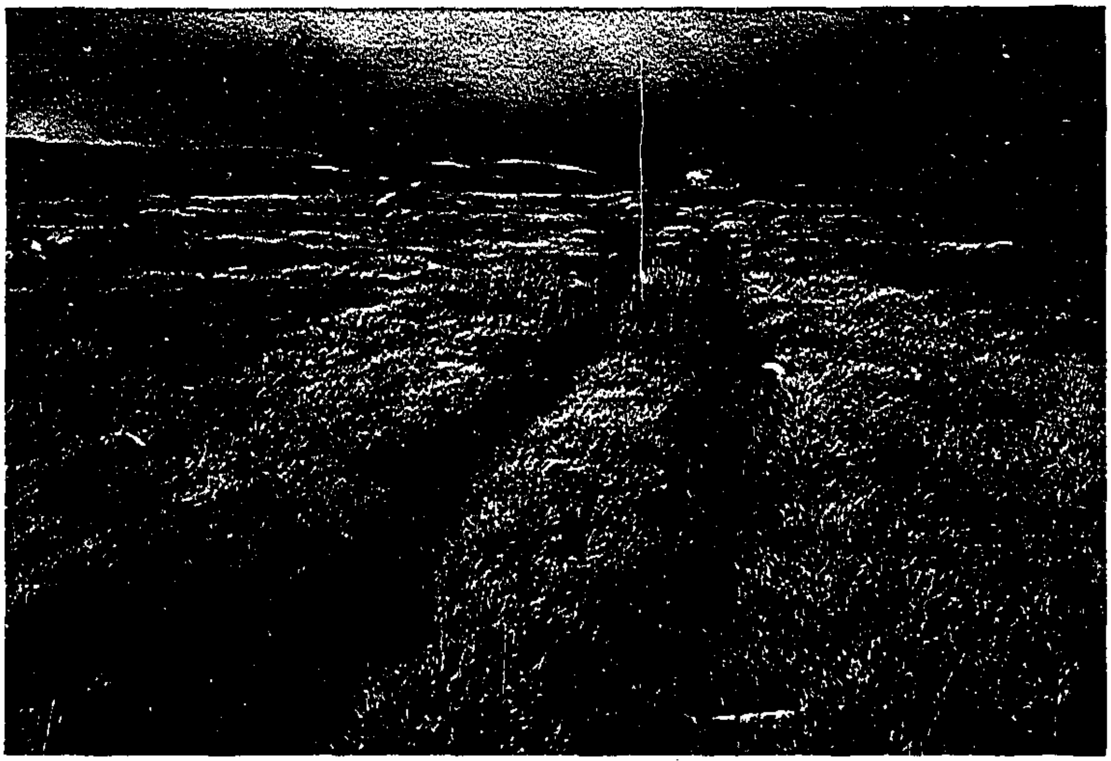
Appendices 29-33 and **34a** illustrate mean seasonal active layer development during 1990 among stands representing various disturbance regimes surveyed at CR. These may be compared to means from many of the same stands during 1989 in **Appendices 34b** and **36-39**. Responses were variable within disturbance regimes apparently depending on local drainage, bulk density of the soil, and the extent to which the organic mat remained compressed, all of which affect insolation. In 1990, for example, hydric single-pass tracks thawed more slowly than undisturbed soils in the early part of the season (**Appendix 29b**). In contrast, the soils of more mesic tracks, with greater bulk densities, thawed at rates similar to controls during the early growing season (**Appendix 29a**). These differences were fundamentally similar in 1989 (**Appendix 36**).

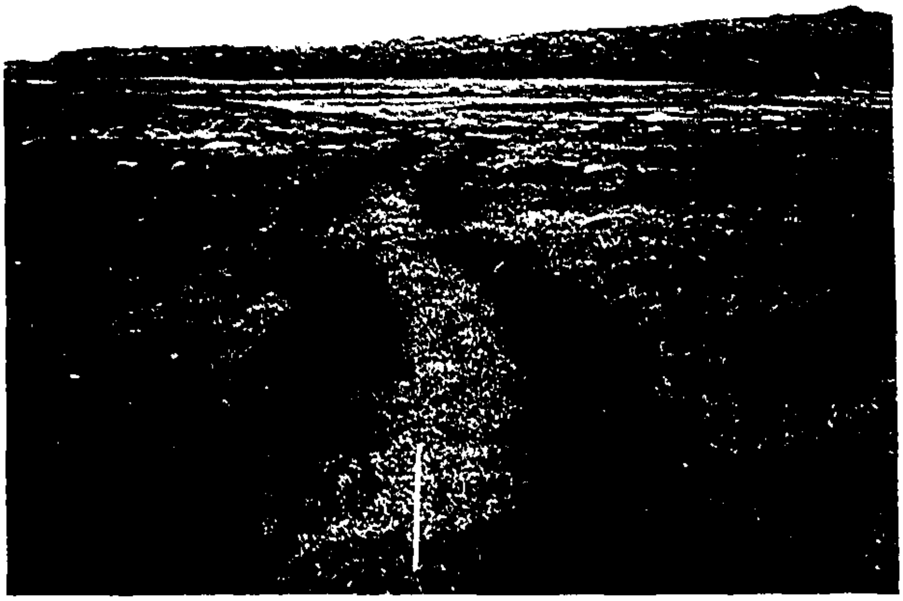
The pattern of thaw differed substantially in the non-hummocky meadows with late-lying snow banks and poorly developed vegetation (**Appendices 30 and 37a**). Here, the organic mat was so thin that even a single-pass track was sufficient to either destroy or severely damage it. The spring runoff was thus able to easily erode the organic mat despite the near absence of slope. Due to the lack of peat in this portion of the study area, most thaw occurred almost immediately after snow melt. In hummocky meadows, comparisons between active layer development in water channels and adjacent interfluves revealed differences between single- and multi-pass tracks, drained areas downslope, and control areas upslope (**Appendices 31, 32 and 37b**). In an interfluve zone, soils beneath single-pass tracks thawed more quickly than controls, as did soils in the drained peatland downslope. Where the same set of single-pass tracks dissected a water channel, the soils beneath were relatively loose (low bulk densities) and saturated and thawed more slowly than the controls. In contrast, drained soils downslope from these tracks thawed more slowly throughout most of the first half of the growing season.

Thaw was delayed in areas drained by multi-pass tracks perpendicular to local slope, at least in the early part of the growing season (**Appendices 32**

Plate 3.9 - General aspect of Stands 9 and 10 showing 'green belting' (*sensu* Abele et al. 1984) in tracks at CR from 100-150 passes over several years (ending ca. 1969) in mesic, Sphagnum meadow (Stands 9 and 10). Undisturbed hummocks in this community display a wide range of heath species and fruticose lichens. Microrelief is virtually lacking in tracks and water runs gently downslope (3.5-4.0°) during spring melt, although no erosion is evident. Peat layer is completely lacking in tracks, where a semi-closed cover of mosses has developed, consisting mainly of Bryum cryophilum, B. pseudotriquetrum, and Hypnum bambergeri, three species which are not found in the adjacent undisturbed vegetation. Vascular cover in the tracks is mainly Carex aquatilis var. stans and Eriophorum angustifolium. Tall culms visible in the center are Alopecurus alpinus, another species lacking in the undisturbed vegetation. Darker, thinner cover of vegetation in tracks contribute to enhanced active layer development (**Appendices 29, 30, 38, 39**). Individual ruts are ca. 50 cm wide. Photo date 13 July 1988.

Plate 3.10 - General aspect of recent multi-pass tracks resulting from 180 passes made by Arnold 'Ranger', a light tracked vehicle, during summer 1986 in mesic meadow at TL. Remnant patches of vegetation can be seen in tracks, especially in micro-depressions where damage was not as severe. These patches were comprised almost exclusively of Carex aquatilis var. stans, as other species have been reduced in cover or eliminated entirely. Adjacent undisturbed vegetation included abundant Eriophorum angustifolium, Juncus biglumis, Arctagrostis latifolia, and lesser amounts of Salix arctica. Many intact rhizomes of C. aquatilis var. stans remained below the tracks and will help this species to revegetate the site more quickly than most. In addition to biomass and species richness, albedo was clearly reduced in tracks. These tracks thawed to significantly greater depths than their controls, in contrast to tracks resulting from 60 passes, as reported by Babb & Bliss (1974a). Stake stands 38 cm high. Photo date 24 July 1989.





and 37b). However, thaw in the tracks themselves was greatly accelerated relative to both drained peatlands and control areas. This pattern was repeated in both years. Thaw rate and overall depth were consistently greater in the tracks where the organic mat was destroyed but a dense cover of sedges and grasses had developed (**Appendices 33 and 38, Plate 3.9**).

Profiles from an abandoned housepad with no added materials (e.g. sand, gravel) and from adjacent trampled terrain revealed a clear gradient in which thaw rate was positively correlated with intensity of disturbance at the beginning of the growing season. This gradient was apparent through both years (**Appendix 34**). Soils beneath lightly trampled areas thawed at about the same rate as undisturbed soils. The driest, most heavily compacted soils, those on the former housepad, thawed significantly faster and to greater depths than any of the trampled soils. The same pattern of thaw occurred on abandoned housepads where sand and gravel were added. Comparisons between wet and mesic trampled meadows showed that maximum thaw depth was slightly reduced in wetter soils, a pattern which was consistent through both years.

b. Truelove Lowland

Mid-season thaw depths in vehicle tracks and adjacent controls at TL are illustrated in **Appendix 40** and reveal a variety of responses. The tracks which remain most severely disturbed, such as those in Stands 1 and 4, contained standing water throughout the growing season, supported only a thin cover of aquatic and emergent plants, and thawed to significantly greater depths than adjacent mesic and hygric sedge meadows. In the wettest meadows with standing or lightly flowing water throughout the summer, naturally recovering areas (Stands 7, 13) and sites of assisted restoration using sod plugs (Stands 11, 12) were no different from adjacent controls. In the recently (1986) disturbed areas (Stands 8, 9, **Plate 3.10**). As at CR, thaw depth was increased in more mesic tracks and controls (Stand 8) compared to an imperfectly drained area nearby (Stand 9). In mesic hummocky meadows where vegetation cover was lacking or remained sparse in the tracks (Stands 5, 6), thaw was significantly greater in tracks, as was the case at CR. Thaw depths in few-pass tracks through hummocky meadows (Stands 2, 10 - not shown) did not differ from their adjacent controls. Probing of thaw depths was not attempted on unexcavated Thule dwellings (Stands 15, 16) for fear of potential damage to artifacts beneath the surface. However, probing along the back wall of the recently excavated and reconstructed Thule dwelling (Stand 14) revealed a mean thaw depth of 37.2 cm, significantly greater ($p \leq 0.01$, Mann-Whitney test) than the mean depth of 26 cm beneath the adjacent beach ridge.

ii. Soil temperature regimes

a. Clyde River

Active layer development is intimately linked to the patterning of surface and near surface temperatures. Sampling of diurnal and seasonal flux of soil temperatures took place in 1989 at depths of 5, 10 and 15 cm. Diurnal measurements were made by sampling every few hours for periods of 26-36 hr. Monitoring among multi-pass tracks and adjacent controls revealed several expected trends. For example, over a 24 hr period under cloud-free skies, soil temperature flux was greatest at a depth of 5 cm in tracks where both vegetation and peat were mostly lacking (**Fig. 3.7a**) and where vegetation was closed but peat was lacking (**Fig. 3.8a**). Diurnal flux was somewhat reduced at greater depths, particularly in the latter, well-vegetated track. In adjacent undisturbed soils with intact vegetation and organic layers at the surface (**Figs. 3.7b and 3.8b**), temperatures at different depths remained mostly distinct from one another throughout the day and 'night'. This was particularly the case in Stand 11, the wetter of the two (**Fig. 3.9b**).

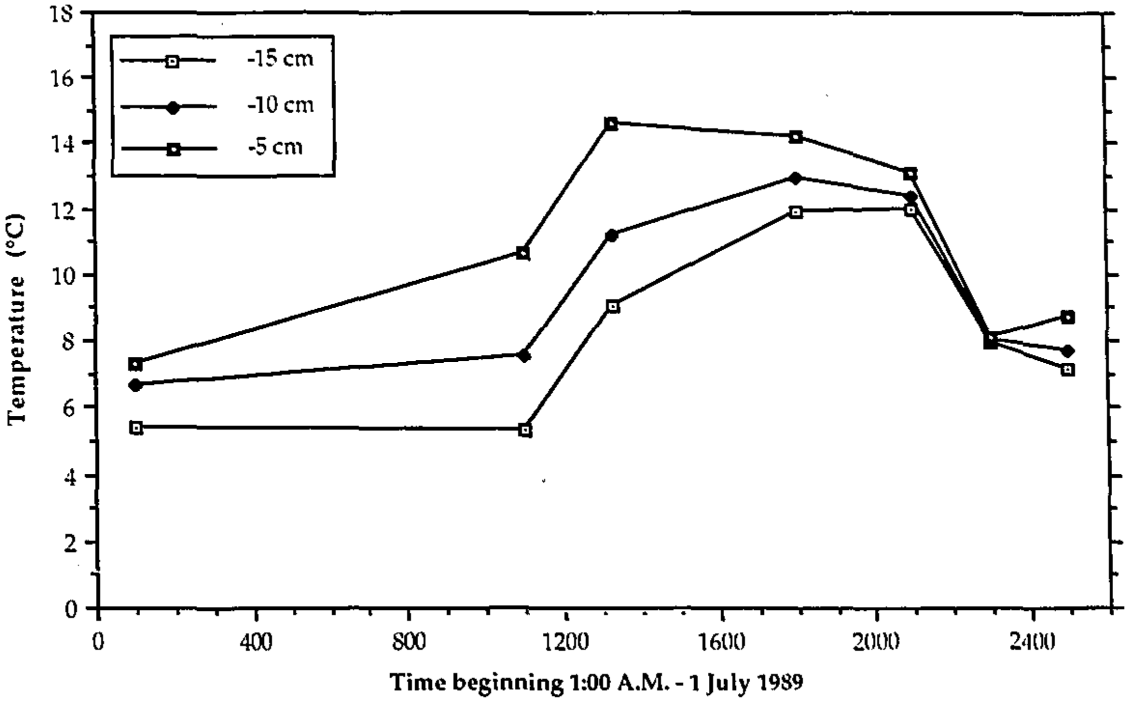
There were great differences between the poorly vegetated track and the control area at a depth of 5 cm. In effect, a lack of vegetation on the tracks in **Fig. 3.7a** has exposed the sandy soils and, despite the generally high relative moisture of these soils, led to a marked increase in albedo (**Fig. 3.10a**) which, in turn, has led to cooler temperatures near the surface relative to the dark, moist and well-vegetated surface of the control area (**Fig. 3.9b**). At greater depths, however, the reverse is true. The closed vegetation and peat of the control area provided enough insulation, even when wet, to keep the mineral soils at 10 and 15 cm cool compared to the tracks. The importance of the organic mat becomes clearest in the evening, when the tracks cooled rapidly and temperature was equal at all depths by about 11:00 P.M. The control area, in contrast, cooled more slowly.

The overall situation was very different in Stand 9, where the tracks were well-vegetated and remained moist throughout most of the growing season, while the adjacent control area was one the more mesic spots in the entire study area. Here, the Sphagnum hummocks were dry to the touch immediately after snow melt and most were capped by a variety of crustose and fruticose lichens, an indication of relatively dry microhabitats. Soil temperatures at all depths were consistently warmer in the tracks (**Fig. 3.8a**), with the notable exception of 5 cm. Soils at this depth had cooled to <3°C the

Fig. 3.7a - Plot of diurnal soil temperature flux under cloud-free skies in multi-pass tracks in a water track zone at CR.

Fig. 3.7b - Plot of diurnal soil temperature flux under cloud-free skies in adjacent controls.

Soil temperature - Clyde River - Stand 11 - Multi-pass tracks



Soil temperature - Clyde River - Stand 11 - Control

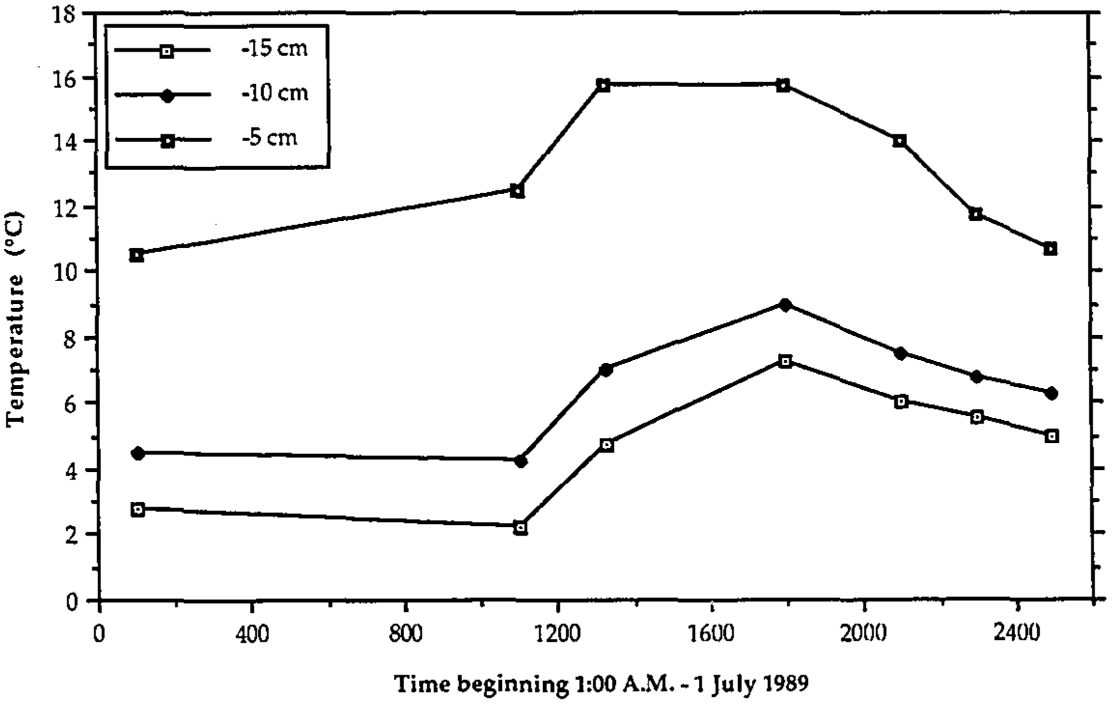
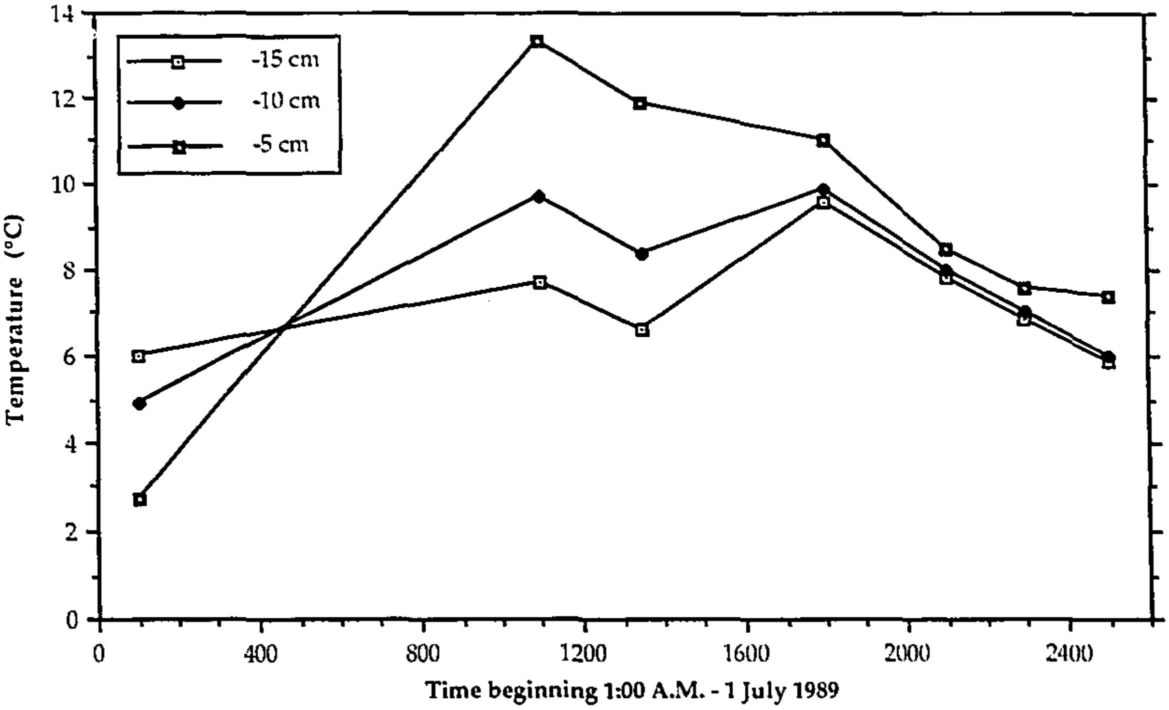


Fig. 3.8a - Plot of diurnal soil temperature flux under cloud-free skies in multi-pass tracks and adjacent controls in a mesic meadow at CR.

Fig. 3.8b - Plot of diurnal soil temperature flux under cloud-free skies in adjacent controls.


Soil temperature - Clyde River - Stand 9 - Multi-pass tracks

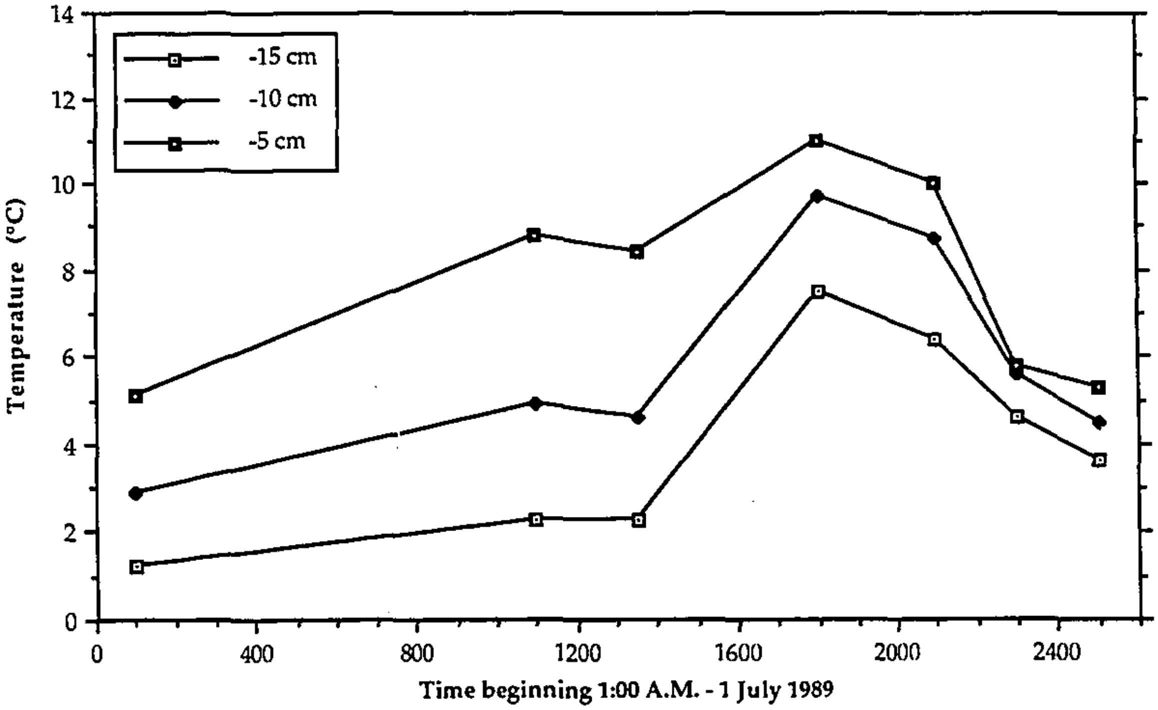
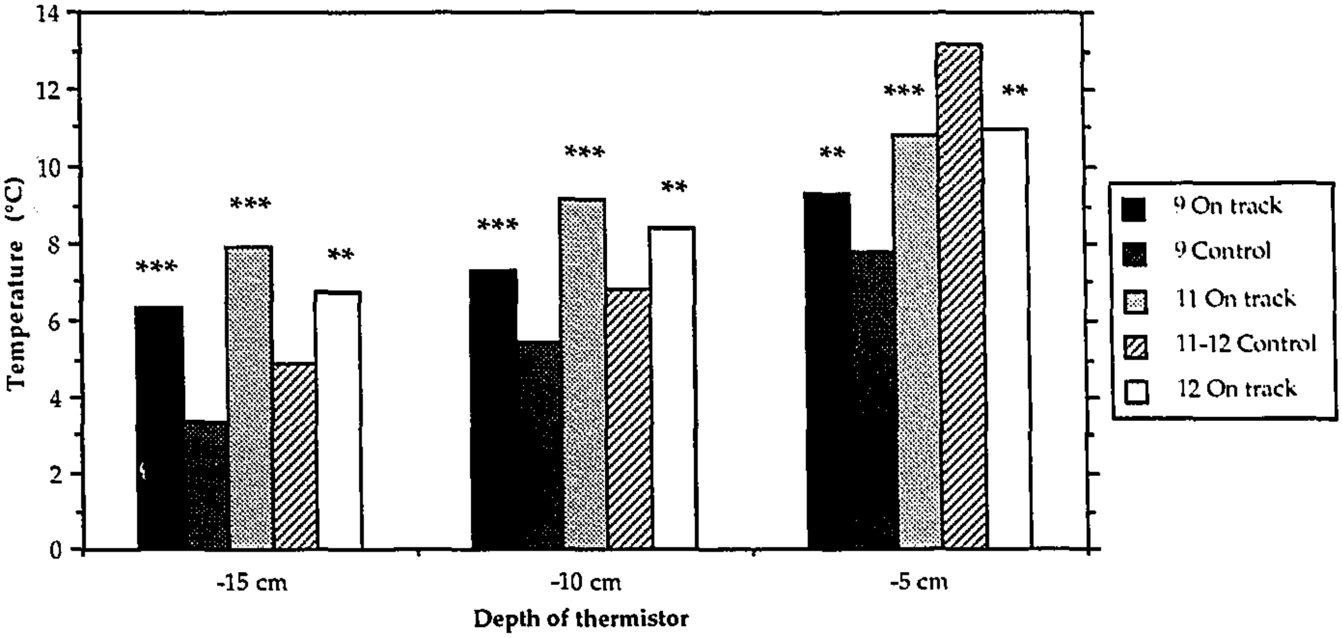

Soil temperature - Clyde River - Stand 9 - Control

Fig. 3.9 - Histogam of pooled means from 34 soil temperature readings from three depths in multi-pass tracks and adjacent controls at CR.

Pooled daily soil temperatures in multi-pass tracks and adjacent controls - Clyde River - 22 June to 13 July 1989

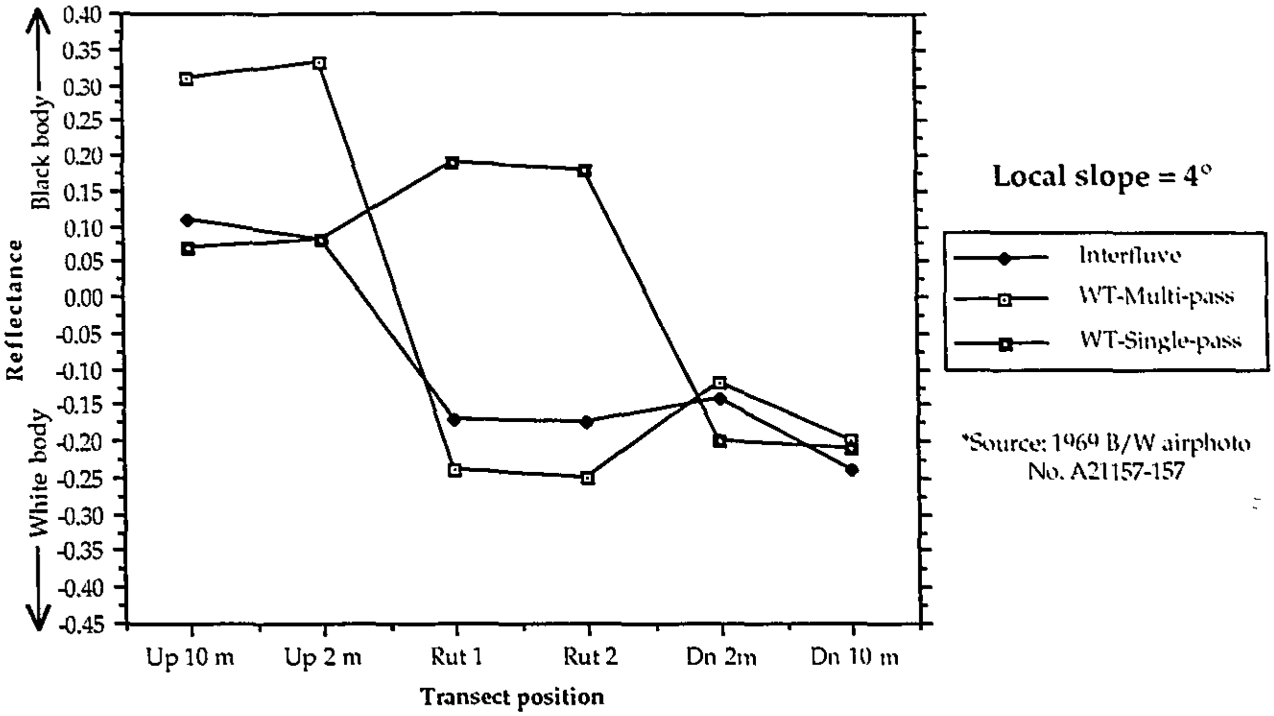


, * = significant at p=0.005 and 0.0005 respectively (t-test)

Figs. 3.10a - Plot of surface albedo (reflectance) in vehicle tracks, drained peatlands, and adjacent controls at CR, summer 1969.

Fig. 3.10b - Plot of surface albedo (reflectance) in multi-pass tracks and adjacent controls in mesic meadow in summers 1969 and 1973.

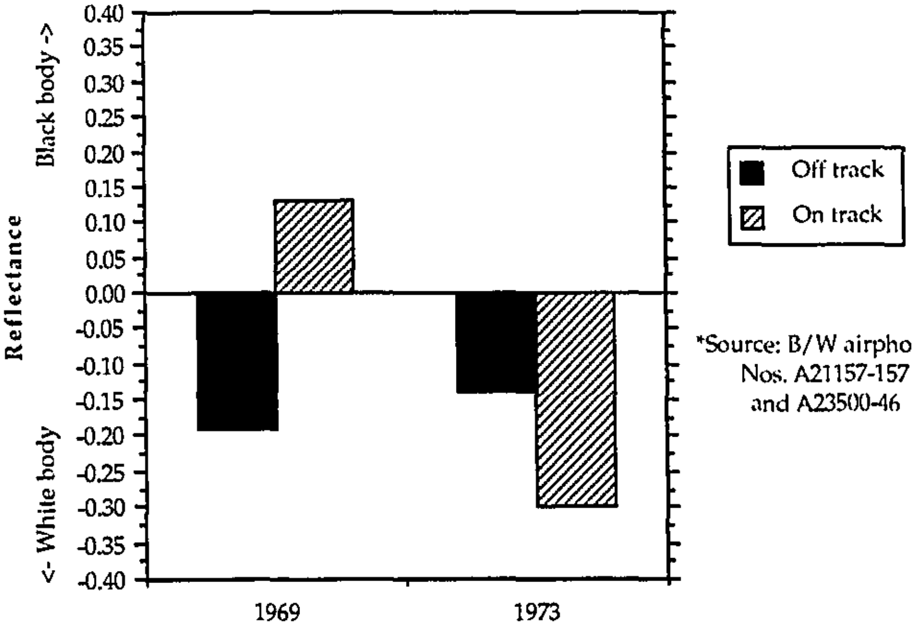
Surface reflectance* - Vehicle tracks, drained peatlands and adjacent controls



Local slope = 4°

*Source: 1969 B/W airphoto No. A21157-157

Surface reflectance* - Multi-pass tracks and adjacent controls
Clyde River, Baffin Island



*Source: B/W airphotos Nos. A21157-157 and A23500-46

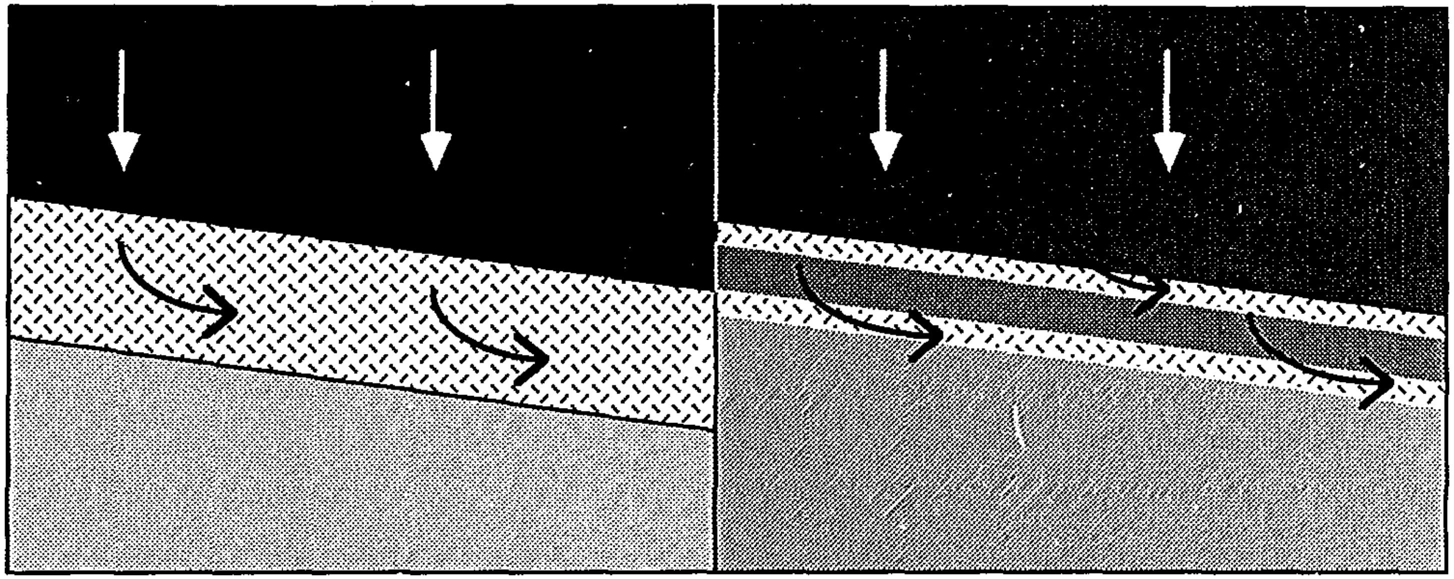


Fig. 3.11. Idealized vertical view showing hydrological effects of vehicle tracks on sloped meadows. Arrows indicate direction of water flow during snowmelt runoff, channelled by major gully from multi-pass tracks (left) and by individual ruts from single-pass tracks (right). Meadow desiccation downslope from tracks is approximately proportional to the severity of the rutting such that surface albedo, as measured from airphotos (see Fig. 3.10), is increased downslope from single-pass tracks. However, reflection is greatest in areas below multi-pass ruts which traverse water channels. These differences in reflectivity are idealized here with variations in the density of stipples (lighter areas represent more xeric surfaces).

night before these measurements began. The same night, soils at the 5 cm depth in the control area (**Fig. 3.8b**) were >5°C. This difference is similarly attributed to the combined insulating effects of a closed vegetation cover and a layer of dry peat. A lag effect, also attributed to the thermal properties of the overlying peat, is seen in the rate of warming during the morning and mid-day periods. The soils in both areas experienced weakly bimodal heating, but the higher peak occurred before noon in the tracks and not until almost 6:00 P.M. in the control area. This bimodal pattern was neither evident in the unvegetated tracks nor in the adjacent undisturbed water channel in Stand 11. The overall pattern of heating and cooling was quite similar during periods of cloud cover (not shown), but both highs and lows were clearly muted.

Apart from the efforts to gauge diurnal flux, soil temperature was measured at least once and often twice daily. Thirty-four temperature readings from each depth were pooled for the period 22 June to 13 July 1989 (**Fig. 3.9**). Relative to control areas, overall soil temperatures were consistently and significantly warmer in the tracks at depths of 10 and 15 cm. On the other hand, pooled temperatures were significantly cooler at a depth of 5 cm in the tracks compared to controls. This fact can be explained by both the nature of the sampling regime and the dynamics of subsurface heating. First, almost 60% of the total number of readings were taken between 9:00 P.M. and 9:00 A.M., the coolest half of the diurnal period. Second, as was apparent from the examples discussed above, diurnal flux was greatest in the top 5 cm of soil, so that a bias toward 'nightime' measurements would certainly indicate a pronounced cooling in this zone after pooling.

Taken together, the combined daily and seasonal measurements indicate that the disturbed soils were generally warmer than immediately adjacent natural soils. However, without a closed cover of vegetation and peat, or simply without peat, diurnal fluxes can be drastic. For example, fluxes of ≥10°C can occur in the top 5 cm of moist, well-vegetated mineral soils under cloud-free skies, and fluxes of ≥7°C can occur in the top 5 cm of moist, unvegetated mineral soils during the same period. Peat and vegetation each provided a measure of insulation which tended to slow heating and cooling of the soil. Wet surfaces tended to heat more quickly than dry ones, due to lower surface albedo and a reduction in the insulating value of the peat layer. On the other hand, exposed mineral soils, even when wet, tended to heat more slowly and to shallower depths than wet organic ones, indicating the relative importance of albedo.

Repeated soil temperature measurements were made for each quadrat in each stand under a variety of cloud cover and temperature conditions during the middle portion of the 1990 growing season. Differences in means between treatments and controls were apparent and statistically significant during both overcast and cloud-free periods. However, depending on the length of each period, differences were usually most pronounced under sunny skies. The following general discussion emphasizes measurements made at mid-day under sunny skies, although the dates and ambient temperatures vary as noted. Measurements most representative of the conditions in each stand, based on examination of the entire series of measurements for that particular stand during the period of observation, are presented in **Appendices 41-45**.

Single-pass tracks through a moist hummocky meadow displayed little difference in the upper layers of soil, but at depths of 15 cm soils beneath tracks were up to 2°C warmer on a 'slightly-above-average' (7.5°C) day early in the growing season. In contrast, single-pass tracks through an area of late-lying snow which lacks hummocks were only slightly warmer than adajcent controls on a very warm (12.5°C) day. In contrast, soils beneath single-pass tracks perpendicular to a water channel were significantly cooler at each depth on a similarly warm day. At depths of 10-15 cm, drained soils downslope from the tracks remained cooler than both tracks and controls.

Among multi-pass tracks, drained peatlands, and controls, temperatures were coolest in the control area, warmest in the tracks and intermediate in the drained area downslope. Active layer profiles from the date of measurement revealed depths of thaw corresponding to this pattern; the control area being shallowest, the tracks deepest and the drained area intermediate. This pattern was apparent in both a water channels and and adjacent interfluve. In multi-pass tracks parallel to local slope, tracked soils were substantially warmer than adjacent controls.

All types of housepads were significantly warmer than adjacent trampled meadows. Where soils in different zones of trampling intensity were measured across a wet meadow, there was a clear temperature gradient at a depth of 15 cm, from coolest (lightly trampled aress) to warmest (heavily trampled areas). A different pattern emerged from the same depth in more mesic meadows. There, lightly trampled portions of the meadows were warmest and heavily trampled areas were coolest. Neither pattern was consistent at shallower depths.

b. Truelove Lowland

Repeated meaurements of soil temperature were also made for all quadrats at TL under a variety of climatic conditions during the 1990 growing season. However, sunny skies were rare during much of the sampling period and the measurements illustrated in **Appendices 46-49** were all made during periods of heavy cloud cover. These serve to provide a contrast to the measurements illustrated from CR, which were made under clear skies.

At TL, temperatures of soils beneath few-pass vehicle tracks compared to adjacent controls exhibited no difference where vegetation cover was complete. However, tracked soils were substantially warmer than controls when the vegetation canopy in was open or lacking in the tracks. A pattern similar to that described for the older few-pass tracks was seen in the more recently tracked meadows. Across the Truelove Lowland, older tracks showed similar patterns. Where vegetation cover remained sparse, usually in more mesic meadows, soils were consistently warmer in the tracks, even under completely overcast skies lasting 48 hr or more. In wetter meadows, the vegetation canopy was generally closed and no significant differences were measured. At the archaeological sites, the peaty soils in the area of both excavated and unexcavated Thule winter dwellings were significantly warmer than immediately adjacent beach ridges.

iii. Surface albedo

Albedo is the percentage of radiant solar energy reflected by a surface. Albedo is an important property of terrestrial surfaces, particularly in permafrost environments because it determines how how fast a surface heats up when exposed to insolation. Consequently, anthropogenic and natural disturbances which induce changes in surface albedo have clear implications for soil temperature, active layer development and, ultimately, plant growth. Albedo was measured at the level of the patch, or the disturbed area, instead of the individual quadrat. **Fig. 3.11** illustrates the general patterns of diverted surface runoff during snowmelt and how these diversions affect surface albedo.

Analysis of surface reflectance in the July 1969 airphoto from CR revealed that vehicle tracks running perpendicular and diagonal to local slope had already impeded local drainage and altered surface albedo prior to abandonment (**Fig. 3.10a**). Changes were evident in tracks, both single- (Stand 16) and multi-pass (Stands 11, 12), and in drained peatlands downslope. At the time, reflectance was apparently increased in multi-pass tracks and decreased in single-pass tracks. In a set of multi-pass tracks parallel to local slope (Stand 9), where the organic mat was mostly destroyed but portions of the sedge mat remained intact, albedo was decreased at the time of abandonment (**Fig. 3.10b**). However, it appears that within four years, the rapid regeneration of rhizomatous graminoids in the tracks had resulted in a substantial increase in albedo compared to adjacent controls.

In 1989 and 1990, mid-season gravimetric water measurements revealed that the drained peatlands remained drier, often significantly, than the controls upslope. Relative to upslope areas, reductions of 3.5-5% were measured 2 m downslope from single-pass tracks and 12.5-15% 2 m below multi-pass tracks. Measurements made at distances of 10 m below the same sets of tracks yielded similar results. In the airphoto analysis, wet areas appeared dark because of the high radiation absorption and generally registered tone densitometer values of >0. Drained areas appear lighter due to the low moisture and relatively high reflectivity of these areas and generally provide values of <0. It should be noted that the changes in reflectance in drained areas induced by single- and multi-pass tracks were essentially equivalent, and that albedo increased slightly with increasing distance downslope from the tracks (**Fig. 3.10a**).

iv. Biomass

The direct impacts of vehicles on biomass can be substantial and persist for periods of up to 20 yr (Forbes 1992b), as shown in **Appendix 50**. In general, total biomass was consistently and significantly reduced in vehicle tracks within mesic meadows at TL and CR, despite the apparent increases common among a few graminoid species. In the wettest meadows at TL, total vascular biomass had nearly recovered to those of adjacent controls after 20 yr, although species richness (including non-vascular plants) often remained significantly reduced. The following sections will include description of some of these direct vehicle impacts, and analysis of variations in biomass along gradients of disturbance intensity.

a. Drainage

The effects of vehicle traffic across peaty slopes at CR and the resulting drainage modifications of downslope areas can be seen in **Figs. 3.12, 3.13 and 3.14a**. Significant changes in peak season aboveground standing crop are evident among the four vascular species with the highest cover/abundance values in this portion of the study site. **Figs. 3.12b and 3.13a** illustrate changes resulting from multi-pass tracks through interfluve and water channel zones, respectively, of the same slope. In the water channel zone (**Fig. 3.13a**), the three graminoid species increased slightly in the tracks while the only deciduous shrub (Salix arctica) was virtually eliminated. In contrast, only Luzula nivalis increased in the tracks through the interfluve zone (**Fig. 3.12b**). In the drained portions of both zones, the general responses of the four species were similar and formed a pattern whereby the standing crops of S.

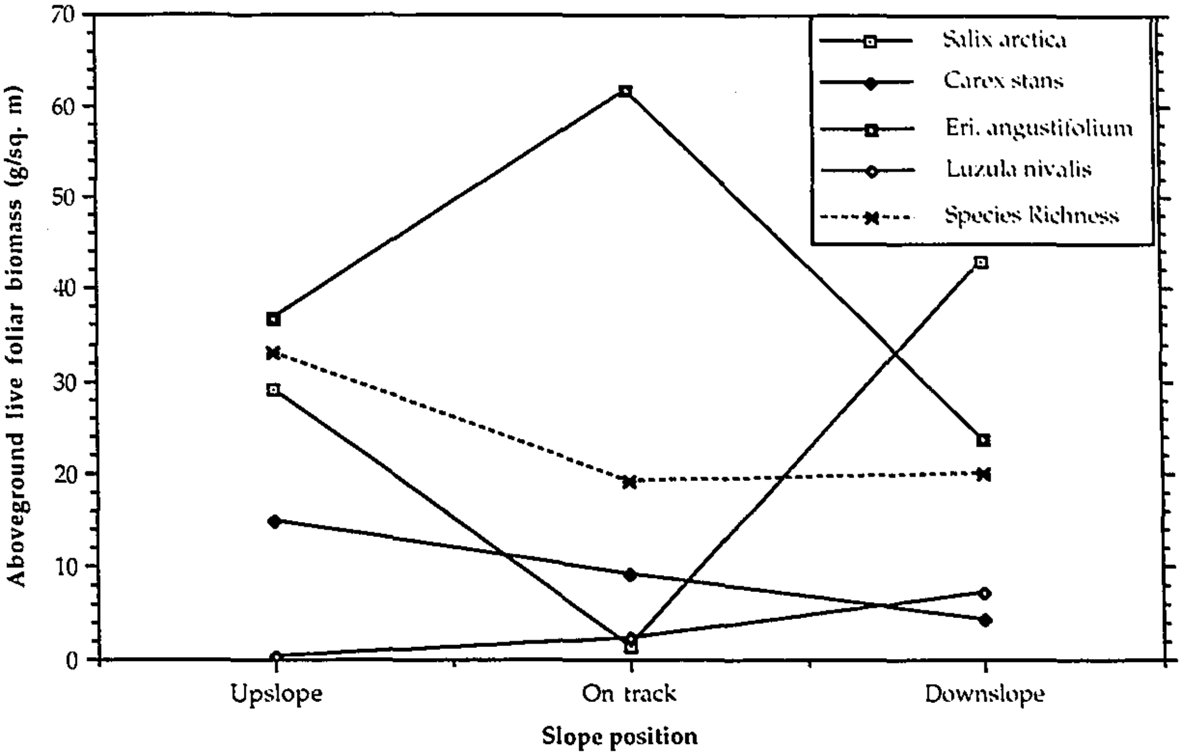
arctica and L. nivalis were increased, and both Carex aquatilis var. stans and Eriophorum angustifolium were decreased. However, the relative magnitude of these changes varied between the two zones. The downslope reduction in biomass of E. angustifolium was greater in the water channel zone, while the downslope increases in S. arctica and L. nivalis were greatest in the interfluve zone. The reduction in C. aquatilis var. stans was also greatest in the interfluve zone. In single-pass tracks (**Fig. 3.12a**), E. angustifolium and L. nivalis increased their biomass. Downslope changes in all four species matched the pattern, though not the magnitude, of change induced by multi-pass tracks.

Vascular biomass in areas drained by single-pass tracks was intermediate between undrained areas and areas drained by multi-pass tracks, at least in interfluve zones. Whereas Eriophorum angustifolium had a standing crop of ca. 37 g/m^2 in undrained or control areas, this dropped to ca. 24 g/m^2 below single-pass tracks in the interfluve zone and ca. 20 g/m^2 below multi-pass tracks in a similar interfluve. Salix arctica, however, increased from ca. 30 g/m^2 in the undrained interfluve, to ca. 42 g/m^2 below single-pass tracks and to ca. 47 g/m^2 below multi-pass tracks. The same pattern was evident for Luzula nivalis, which increased from <1 g/m^2 in undrained portions of the interfluve, to ca. 7 g/m^2 below single-pass tracks and ca. 20 g/m^2 below multi-pass tracks. The pattern of decreasing standing crop for Carex aquatilis var. stans was similar to that described for E. angustifolium. Total foliar standing crop did not exhibit substantial change in drained areas relative to undrained areas (**Fig. 3.14a**). This was because losses among the aquatic sedges were essentially offset by gains among S. arctica and L. nivalis. Totals remained significantly lower ($p \leq 0.01$, Mann-Whitney Test) in all multi-pass tracks, and in many single-pass tracks, especially when woody

Fig. 3.12a - Plot of foliar biomass of of dominant species and species richness in single-pass tracks, drained peatlands, and adjacent controls in imperfectly drained interfluve zone at CR. Tracks run diagonal to local slope (3.5 to 4°).

Fig. 3.12b - Plot of foliar biomass of of dominant species and species richness in multi-pass tracks, drained peatlands, and adjacent controls in interfluve zone at CR. Tracks run perpendicular to local slope (2.5-3°).

Biomass of dominant species & species richness (spp./1350 sq. m) - Single-pass tracks, drained peatlands and adjacent controls - Stand 16 - Clyde River - 10 July 1990



Biomass of dominant species & species richness (spp./1350 sq. cm) - Multi-pass tracks drained peatlands and adjacent controls - Stand 12 - Clyde River - 10 July 1990

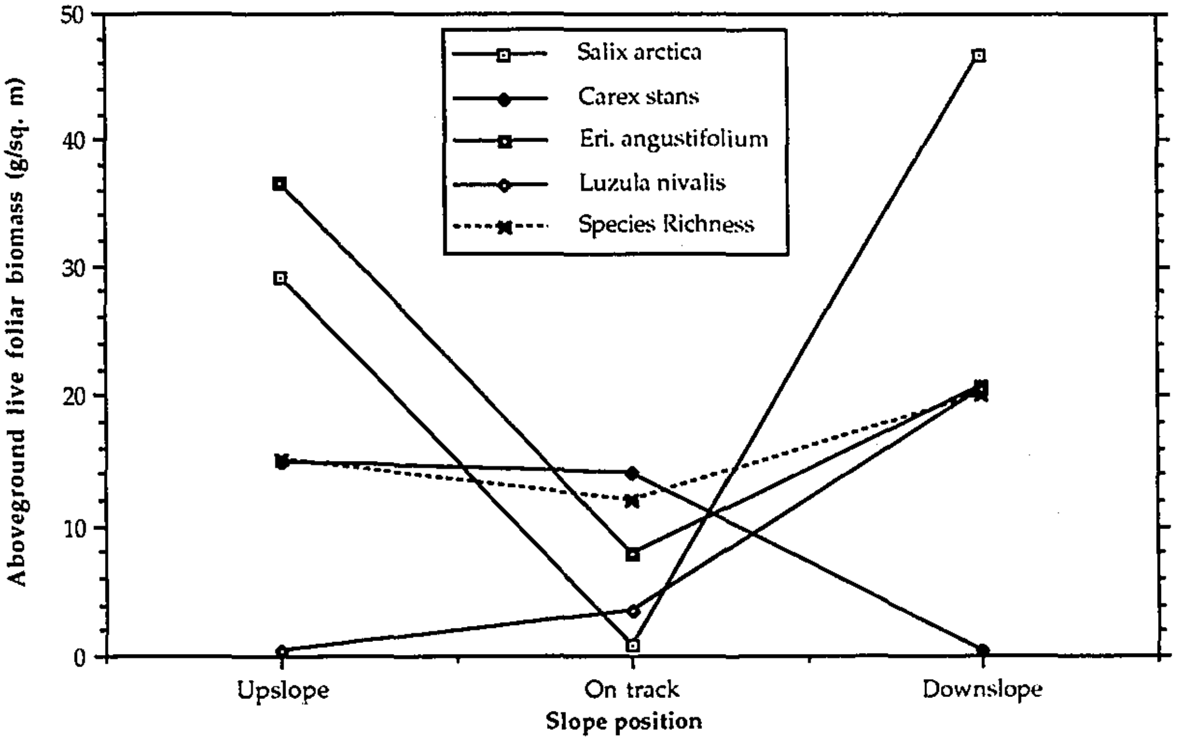
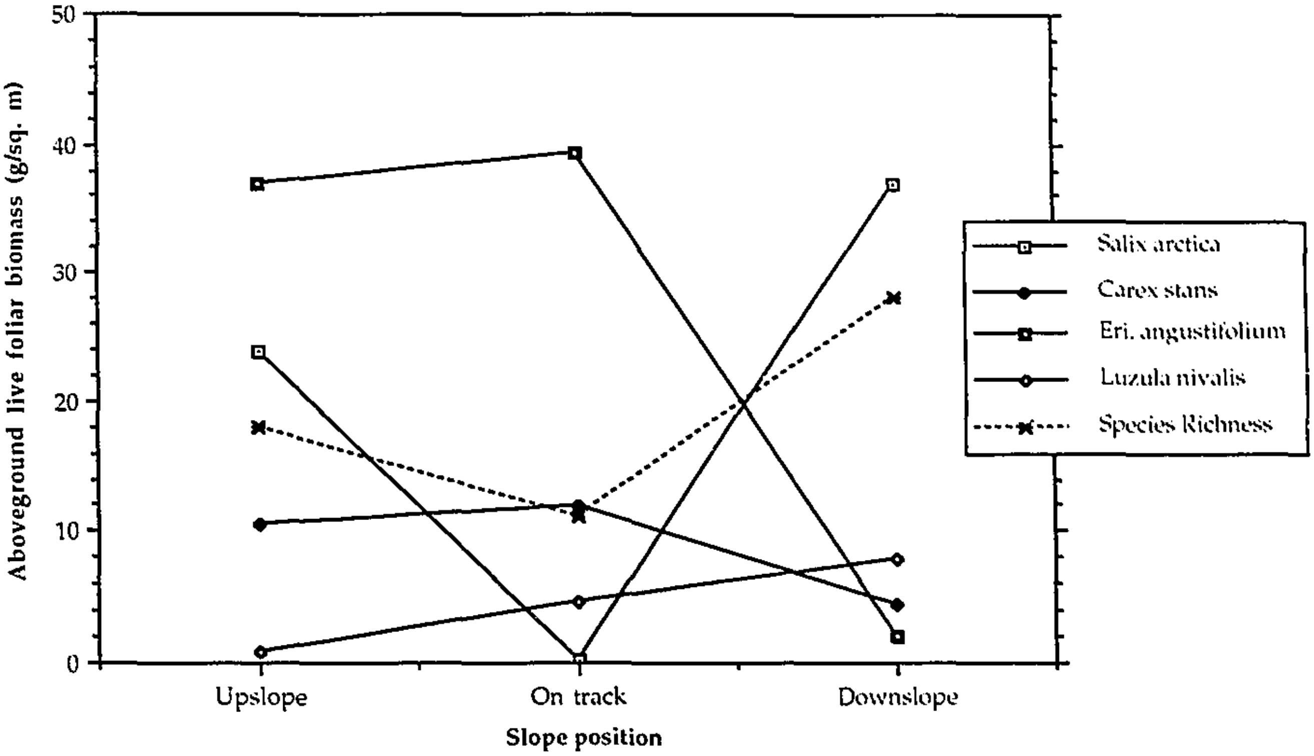


Fig. 3.13a - Plot of foliar biomass of of dominant species and species richness in multi-pass tracks, drained peatlands, and adjacent controls in water channel zone at CR. Tracks run perpendicular to local slope (2.5-3°).

Fig. 3.13b - Plot of foliar biomass of of dominant species and species richness on Housepad Type A and adjacent trampled and natural meadows. Note that the highest total biomass is on heavily trampled ground and that most of this is comprised of Alopecurus alpinus **(Plate 4.13)**, a highly nutritious forage grass, selectively grazed by caribou (cf. Hjeljord 1975) and other herbivores in the High Arctic.

Biomass of dominant species & species richness (spp./1350 sq. m) - Multi-pass tracks, drained peatlands and adjacent controls - Stand 11 - Clyde River - 10 July 1990



Biomass of dominant species & species richness (spp./1350 sq. m) - Housepad Type A and adjacent trampled and natural meadows - Stand 18 - Clyde River - 11 July 1990

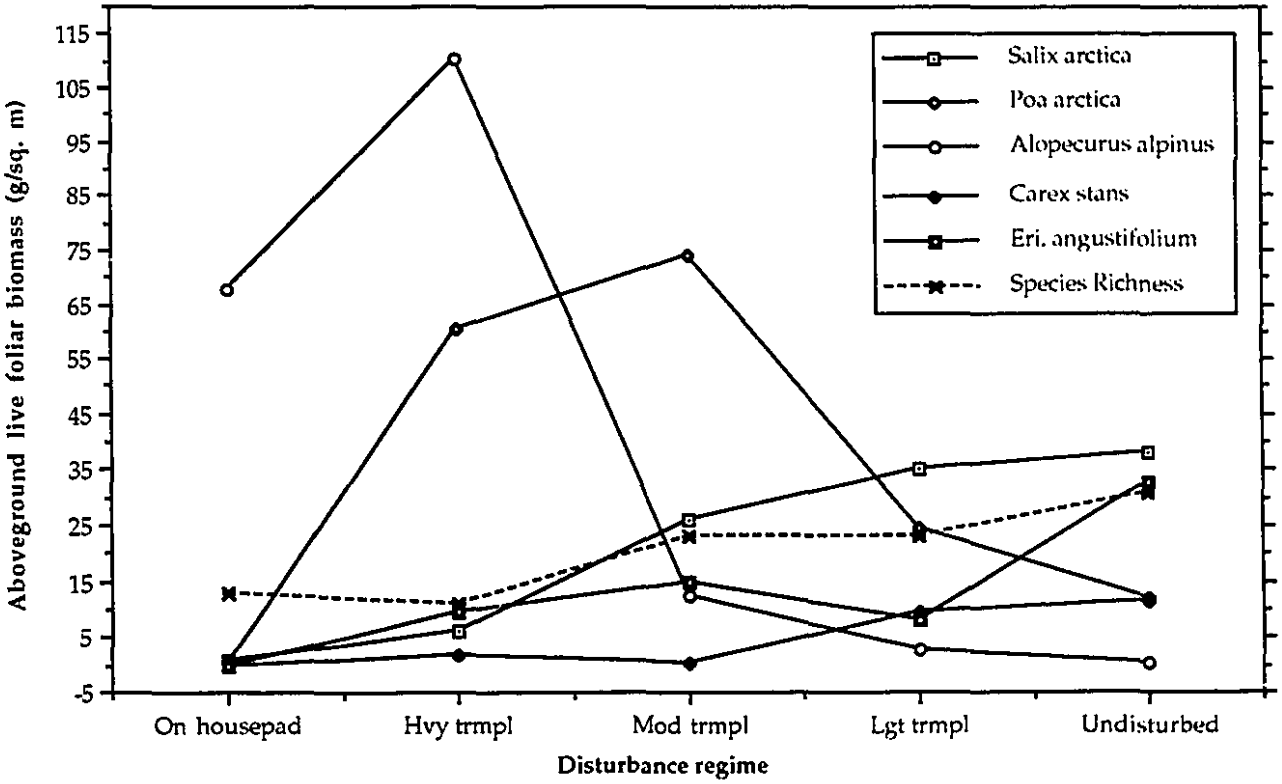
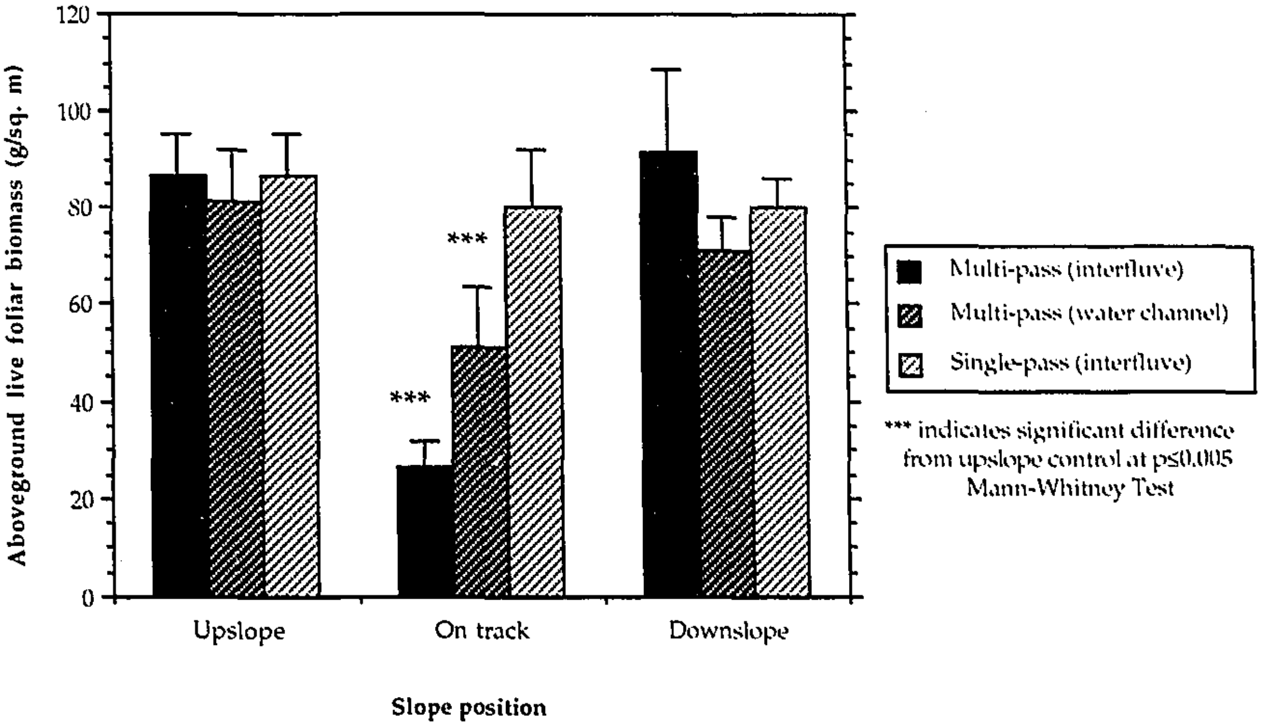


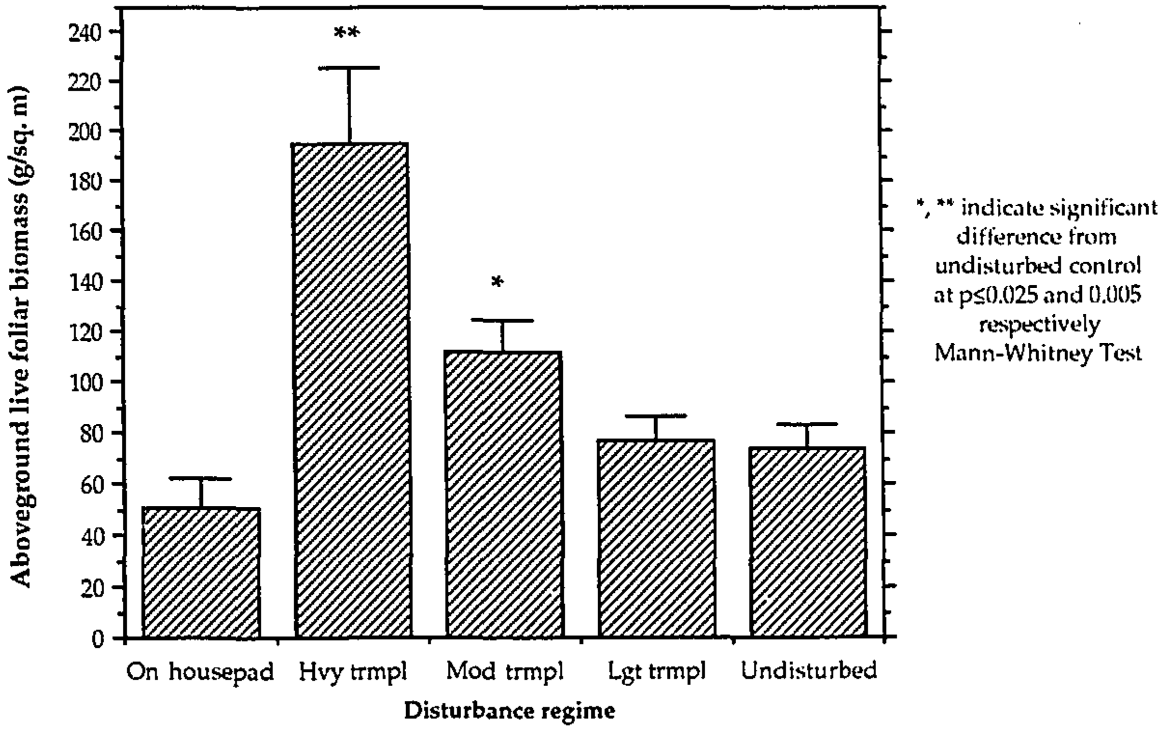
Fig. 3.14a - Histogram of total foliar standing crop in vehicle tracks, drained peatlands, and adjacent controls at CR.

Fig. 3.14b - Histogram of total foliar standing crop on Housepad Type A, and adjacent trampled and undisturbed meadows at CR.



Total foliar biomass - Vehicle tracks, drained peatlands and adjacent controls - Stands 11, 12 & 16 - Clyde River - 10 July 1990

*** indicates significant difference from upslope control at p≤0.005 Mann-Whitney Test



Total foliar biomass - Housepad Type A and adjacent trampled and natural meadows - Stand 18 - Clyde River - 11 July 1990

*, ** indicate significant difference from undisturbed control at p≤0.025 and 0.005 respectively Mann-Whitney Test

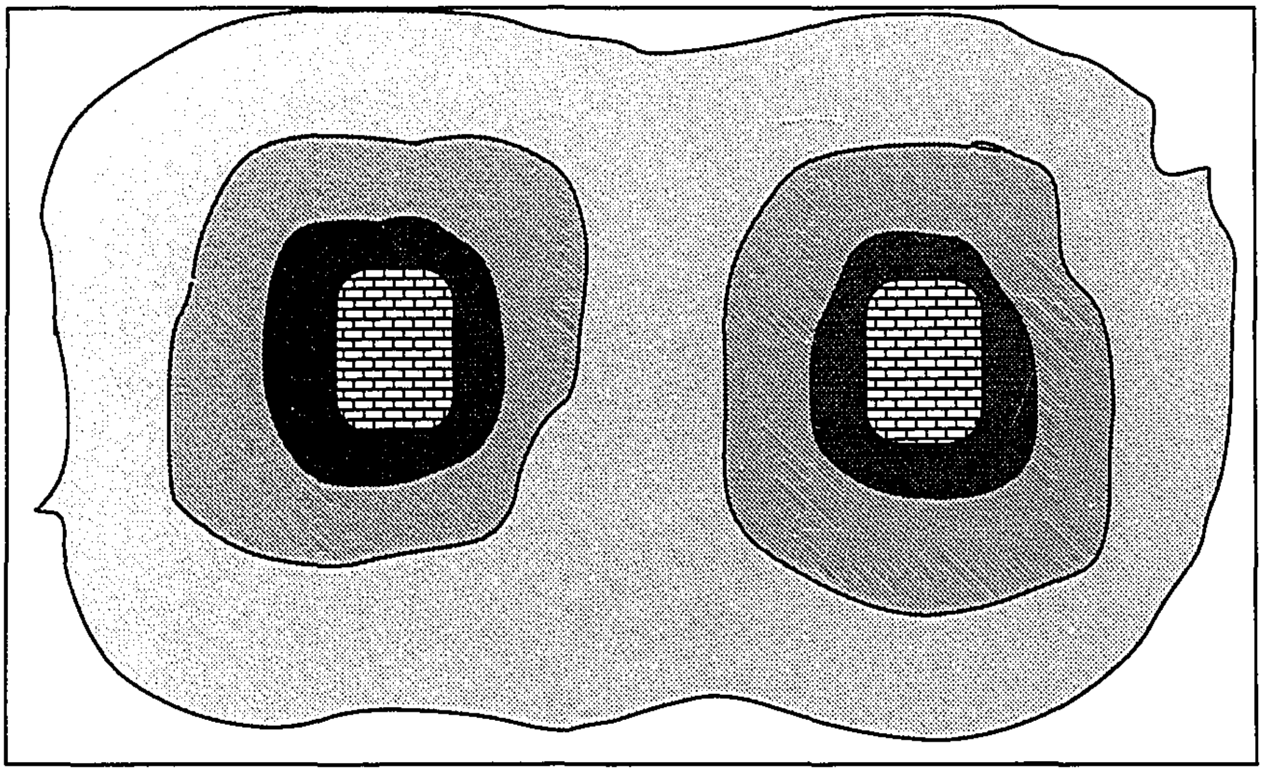


Fig. 3.15. Idealized sketch of disturbance gradient from abandoned housepad across trampled ground into adjacent undisturbed meadows.

▦ = Housepad

● = Heavily trampled meadow

▨ = Moderately trampled

░ = Lightly trampled

○ = Natural meadow

tissues were included in the analysis (Forbes 1992b).

b. Trampling

Housepad Type A was chosen as the high endpoint of the trampling intensity gradient because no materials (i.e. sand, gravel) were added to level or otherwise modify the tundra surface, except for small wooden blocks on which to lay the houseframe and which were apparently embedded from the weight of the house. The house did rest on the tundra surface and crush (but not tear) the vegetation and compact the soils beneath. It was considered to be nearly equivalent to an excessive amount of trampling. The persistence of partially bared mineral soils visible in an airphoto (**Plate 2.10**) taken four years after abandonment serves to reinforce this conclusion. **Fig. 3.15** illustrates the trampling gradient.

Fig. 3.13b compares the biomass of the five species which together had the highest cover/abundance values over the gradient from the housepad, across trampled vegetation to undisturbed vegetation. Two grasses, Alopecurus alpinus and Poa arctica, comprised the bulk of biomass on trampled ground. Almost all of the biomass on the housepad was provided by A. alpinus, with a small amount provided by Saxifraga cernua (not shown). P. arctica was usually present at low cover/abundance and biomass values. A. alpinus achieved its greatest biomass on heavily trampled ground immediately adjacent to the abandoned housepad, while P. arctica reached its peak on moderately trampled terrain.

Standing crop values for Salix arctica were highest away from the disturbance and declined fairly consistently with increasing disturbance intensity. Standing crops of Carex aquatilis var. stans and Eriophorum angustifolium were also highest in undisturbed vegetation, although a clear relationship with increasing disturbance intensity did not emerge for either species. The pattern for S. herbacea, another important deciduous shrub species in the undisturbed vegetation (not shown), was basically identical to that shown for C. aquatilis var. stans, except that it was completely absent on heavily trampled ground. Total foliar biomass on heavily trampled ground was nearly 2.5 times that found on lightly trampled and undisturbed ground (**Fig. 3.14b**). Totals were also significantly higher ($p \leq 0.025$) on moderately trampled ground compared to undisturbed ground, despite the reduction of woody species on the former.

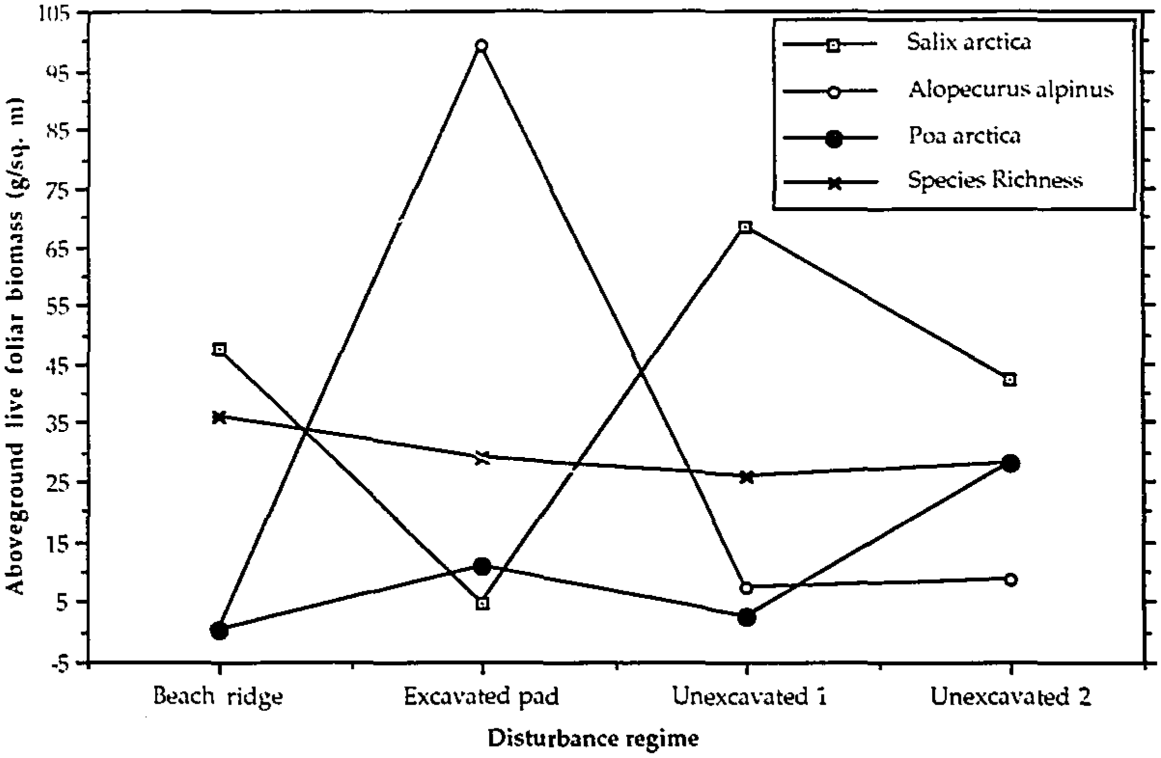
c. Archaeological sites

Fig. 3.16a illustrates the standing crops of the three dominant vascular species on the Thule winter dwellings and the adjacent beach ridge at TL. Despite their apparent floristic similarity (Section 3.2.iii), the two unexcavated dwellings differed significantly from one another in terms of the standing crops present for Poa arctica and Salix arctica. These grasses were present at low levels of cover and biomass on the beach ridge. Alopecurus alpinus was abundant on all three dwellings but comprised by far the majority of the biomass on the recently excavated dwelling (**Plate 3.11**). Total biomass on the excavated dwelling was more than twice that found on the unexcavated pads and the beach ridge (**Fig. 3.16b**), though species richness was highest on the beach ridge (**Fig. 3.16a**). S. arctica provided the bulk of the biomass on the beach ridge.

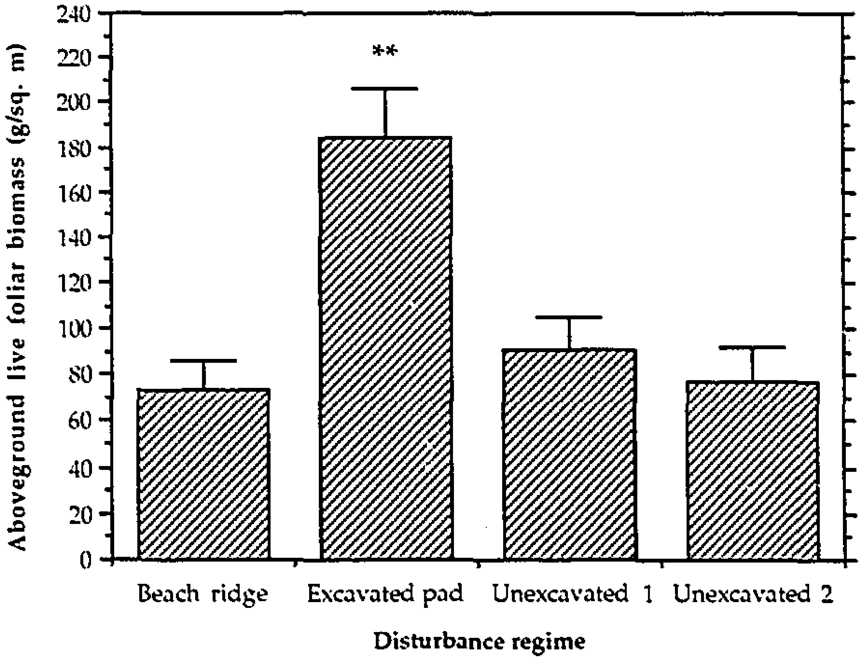
Fig. 16a - Plot of foliar biomass of dominant species and species richness on Thule winter dwellings and adjacent beach ridge at TL.

Fig. 3.16b - Histogram of total foliar standing crop on Thule winter dwellings and adjacent beach ridge at TL.

Biomass of dominant species & species richness (spp./1350 sq. cm) - Thule winter dwellings and adjacent controls - Stands 14, 15 and 16 - Truelove Lowland - 28 July 1990



Total vascular biomass - Thule winter dwellings and adjacent controls Stands 14, 15 and 16 - Truelove Lowland - 28 July 1990



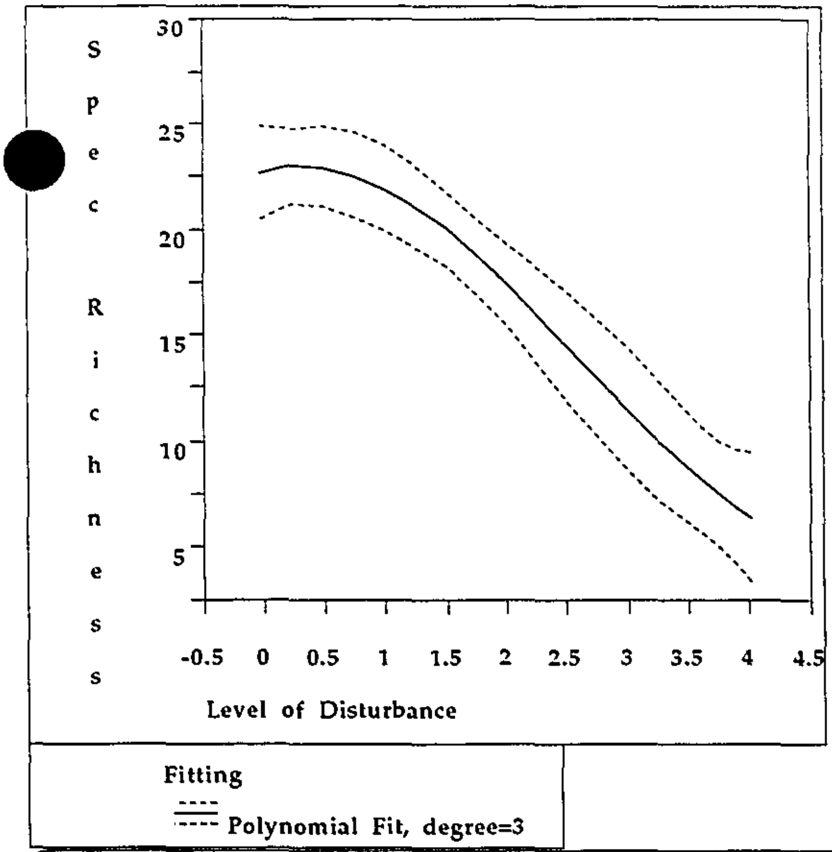
** indicated significant difference from beach ridge control at $p \leq 0.005$ Mann-Whitney Test

v. Species richness

Species richness is defined here as species per 1350 cm^2. In vehicle tracks through saturated meadows at TL, species richness (including non-vascular plants) often remained significantly reduced after 20 yr, despite the fact that total vascular biomass had nearly recovered to predisturbance levels. Species richness was consistently and significantly reduced in mesic meadows at both TL and CR, despite apparent biomass increases common among individual graminoid species (Forbes 1992b).

Species richness was invariably increased in gently sloped meadows drained by multi-pass tracks at CR (**Figs. 3.12b and 3.13a**). Along the trampling gradient, species richness displayed an inverse relationship with trampling intensity (**Figs. 3.13b, 3.17 and 3.18**). The greatest species richness occurred at intermediate levels of total biomass along the trampling gradient (**Fig. 3.19**). Only one pattern emerged from total species richness among the Thule sites at TL (**Fig. 3.16a**); the total was highest on the beach ridges. However, fully one third of the species on the beach ridges were macrolichens, whereas on each of the archaeological sites only one lichen species was common (Peltigera aphthosa). Only one other lichen species (Thamnolia subuliformis) occurred there, exhibiting low cover/abundance values. The balance was made up by bryophytes and several species of forbs (e.g. Draba spp., Saxifraga spp., etc.), which occurred at low cover/abundance and biomass values, but at fairly high frequencies.

Fig. 3.17 - Fitted line showing relationship between disturbance (trampling) intensity and species richness in a mesic meadow at CR (**Stand 18**). Analysis includes all plant life forms. Disturbance levels are as follows: **0**=undisturbed, **1**=lightly trampled; **2**=moderately trampled; **3**=heavily trampled; **4**=former housepad without materials added (vegetation completely absent at cessation of human activity in 1969).



```
Polynomial Fit, degree=3

  Summary of Fit

  Rsquare                              .7847323
  Root Mean Square Error               3.272521
  Mean of Response                     17.90909
  Observations (or Sum Wgts)                 33

  Analysis of Variance
  Source        DF   Sum of Squares   Mean Square    F Ratio
  Model          3        1132.1548       377.385    35.2387
  Error         29         310.5725        10.709   Prob > F
  C Total       32        1442.7273                   0.0000

  Parameter Estimates
  Term                          Estimate    Std Error   t Ratio   Prob>|t|
  Intercept                    22.706642      1.08600     20.91     0.0000
  Level of Disturbance          1.888028      3.07404      0.61     0.5439
  Level of Disturbance^2       -3.029055      2.13860     -1.42     0.1673
  Level of Disturbance^3       .38559504      .367053      1.05     0.3022
```

Fig. 3.18 - Histogram of species richness along the same trampling disturbance gradient at CR analyzed in **Fig. 3.17**.

Vascular and non-vascular species richness - Housepad Type A and adjacent trampled and natural meadows - Stand 18 - Clyde River - July 1990

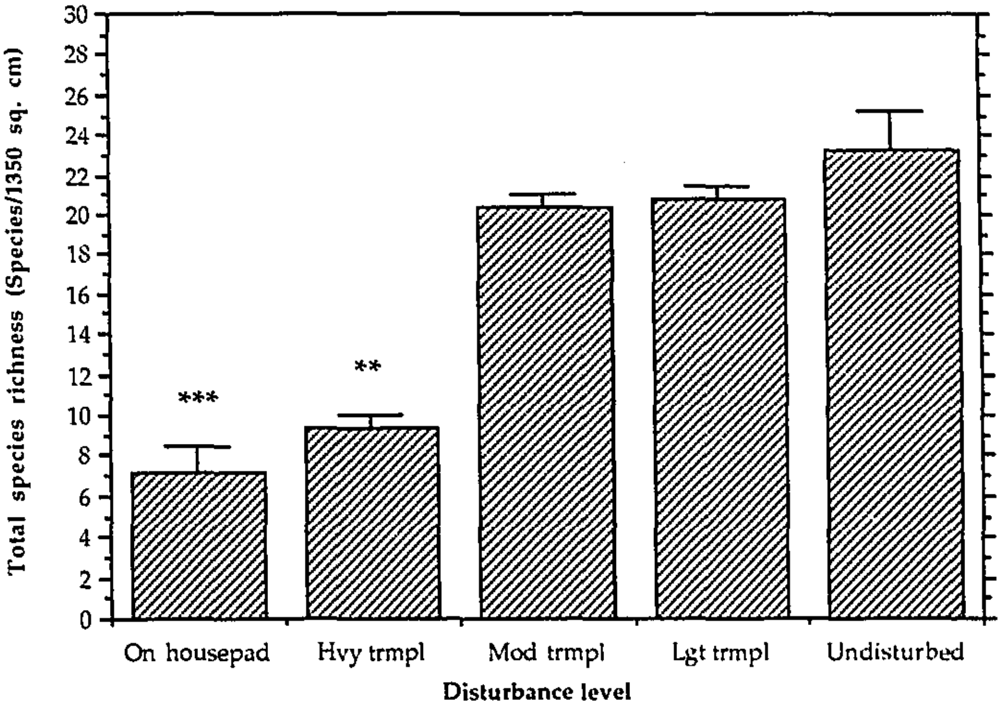
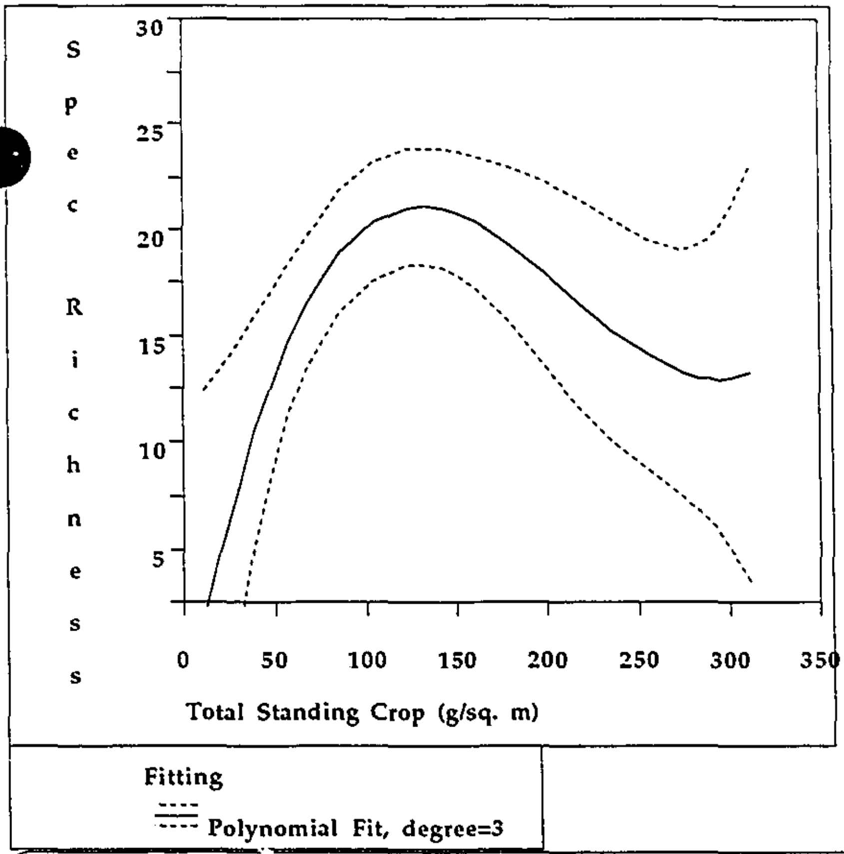


Fig. 3.19 - Fitted line showing relationship between above-ground vascular standing crop and species richness along the same trampling disturbance gradient at CR analyzed in **Figs. 3.17** and **3.18.**



```
Polynomial Fit, degree=3

Summary of Fit

Rsquare                          .3099949
Root Mean Square Error           5.858942
Mean of Response                 17.90909
Observations (or Sum Wgts)             33

Analysis of Variance

Source     DF   Sum of Squares   Mean Square   F Ratio
Model       3         447.2381       149.079    4.3429
Error      29         995.4891        34.327   Prob > F
C Total    32        1442.7273                  0.0121

Parameter Estimates

Term                                  Estimate   Std Error   t Ratio   Prob>|t|
Intercept                            -3.160301     6.78803     -0.47     0.6450
Total Standing Crop (g/sq. m)        .43396986     .156178      2.78     0.0095
Total Standing Crop (g/sq. m)^2      -.0023904     .001067     -2.24     0.0330
Total Standing Crop (g/sq. m)^3      .00000374     .000002      1.75     0.0901
```

vi. Growth forms

Life forms are considered types of plants having the same kind of morphological and/or physiological adaptation to a certain ecological factor. Growth forms are types of plants with the same gross morphology (architecture). The growth form concept is therefore free of any hypotheses about adaptation (Barkman 1988). Vascular taxa encountered at CR, TL and RB are categorized according to growth form in **Appendix 51** using a system based on that of Barkman. Species occurring in only one quadrat at any site were excluded from the table. It is apparent that deciduous shrubs provided about twice as much cover in undisturbed formations at CR than they did at TL. Although the sample pool at TL included more beach ridge stands than did that at CR, the shrub cover figure changes little if we remove them from consideration. The proportions of taxa in each growth form, on the other hand, are quite similar. Non-vascular plants were categorized as well. Mosses were divided into pleurocarpous and acrocarpous forms, hepatics were divided into thallose and leafy forms, and lichens were divided into crustose, foliose and fruticose forms.

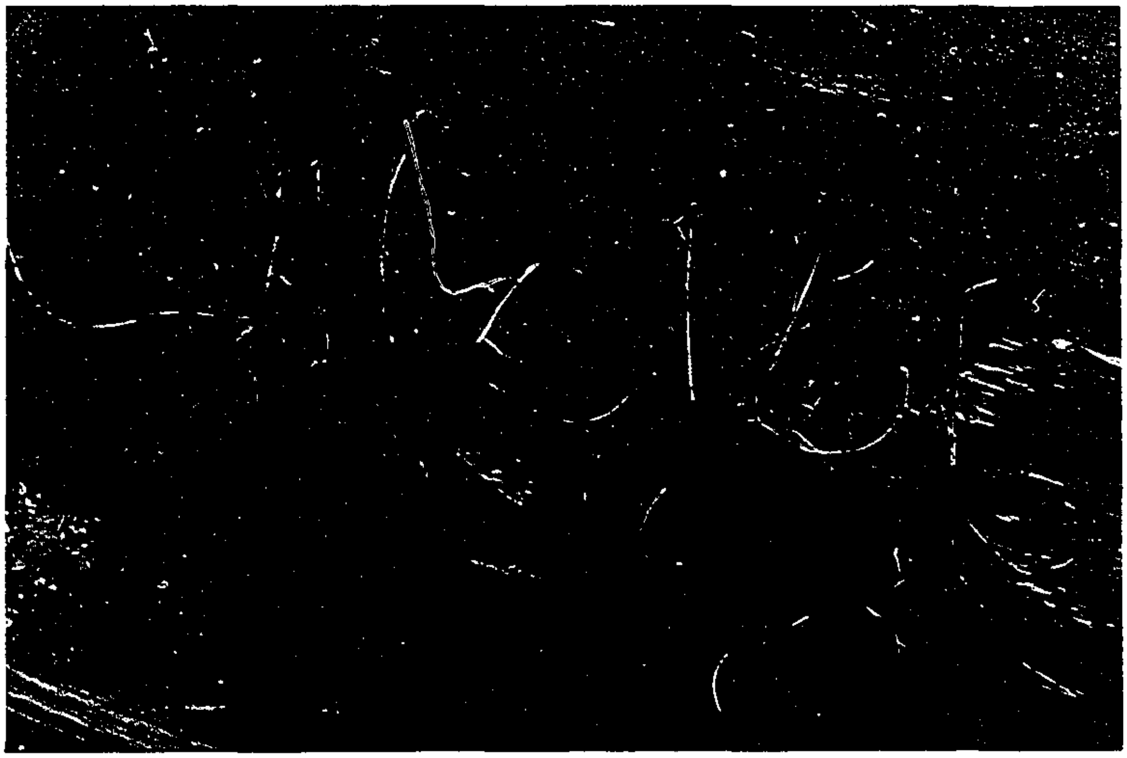
In this study, presence of the moss growth forms was about evenly split between acrocarps (56%) and pleurocarps (44%) in the wetter undisturbed meadow stands at TL, although 78% of the bryophytic cover in wet meadows at TL was provided by two pleurocarps (<u>Drepanocladus</u> <u>revolvens</u>, <u>Calliergon giganteum</u>) and one acrocarp (<u>Meesia</u> <u>triquetra</u>) (Vitt & Pakarinen 1977). These proportions shifted somewhat in hummocky meadows and on beach ridges. 65% of the taxa (not including Sphagna) were acrocarps in the hummock/hollow complexes at CR, although Sphagna comprised much of the cover and bryomass of the hummocks themselves. On beach ridge crests

Plate 3.11 - General aspect of recently excavated (1986) Thule winter dwelling (foreground) and unexcavated dwelling (rear) on beach ridge at TL. Alopecurus alpinus was abundant on all three dwellings surveyed, but comprised by far the majority of the biomass and was most densely flowering (**see also Plate 3.17**) on the recently excavated dwelling (Stand 14). Prominent flowers visible on excavated dwelling are those of Papaver radicatum. Here, and on the adjacent spoil heap, nearly all Papaver flowers were white, in contrast to the more common yellow occurring elsewhere in natural vegetation. Interestingly, the only other white Papaver flowers observed during the course of this study were on Inuit residences at Eglinton Fiord on Baffin Island, which were abandoned early in this century. Photo date: 25 July 1990.

Plate 3.12 - Portion of excavated clone of Carex aquatilis var. stans, showing extensive rhizome system and arrangement of ramets (**see also Fig. 3.20a**). C. aquatilis and C. bigelowii are taxonomically complex, closely related, and frequently hybridize in the eastern Canadian Arctic and elsewhere (Polunin 1940; Duman & Kryszczuk 1958; Drury 1962). Barrett (1975) considered them 'functionally equivalent' in his studies at TL. Nearly four dozen shoots were dug up intact. Many more broke off. This clone was excavated from a sandy multi-pass vehicle track in water channel zone, in which the tillers extended from the undisturbed vegetation on one side, nearly across the track (>50 cm) and part way back again. From left to right the specimen here measures 76.5 cm. Photo date: 28 June 1990.

Plate 3.13 - Excavated clone of Eriophorum angustifolium, showing extensive rhizome system and arrangement of ramets (**see also Fig. 3.20b**). It was excavated from the same vehicle track as the Carex specimen in **Plate 3.12**, where it exhibited a similar pattern of spread and also traversed the track more than once. From left (slightly cut off) to right the specimen here measures 101 cm. Photo date: 28 June 1990.

Plate 3.14 - Captive lemmings after being fed a choice of live and dead shoots of Alopecurus alpinus, Carex aquatilis var. stans and Eriophorum angustifolium at CR. Seen here are mostly overwintered tissues of A. alpinus. The lemmings apparently preferred live shoots of A. alpinus and, when that was finished, chose dead tissue of A. alpinus in preference to the sedges. Photo date: 18 June 1988.

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FIRST AIR AGENT
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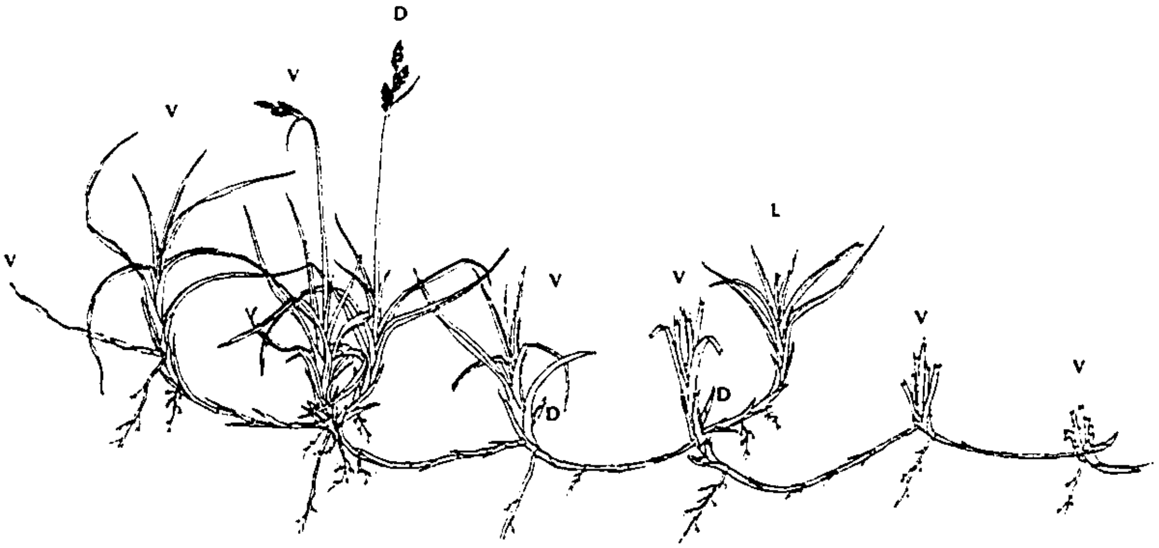
Fig. 3.20a - Sketch of Carex bigelowii showing root system and sympodial pattern of tillering. Tillers are produced ventrally (V), dorsally (D) or laterally (L). C. bigelowii is closely related to C. aquatilis, with which it often hybridizes in arctic and subarctic regions. Both species are clonal, producing thick rhizomes and multiple generations of interconnected tillers which are capable of covering several square meters. The 'guerilla' growth form (*sensu* Lovett-Doust 1981) is seen here (**see also Plate 3.12**). This growth form consists of long ramet connections, to better explore new habitats, and a high degree of branching. Source: Carlsson & Callaghan (1990). Used with permission of authors.

Fig. 3.20b - Sketch of Eriophorum angustifolium showing root system and pattern of tillering. As with Carex aquatilis and C. bigelowii, E. angustifolium is capable of producing guerilla-type ramets to probe for new, unoccupied substrates (**see also Plate 3.13**). Modified from Kutschera-Mitter (1984).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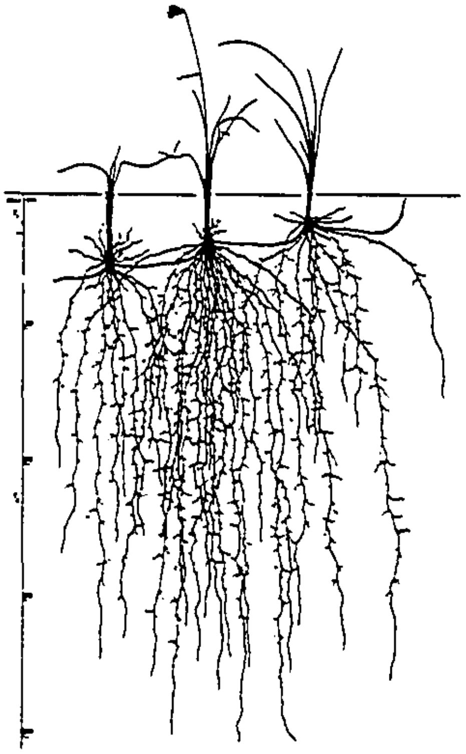
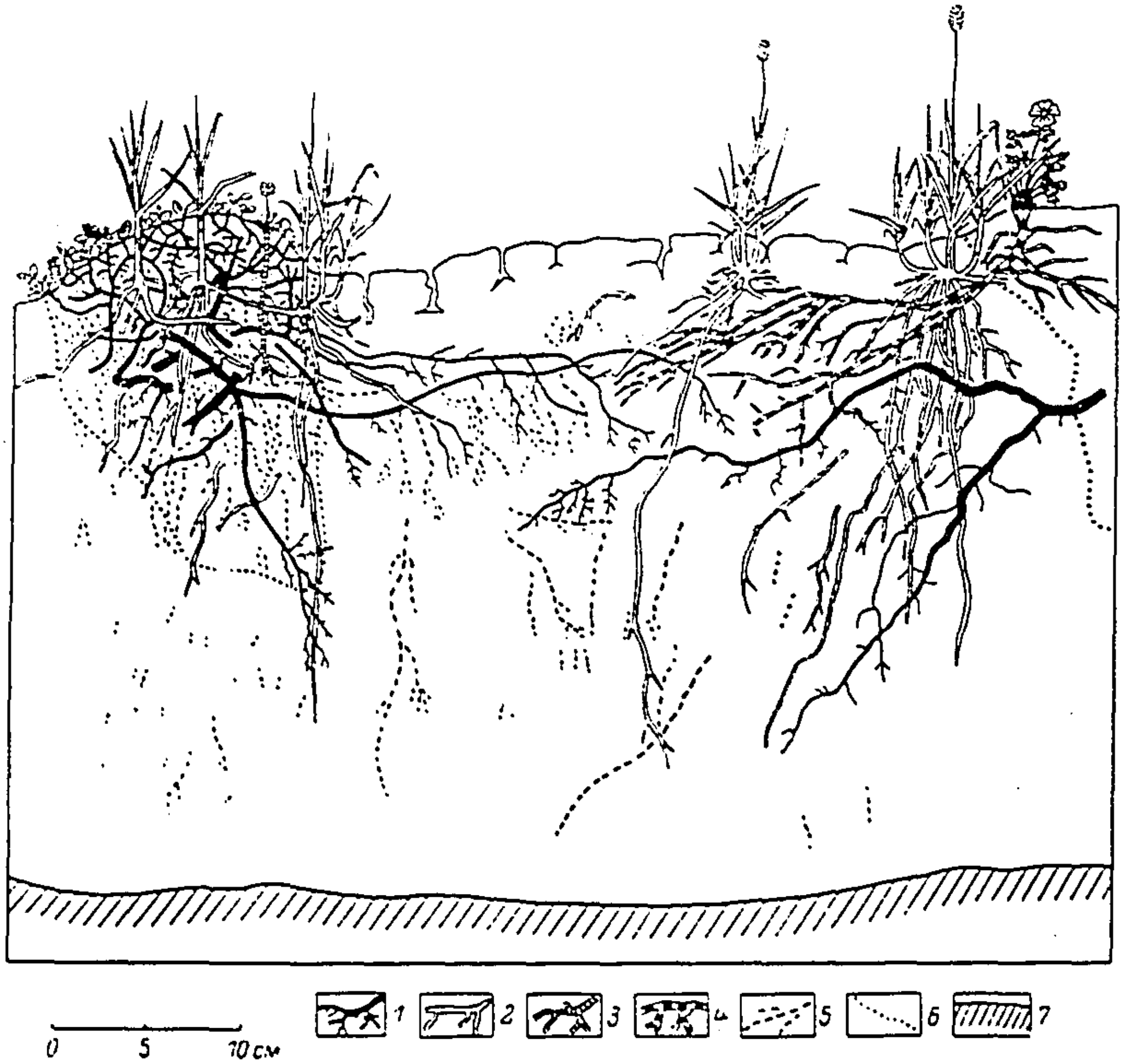


Fig. 3.21 - Vertical section of naturally occurring tundra plant-soil unit, showing relative depths of root systems. Roots of Alopecurus alpinus can penetrate rapidly to great depths in soils ranging from extremely dense clays to loose gravels, a competitive advantage in the context of disturbance. Even in the absence of anthropogenic disturbance, as seen here, A. alpinus tends to send roots deeper than other cooccurring species. Root systems depicted are: 1 Salix polaris; 2 A. alpinus; 3 Draba pseudopilosa; 4 Potentilla hyparctica; 5 unidentified roots; 6 limit of root masses for majority of roots; 7 permafrost surface in August. Source: Aleksandrova (1988). Used with permission of the publisher.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and slopes at TL and RB examined for this study, 66% of the taxa were acrocarps, but cover was often minimal relative to lichens. Among liverworts, leafy forms comprised 75% of the taxa in sampled stands at TL and RB and 60% at CR. However, thallose forms were rare.

As seen in **Appendix 51**, pedestrian trampling at CR has had a profound effect upon the presence and abundance of certain growth forms. The only shrubs present (mostly Salix arctica and S. herbacea) were those that appeared to have survived the initial impact of light trampling. Both deciduous and evergreen growth forms were apparently unable to withstand even a single-pass of a heavy tracked vehicle and, after ≥20 yr, showed little evidence of reinvasion. On the other hand, the presence at the outset of an essentially closed mat of rhizomes in the soil meant that while heavy trampling bared the surface of most shoots, stems, leaves, and litter, the 'root mat' of species such as Carex aquatilis var. stans held more or less intact through the more than six years of settlement. Consequently, surface erosion was minimal and regrowth was facilitated. In this sense, the rhizomatous graminoid was the most resistant of the vascular growth forms present (**Plates 3.12 and 3.13, Fig. 3.20**). Another species with an extensive root system is Alopecurus alpinus (**Fig. 3.21**). The dense turf which developed on moderately and lightly trampled ground at CR was dominated by the viviparous Poa arctica and, to a lesser extent, A. alpinus and Arctagrostis latifolia ssp. latifolia. The former two grasses have successfully displaced much of the original sedge cover (C. aquatilis var. stans, Eriophorum angustifolium and Juncus biglumis). Unlike the sedges, establishment and spread by the former species appeared not to be limited by the hummock and hollow microenvironments.

Among cryptogams, fruticose lichens were completely lacking in all trampled and tracked vegetation. A few crustose species (Ochrolechia and Collema spp.) remained on tops of moderately and lightly trampled hummocks but not in vehicle tracks. Relative to adjacent undisturbed vegetation, the foliose lichen Peltigera aphthosa apparently increased slightly in frequency and cover on the sides of moderately and lightly trampled hummocks but it, too, was lacking in vehicle tracks. No species of Sphagnum remained on trampled sites at CR and there was no evidence of recolonization. Although no Sphagna survived multi-pass vehicle tracks, S. capillifolium var. tenellum remained in 75% of single-pass tracks while S. squarrosum was limited to 20% of the same tracks. Responses among other bryophytes varied.

On housepads where sand/gravel was added, all species were acrocarpous; it was apparent that the addition of soil favored those forms in which the reproductive organs were able to remain above or quickly penetrate any added materials. On adjacent mesic, moderately trampled ground, only 25% of the species present were pleurocarps. This figure jumps to 43% on wet ground, where most of the cover was provided by Brachythecium salebrosum and the acrocarps Aulacomnium palustre and Bryum pseudotriquetrum. A similar pattern of differentiation existed between trampled hummocks and hollows. The frequency of pleurocarps (e.g. Calliergon sarmentosum, C. stramineum, Cirriphyllum cirrosum) increased in hollows, while acrocarps were more frequent on hummocks. There were exceptions to this pattern. One of the most frequent and extensive ruderals on drier substrates was Drepanocladus uncinatus, a pleurocarp. Conversely, the acrocarp A. palustre was both frequent and extensive in wet microenvironments.

vii. Nutrient cycling

a. Tissue nutrients

Mid-season concentrations of macronutrients in vascular plant tissue are illustrated for dominant species and growth forms along disturbance gradients at CR and TL in **Appendices 53-57**. Analyses were made from live shoots of graminoid species and from live leaves of deciduous shrubs. All measurements in sloped areas were made along a transect perpendicular to local slope so as to restrict sampling to sites with a unidirectional flow of water. This was done in accordance with recommendations made by van Leeuwen (1966) and Damman (1988) on investigations of vegetation change along resource gradients in peatlands (see also de Molenaar 1987). Levels of statistical significance for these and related data are summarized in **Appendix 57.**

Some patterns emerge among data for species, growth forms, study sites, disturbance regimes and individual nutrients. Relative to controls, levels of nitrogen in rhizomatous graminoids were somewhat increased in single-pass vehicle tracks in an interfluve at CR. However, nitrogen levels were greatly reduced in the deciduous shrub Salix arctica. In drained areas below multi-pass tracks perpendicular to the same interfluve, nitrogen content was significantly decreased in all three species, but the magnitude of change was greatest in the two rhizomatous sedges. In few-pass tracks through a wetter calcareous meadow at TL, nitrogen increased significantly in E. angustifolium, but decreased significantly in Carex aquatilis var. stans **(Appendix 57c).**

At CR, levels of phosphorus content among the sedges displayed a pattern similar to that described for nitrogen (**Appendix 53**). Leaf tissue of Salix arctica registered a significant reduction in the same set of tracks, but phosphorus levels remained unchanged in drained areas, relative to controls upslope. Potassium levels increased in tracks in all species at both study sites, significantly in several cases (**Appendix 57**). Potassium was significantly lower in drained areas relative to controls in E. angustifolium and S. arctica (**Appendix 54a and 57a**). Differences in levels of magnesium were rare. Calcium levels decreased in all three species in tracks at CR, significantly so in Carex. At TL, calcium decreased significantly in Eriophorum in few-pass tracks. Decreases in calcium were registered in drained areas for all three species and were significant for the two sedges.

Tissue nutrient status was also measured for trampled vegetation at CR. Leaves of Salix arctica registered significant increases in concentrations of most nutrients measured relative to adjacent undisturbed ground. The only exception was nitrogen, for which Salix leaf concentrations were significantly lower in lightly trampled areas compared to controls. However, the nitrogen content of Salix displayed a positive relationship with increasing disturbance intensity so that N concentrations in heavily trampled populations approached those in undisturbed populations.

Other plant species sampled in pairs along the same gradient revealed interesting patterns of nutrient content. Alopecurus alpinus, for example, did not occur in the undisturbed vegetation, but its leaves registered substantial changes between moderately trampled ground and the adjacent housepad (**Appendix 57b**); leaf concentrations of nitrogen, phosphorus and calcium all increased significantly, and potassium decreased significantly. In leaves of Eriophorum angustifolium, nitrogen content increased significantly from lightly to moderately trampled ground. In effect, the tissues of these species exhibit significant changes in macronutrient concentrations over distances of 50-200 cm. Substantial changes in the concentrations of all five nutrients were associated with different levels of disturbance intensity, including light trampling, relative to adjacent undisturbed vegetation.

At TL, tissues of Salix arctica registered pronounced differences in macronutrient concentrations among two different Thule winter dwellings and the adjacent beach ridge. This gradient is illustrated in **Appendix 56b**. Concentrations of most nutrients were significantly higher on one or both of the Thule dwellings relative to the beach ridge (**Appendix 57c**). Alopecurus alpinus was not abundant enough on the beach ridge to sample. However, Nosko (1984) did extensive sampling of nitrogen and phosphorus concentrations in this species on the lowland. His samples from 19-20 July 1980 indicate that percent nitrogen content was reduced on a 'Thule camp' site compared to a 'willow-cushion plant-moss' site, but that phosphorus content was increased on the Thule camp. He showed that concentrations of both nutrients tended to be lower in flowering plants compared to non-flowering plants, and that concentrations on the same 'control' site declined over an eight-day period from 19 to 27 July. He also showed that nitrogen increased in plants growing in vehicle tracks through the 'willow-cushion plant-moss' site. My own data show that there were clear differences in the nutrition of this species between the unexcavated and recently excavated Thule dwelling. Concentrations of all nutrients except magnesium were significantly lower on the latter (**Appendix 57c**).

b. Soil nutrients

The soil nutrient data are not directly comparable to the tissue nutrient data in most cases. In only a few instances did my soil sampling precisely match the quadrats used for tissue sampling. However, the sampling did detect many proportional changes in the nutrient content, pH and corrected conductivity of mineral soils analyzed along essentially the same transects used for the other analyses. These are presented graphically in **Appendices 58-60**. No attempt has been made to directly compare the soils data to any of the measured biological responses, since the latter are certainly highly covariate and not likely to be tied to soil nutrients at one point in time assayed by 'availability' methods developed for southern agriculture (Lechowicz 1992, pers. comm.).

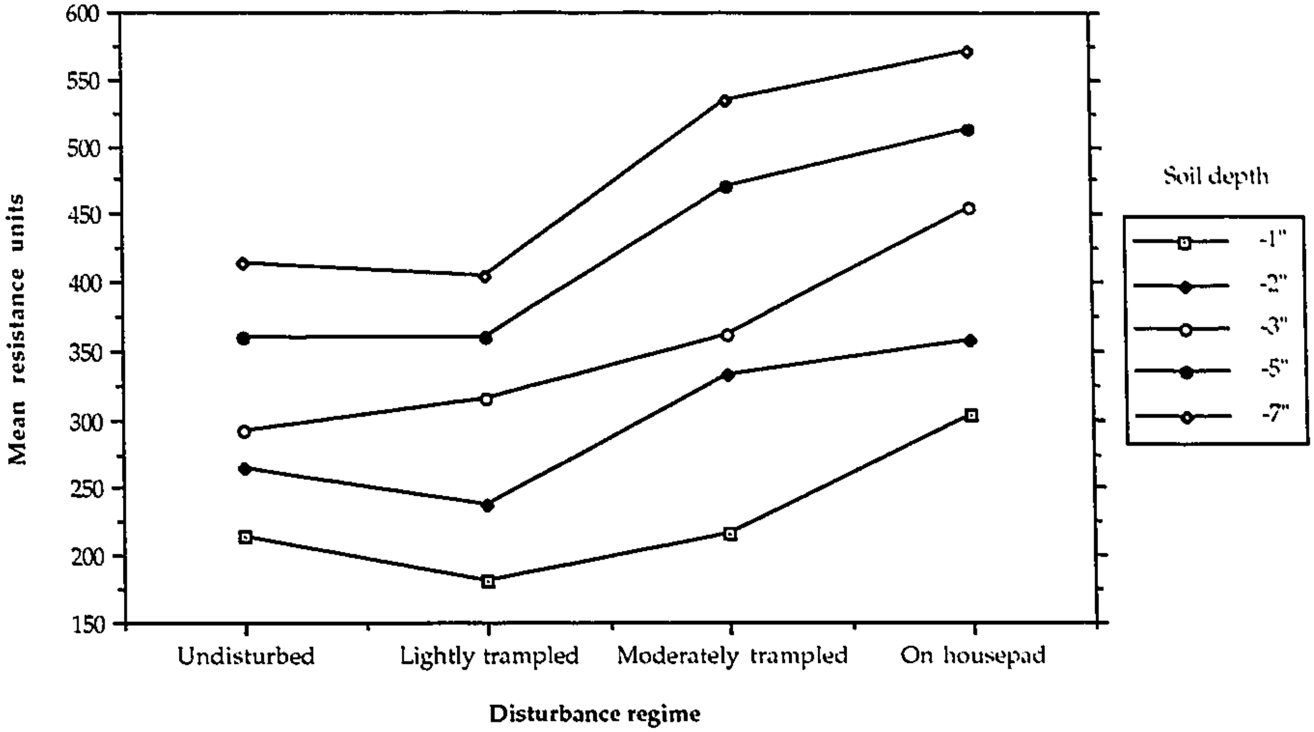
Most soil parameters measured (organic matter, pH, corrected conductivity, etc.) increased significantly in single-pass tracks, and also in multi-pass tracks. Many of these also increased in drained areas downslope from multi-pass tracks (**Appendix 58**). These same parameters differed little or not at all in areas drained by single-pass tracks compared to controls upslope. On the trampling gradient, most parameters increased relative to undisturbed ground (**Appendix 59**). An exception was phosphorus content, which was unchanged on moderately trampled ground. Corrected conductivity declined with light and moderate trampling, but increased significantly, along with phosphorus, potassium, organic matter, and carbon, on heavily trampled ground. On the Thule winter dwellings, soils were significantly enriched compared to the adjacent beach ridge, with the soils of the excavated dwelling having the highest organic matter, carbon and phosphorus contents (**Appendix 60a**). Potassium content was highest in the soils of the second housepad (**Appendix 60b**). Soil pH (**Appendices 58-59**) was significantly higher under each disturbance regime at CR relative to controls. At TL, pH was significantly lower on each of the Thule dwellings at TL compared to the beach ridges (**Appendix 61**). Thus, virtually all aspects of soil nutrition and chemistry varied substantially at scales congruent with each of the disturbance regimes investigated.

viii. Soil compaction and particle size distribution

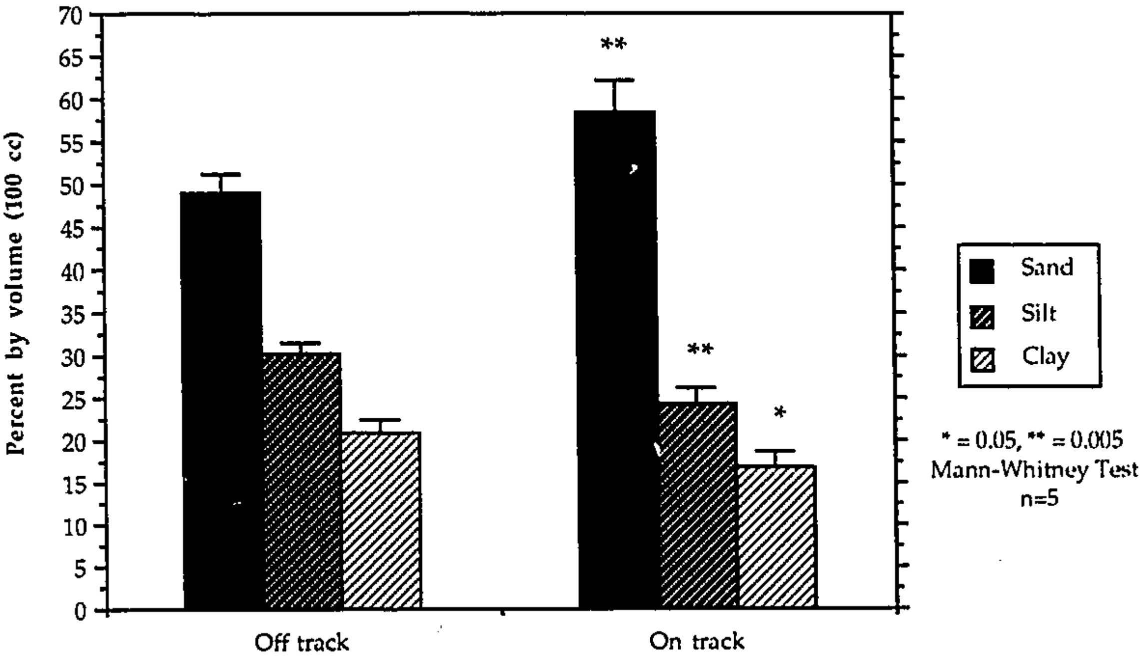
Although only soil compaction data from a depth of 3" was used in the multivariate analysis, many additional measurements were made, with readings taken at depths of 1", 2", 3", 5" and 7". Compaction was invariably greatest on trampled ground and in some multi-pass vehicle tracks, particularly where the organic mat was completely destroyed. As seen in **Fig. 3.22a**, compaction increased fairly consistently with depth in both disturbed and undisturbed soils. This pattern was repeated in other mesic stands at CR, except in single-pass tracks, where soil moisture was often increased and compaction and bulk density were significantly decreased. This was revealed by CANOCO and is shown in **Appendix 20**. At TL, the soils were generally much wetter and differences in compaction between treatments and controls were minimal or lacking. Other physical analyses of soils not included in the multivariate analyses were particle size distribution in each disturbance regime. The only significant changes detected were those in multi-pass vehicle tracks at CR where the organic mat was destroyed and thus allowed the removal of fines by runoff during Spring snowmelt. **Fig. 3.22b** illustrates these changes for a water channel zone at CR. Predictably, sands were significantly increased in the multi-pass tracks, while silts and clays were

Fig. 3.22a - Plot of soil compaction versus depth for Housepad Type A and adjacent trampled and natural meadows at CR.

Fig. 3.22b - Histogram of soil particle size for multi-pass tracks and adjacent controls in a water track zone at CR.



Soil compaction vs. depth as measured by cone penetrometer - Housepad Type A and adjacent trampled and natural meadows - Stand 18 - Clyde River - 12 July 1989



Soil particle size analysis - Multi-pass tracks and adjacent controls - Stand 11 - Clyde River - 7 July 1989

* = 0.05, ** = 0.005
Mann-Whitney Test
n=5

decreased.

ix. Herbivore activity

Nominal classes of faeces cover/abundance were determined for each species for which evidence could be recognized in each quadrat. The results shown in **Appendix 52** are for disturbance regimes where the results appeared to be of significance and for their adjacent controls. Patterns of nesting and grazing (clipping) were also observed and photographed in some instances, allowing several tentative conclusions. Direct observations of collared lemmings (Dicrostonyx groenlandicus) were made almost daily throughout each of the three field seasons at CR, but this species was rarely observed at TL and was not seen at all at RB. At the start of the 1988 growing season, I conducted an informal grazing experiment with a trio of lemmings captured by young Inuit and presented to me as a gift (**Plate 3.14**). Being aware of the forage value of the genus Alopecurus in temperate regions, I offered the lemmings a choice of live and dead standing A. alpinus tissue from a housepad. I offered roughly equivalent amounts of live (new shoots) and dead (overwintered) Carex aquatilis var. stans and Eriophorum angustifolium from an adjacent lightly trampled meadow. After several hours I returned and found that virtually all of the green A. alpinus material had been consumed, but little if any of the green or dead material from the sedges appeared to have been touched. From then on I continued to feed them only A. alpinus until the children departed, after which I released the lemmings.

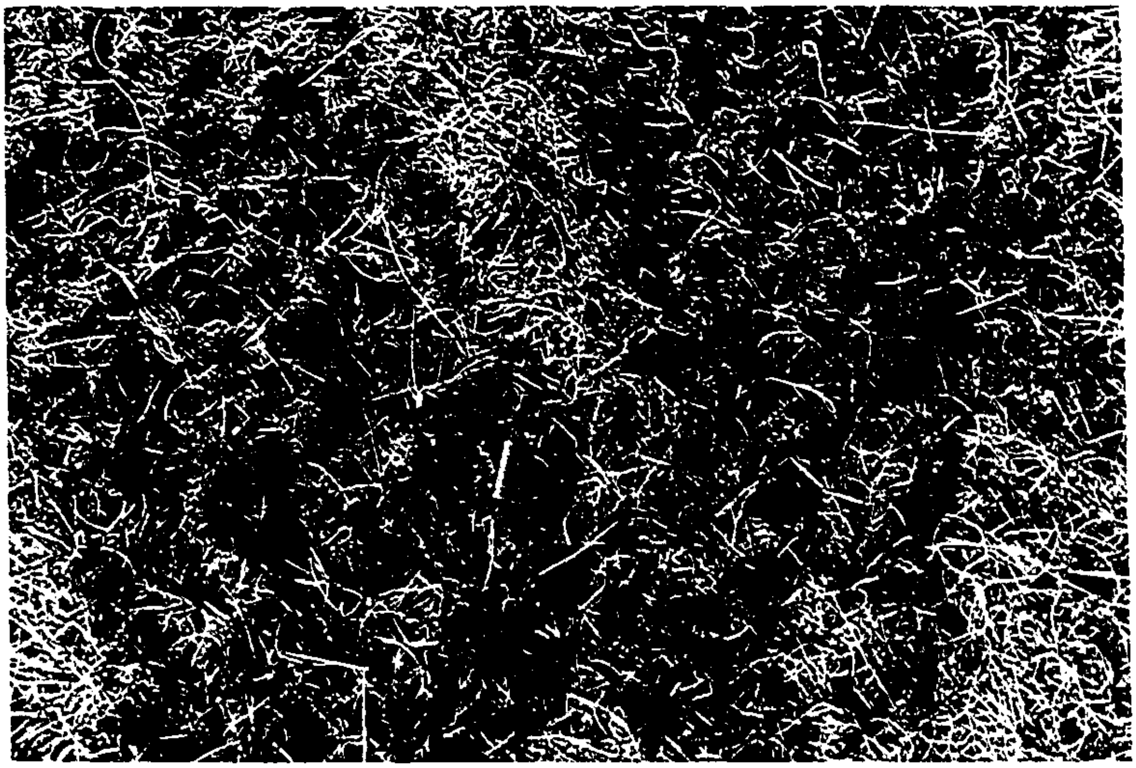
The only grazing bird in evidence at CR was, in all likelihood, the greater snow goose (Anser caerulescens atlanticus). Snow geese were not observed directly but had intensively grazed within a small area, the only truly hydric meadow sampled at this study site. The grazing was presumed to have taken place immediately prior to my arrival at the study site each year, as the migratory birds were en route to northern Baffin and adjacent Bylot Island (Giroux et al. 1984). Early each June, field evidence indicated that the birds had grazed selectively on subterranean portions of the dominant graminoids at the site (Carex aquatilis var. stans and Dupontia fisheri ssp. psilosantha,), since the pattern of grazing matched precisely that described for the region by Giroux et al. (**Plate 3.15**).

From **Appendix 52** it is apparent that the most common grazer in the areas sampled was the lemming, which was active within both naturally and anthropogenically disturbed stands and at all three study sites. Evidence of nesting was absent from virtually all of the undisturbed meadow vegetation sampled at CR and TL, as were signs of manuring. In three seasons of traversing many square kilometers of terrain at CR on foot, I observed neither scattered nor concentrated signs of lemmings even short distances away from patches that had some sort of disturbance in evidence. The disturbances included frost-heaving, trampling, tracking, etc. These observations were repeated over a similar amount of terrain during portions of two growing seasons at TL.

Ancedotal evidence of the importance of disturbance in providing suitable habitat for lemmings is provided again by the children of CR, for whom 'akiani' (the other side, a.k.a. Old Clyde River) has been a favored hunting ground for lemmings for many years. I, too, failed to observe more than one or two lemmings in my many wanderings in the vicinity of 'New' Clyde River. At New CR, I repeatedly travelled through areas similarly

Plate 3.15 - Close-up of grazing effects from greater snow geese in hydric meadow at CR. Meadow is dominated by Carex aquatilis var. stans, Dupontia fisheri ssp. psilosantha, Aulacomnium spp. and Bryum spp. Photo date: 21 June 1990.

Plate 3.16 - General aspect of Housepad Type B and adjacent meadows at CR showing an example of the pattern of snowmelt which was similar each year. With little or no snowcover after the winter, raised housepads such as this one were among the earliest patches to emerge and experience plant growth. The pads themselves typically had substantial faecal deposits from lemmings (**see also Plate 3.17, Appendix 51**). In contrast, the meadows adjacent to the housepads often had wind-compacted snow at a depth of ≤30 cm which, after melting out quite late, revealed numerous lemming tunnels, nest sites, and additional deposits of manure. Note the 4" x 4" wooden blocks at center, embedded in succesive layers of sand (top) and gravel (bottom), on which the house once rested. The discrete graminoid clones with tall culms are Alopecurus alpinus. The caespitose tufts are mostly Phippsia algida. Bryophyte patches are only scattered and vegetation cover is open. The barrels scattered about were cleaned up less than two months after this photo was taken. Photo date: 23 June 1989.

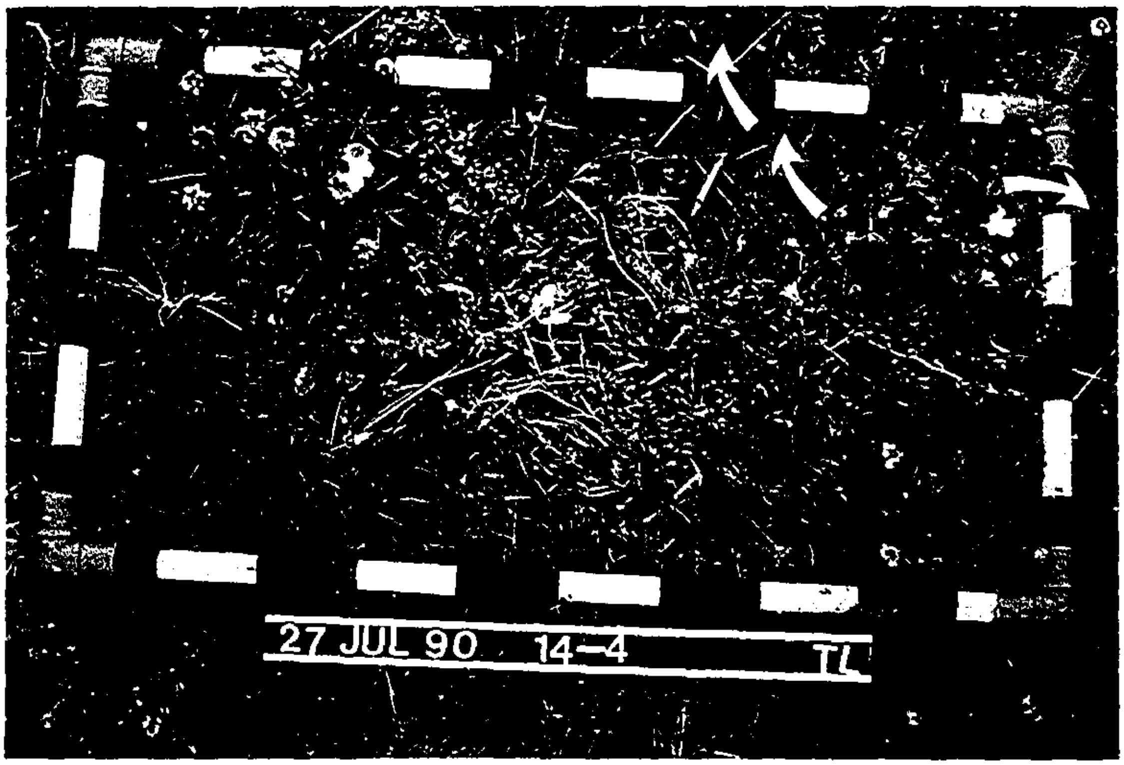


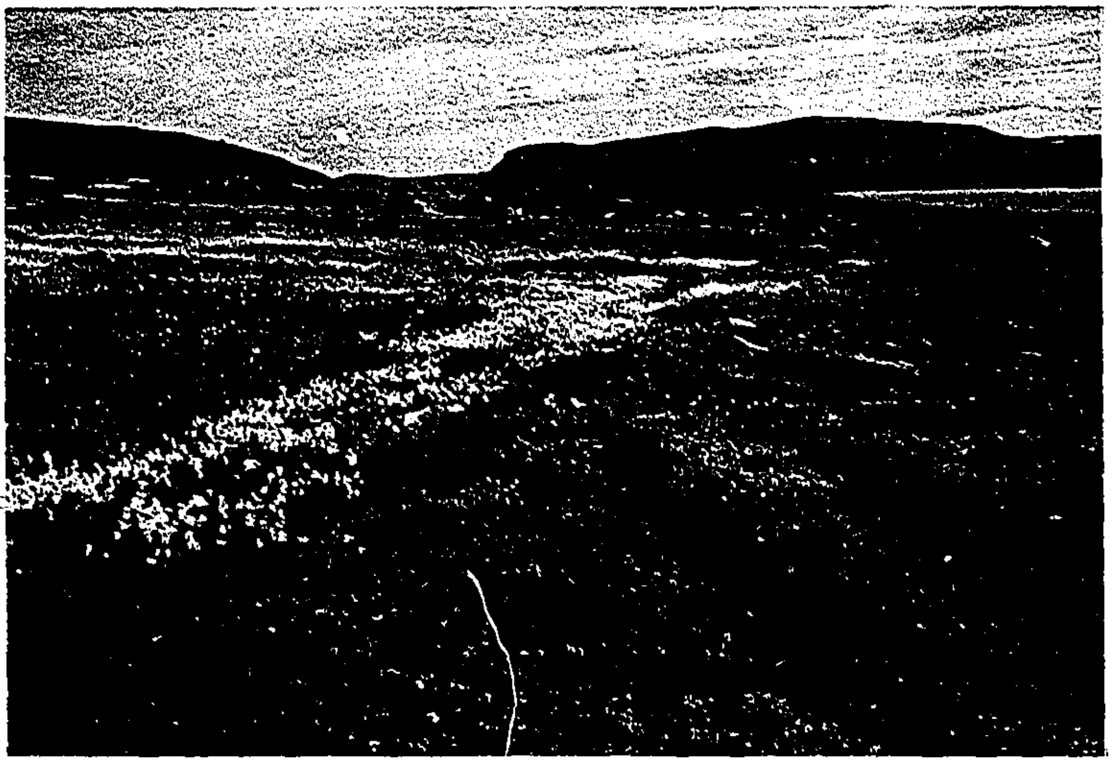
disturbed to many of my samples, but noted that lemmings were present in far greater numbers annually at akiani. Key factors in this abundance may include the general lack of current human activity, including hunting children, at the study sites. Both settlements have innumerable oil drums and other random trash strewn about, which provide excellent cover from predators. However, additional evidence indicates that the habitat at akiani is suitable in other ways. Each Spring I measured snow melt in the sampled stands. It was apparent that while housepads were raised and tended to be more or less exposed, and had substantial quantities of lemming faeces on the surface, the immediately adjacent trampled meadows were typically under at least 20-25 cm of compact snow (**Plate 3.16**). As the latter eventually melted away, a maze of tunnels, numerous nesting sites, and additional layers of fresh faeces were exposed and it was clear that these had been active denning and feeding areas for lemmings during the winter. With increasing distance from the housepads, and moderately to heavily trampled areas, these indicators were increasingly rare.

Appendix 52 also shows that lemming manure was most abundant on recently disturbed housepads (both palaeo and contemporary) and heavily trampled meadows. As was shown earlier, these sites were dominated by Alopecurus alpinus in terms of both cover and aboveground standing crop. A notable exception is Housepad Type C at CR, which was dominated by the caespitose grasses Festuca brachyphylla, Puccinellia langeana, and only lesser amounts of A. alpinus. An abundance of faeces from hare (Lepus arcticus), ptarmigan (Lagopus mutus) and even musk-ox (Ovibos moschatus), were recorded on the recently excavated Thule dwelling at TL, but seldom on the adjacent beach ridges. Faeces of lemming, hare and ptarmigan were occasional

Plate 3.17 - Quadrat from back wall of recently excavated Thule winter dwelling at TL (see **Plate 3.11**) showing vigorous plant growth and high density of faecal pellets from arctic hare. Nine pellets were counted in the field of the photo, some of which are unobscured by vegetation (top arrows). All but one of the pellets appeared fresh (arrow at right). After clipping, lemming manure was revealed to be very abundant with >10% cover within the quadrat. Faeces of ptarmigan and muskoxen were also common on and immediately adjacent to the pad, but not on the beach ridge. The dominant vascular plant is Alopecurus alpinus, which has a significantly higher density of inflorescences and taller culms than on unexcavated pads nearby. Other prominent species include Poa arctica, Papaver radicatum and Saxifraga cernua.

Plate 3.18 - General aspect of multi-pass tracks in water track zone at CR showing extremely high density of Eriophorum angustifolium inflorescences. Moderate density is visible in area upslope from track (left rear), which contrasts with the virtual absence of inflorescences in the downslope area (right). Photo date: 19 August 1990.


27 JUL 90 14-4 TL



to abundant on unexcavated Thule dwellings at TL. Among the many control areas at all three study sites, lemming faeces were observed only in a single frost-boil meadow at TL. Hare pellets were rarely observed on the beach ridge immediately adjacent to the recently excavated Thule dwelling, but were observed in great numbers on the dwelling itself (**Plate 3.17**). In many cases, specialist ('dung-loving') bryophytes (e.g. Splachnum vasculosum ssp. heterophyllum, Voitia hyperborea) occurred at high frequencies within heavily manured stands (e.g. Stands 2on, 3on, 4off and 14on at TL).

x. Graminoid flowering

The percentage of flowering shoots is thought to be a good measure of the vitality of many northern wetland plants (Bernard & Gorham 1978; Grootjans & van Tooren 1984), although allocation to sexual reproduction may vary widely among years (Shaver & Kummerow 1992). Inflorescence density counts (number of inflorescences per square meter) made among dominant species of graminoids revealed definite patterns associated with several disturbance regimes. The highest numbers of inflorescences were in multi-pass vehicle tracks, on housepads and dwellings of all but one type, and on heavily trampled ground. In the latter situation at CR, for example, almost every culm of Alopecurus alpinus was found to be flowering and the mean number of inflorescences (98.64±14.88 inflorescences/m^2) was significantly higher (p =0.01) than that which was recorded on the housepad itself in 1990 (mean = 65.60±8.24 inflorescences/m^2). However, the numbers of A. alpinus inflorescences found on this and each of the other three housepads at CR was significantly higher (p =0.01) than on adjacent moderately and lightly trampled ground and in control areas. Virtually no inflorescences were recorded in the latter. Flowering among the dominant sedges was not significantly different from controls in any of the trampling treatments.

In multi-pass tracks which traversed water channels at CR, Eriophorum angustifolium was observed flowering profusely in each of the three field seasons (**Plate 3.18**). On-track means for this species (69.49±8.7) were significantly higher (*p* =0.05) than upslope controls (34.64±19.2). Few inflorescences of were recorded in the drained areas below the multi-pass tracks here and in Stand 12.

At TL, by far the greatest numbers of inflorescences were, observed on the recently excavated Thule dwelling in 1989 and 1990 (**Plates 3.11 and 3.17**). Here, A. alpinus had 192±19.92 inflorescences/m^2 in 1990, while none were observed on the adjacent beach ridge. This was significantly higher (*p* =0.01) than the number of inflorescences of this species which occurred on either of the unexcavated Thule dwellings at TL (mean = 9.6±1.6 in Stand 16; none in Stand 15) and the unexcavated dwelling at RB (mean = 92.8±28.0). The only other species for which a significant change in the numbers of inflorescences was measured on a disturbance was Eriophorum scheuchzeri. Patterns of cover/abundance and flowering for Poa spp. were often similar to A. alpinus, but inflorescences were not counted for this species. Carex aquatilis var. stans typically flowered in greater abundance in wet meadows than mesic ones, but flowering within this species did not appear to respond to disturbances except for, perhaps, a slight negative response in drained areas at CR. E. scheuchzeri appears to have germinated from seed in a wet meadow at TL (Stand 11) soon after Barrett (1975) transplanted cuttings of C. aquatilis var. stans and blocks of bryophytes in his attempt to restore multi-pass tracks in 1972. This species was observed producing 126.4 inflorescences/m^2 (±29.52) in 1990 within a sharply circumscribed patch which matched almost precisely the dimensions of

Barrett's original manipulation. No flowering culms were observed away from the track.

CHAPTER IV. DISCUSSION

4.1 Discussion of multivariate analyses

i. Vegetation patterns

Several conclusions can be drawn from the numerical classification and ordination analyses. First, interlowland floristic gradients from the three islands surveyed in this study were longer than those derived from multivariate analyses by Henry (1992). The latter compared data from the sedge meadows of five lowlands on three high arctic islands and, using DCA, derived a first axis of only 1.92 s.d. Henry defined a 'core group' of eight vascular species which were common in all meadow stands, with an additional 4-6 species found in most stands, most of which have been shown to possess considerable ecological amplitudes (Muc et al. 1989). The soils of the lowlands Henry surveyed were generally of circumneutral pH, but ranged from mildy acidic (at Alexandra Fiord) to mildly alkaline (Truelove Lowland).

Included in my own data set is a comparison of natural vegetation from a site with moderately acidic soils (CR) to sites with mildly alkaline soils (TL, RB), sites which share 82.5% of their taxa, including all of Henry's core species except Equisetum arvense. Of the 17.5% which do not overlap, none contribute significantly to the cover or biomass of the sampled vegetation. Henry (1987) also showed that simply including 'moss prominence', or total moss cover, values in ordination procedures increased the geographic separation of three high arctic meadows, a fact he attributed to different grazing intensities by muskoxen. The results from the three sites sampled for this study show that the sampled bryofloras share only 31.8% of their total taxa and that detection of subregional geobotanical differences is greatly enhanced by the inclusion of non-vascular compositional data in the analysis, particularly the bryophyte data. The implication is that floristic data contain the great majority of the variation in the vegetational data and more holistic sampling of the vegetation at each of a number of sites can give a much better picture of geobotanical variation than can the vascular flora alone.

A second, related conclusion is that intralowland definition of plant communities was improved with the use of non-vascular plants. Only Sheard & Geale (1983a, b) have used multivariate analysis (PCA) to objectively (quantitatively) define discrete plant communities and vegetation-environment relationships, including a complete survey of the non-vascular flora, in a single high arctic lowland.

Webber (1971) used a modified Bray-Curtis ordination to describe vegetation-environment relationships on an upland of interior Baffin Island, ca. 250 km from CR. Although Webber identified common cryptogams in most of his analyses, the youth of his substrates (≤500 yr), and the different vegetation structure, composition and mesoclimate make his data set less useful for comparative purposes. Apart from Sheard & Geale, phytosociologists in North America and Europe have shown that high arctic communities can be formally classified in the manner of Braun-Blanquet, with diagnostic species derived from each of the three main life forms (Barrett 1972; Elvebakk 1985; Hadac 1989). These phytosociologists and Sheard & Geale have relied heavily on the often relatively narrow ecological amplitudes of the non-vascular plants to determine the extents of their respective communities. In so doing, they have defined their lowland communities with greater floristic and spatial precision than others whose classifications were derived from surveys of the vascular vegetation and total moss cover (e.g. Bergeron 1988; Muc et al. 1989).

Each of the studies cited above concerned 'natural' vegetation. The data from the present study were derived from both natural and anthropogenically disturbed vegetation. Comparisons of multivariate analyses with and without non-vascular floristics showed that differentiation between communities was greatly enhanced with the inclusion of non-vascular plants, particularly bryophytes (Forbes 1992d).

Subtle differences among the various disturbance regimes and/or natural vegetation units were repeatedly detected through random splits of the data into subsets, within lowlands of contrasting lithologies and dissimilar bryofloras. On the other hand, when only vascular vegetation was used in the analyses, starkly contrasting vegetation types (i.e. those with and without Sphagnum hummocks), were routinely classified and ordinated together. These results show that in floristic surveys, the inclusion of the non-vascular vegetation with vascular vegetation, even if only consisting of presence/absence or frequency, can yield more rigorous floristic definition of high arctic vegetation units at the scale of the patch than is possible with only the vascular flora, whether or not disturbance is a factor.

The range of species presences, frequencies and abundances visible in the dendrograms successfully relate a wealth of general information at a glance. For example, **Table 3.1** shows that the presence of Aulacomnium palustre is indicative of the entire suite of natural meadow types at CR. Other species in this section of the dendrogram indicate that the habitats at CR are more mesic (Dicranum angustum, Drepanocladus uncinatus) and acidic (Calliergon sarmentosum, Conostomum tetragonum) than those at TL. At TL, the species tabulated are more indicative of hydric conditions and calcareous substrates (e.g. Bryum calophyllum, Calliergon giganteum, Drepanocladus brevifolius, Lophozia rutheana, Meesia triquetra).

Similar information is apparent in the dendrogram of anthropogenically disturbed vegetation, although the great diversity of disturbance regimes makes it more useful to place emphasis on lower level divisions (**Table 3.2**). Thus at the fourth level, on the left-hand side, it appears that stands are generally hydric based on the presence of Bryum cryophilum, Drepanocladus revolvens and an abundance of Eriophorum angustifolium. At this and especially at lower levels in the same portion of the dendrogram are species indicating relatively alkaline conditions (Calliergon giganteum, Catoscopium nigritum, Cinclidium arcticum, C. latifolium). In the center and right-hand portions of the dendrogram are species more indicative of mesic or acidic conditions, such as an abundance of Salix arctica and the presence of Anastrophyllum minutum and Tomenthypnum nitens. Disturbed conditions are generally represented by the presence of species such as Bryum argenteum, Alopecurus alpinus, Phippsia algida, and an abundance of Poa arctica.

TWINSPAN

In effect, the classification procedure was useful in identifying floristic patterns at both higher (subregional) and lower (community) levels of vegetation organization. Even a casual ecological knowledge of the species used to differentiate among sites could also be used to characterize the general range of environmental conditions, such as hydric vs. mesic, minerotrophic vs. oligotrophic, and disturbed vs. undisturbed. This was especially true with bryophytes. However, since the ecologies of individual species are often variable within different segments of their ranges, it is important to be aware of the geographic limitations of such an analysis when assigning general characterizations to species. A. alpinus and Phippsia algida for example, are quite common apart from natural and anthropogenic surface disturbances in the lowlands of the northwestern Queen Elizabeth Islands, and in uplands of the central archipelago where more severe conditions are prevalent (Bliss & Svoboda 1984). Recently disturbed sites also raise the question of how well the present vegetation reflects the potential vegetation of the site (see below). Still, within the set of lowland landscapes reported here, A. alpinus and several other species were typically restricted to disturbance niches such as bird perches, the margins of ice-wedge polygons, and on trampled, tracked, or otherwise enriched terrain. Yet within the general context of disturbance many of the vascular species, such as A. alpinus and Arctagrostis latifolia ssp. latifolia, exhibited wide ecological amplitudes. Given these considerable amplitudes, and the lack of additional floristic studies addressing disturbance in the region, no attempt was made in this study to classify the vegetation syntaxonomically.

DCA

The DCA ordinations reinforced many of the interpretations of pattern (both within and among study sites) that were illustrated in the classification analyses. Ordination of the larger data sets mirrored the geographical and ostensibly geobotanical gradients derived from TWINSPAN. However, more local gradients tended to be obscured by crowding in the biplots. Data subsets proved far more interpretable and made sense given the diversity of disturbance regimes sampled and the potential for reducing overlap among environmental gradients. On the other hand, where floristic convergence existed between stands, such as the trampled meadows at CR and the Thule housepads at TL and RB, this was consistently detected in large, small and randomly split data sets. That the same convergence/divergence patterns were detected by both the classification and ordination procedures lends credence to the methodology.

DCA detected heterogeneity in undisturbed meadows at CR relative to the meadows at TL, causing the 'tongue effect' to appear in the biplot (**Fig. 3.2**), a fact I attributed to the more subdued microtopography at the latter site, and the concomitant absence of mesic microhabitats for non-vascular plants. The vascular floras differed little between the sites, but the vegetation cover of CR was comprised of a greater proportion of deciduous and evergreen shrubs. This pattern reflected the availability of mesic habitats associated with hummock tops and sides there (see section 3.10.vi).

The ordinations of anthropogenically disturbed vegetation with their adjacent controls ecludicated patterns of local species extinction and colonization. These ordinations also allowed an estimate of the changes in ecological (chi-square) distance which separated the two vegetation types. Even without the inclusion of environmental data, floristic patterns emerged, indicating consistent vegetation differences between stands which were often only a few centimeters apart. Examples include different levels of impact, such as trampling and vehicle traffic, and the importance of a thick layer of peat in determining both the level of impact initially sustained and the patch-level response to the disturbance. Colonists not originating from adjacent controls were most common on disturbances where the organic mat had been mostly or completely destroyed, and in stands characterized by more 'mesic' species, such as drained areas.

ii. Vegetation-environment relations

The addition of environmental variables to the ordination analyses explained much of the variation in species composition within some data subsets but not in others. Where much of the variation was explained, such as in the natural meadows at CR, it was sometimes apparent that a key factor like slope indirectly affected differences within a whole suite of temporally and spatially variable factors such as snow depth, snow melt, and insolation. This points out one of the limitations of ordination with environmental variables: it is ultimately a 'snapshot' approach to summarizing variation within what is essentially a temporally dynamic patch or set of patches and, as a result, much of the temporal variation in the data set sampled had to be treated separately (Section 4.2). However, much information is evident within a given snapshot or set of snapshots, particularly as relates to the amplitudes of the various species involved when genuine gradients have been bracketed by the sampling. In some cases, such as pedestrian trampling, disturbance intensity appeared to be the dominant gradient, overriding such important ecological factors as soil pH and moisture. Belsky (1979) and Sackett (1980) ordinated similarly disturbed alpine and subalpine communities and felt that the two primary axes were moisture and degree of disturbance, although disturbance was considerably less distinct in the subalpine sites. This suggests that in increasingly marginal environments disturbance exerts a stronger control over vegetation composition.

In ordinating low arctic Alaskan tundra vegetation, Ebersole (1985) found that, overall, the controlling environmental factors for anthropogenically disturbed and natural vegetation were quite similar. Moisture and pH were the two most important controlling factors in both cases; thaw depth and organic matter were of secondary importance. Ebersole also reported (p. 155) that "the assemblage of plants on a recently disturbed site gives a less precise indication of the environment at that site than the community on a site that has been disturbed for some time". My own data indicate that this may be especially true on more mesic and xeric substrates in the High Arctic. These patches tend to be colonized by ruderal taxa of wide ecological amplitude, species that are often lacking in the adjacent natural vegetation, that may persist for decades or perhaps even centuries. Thus, what constitute 'recent' and 'some time' (*sensu* Ebersole 1985) are potentially quite different in the High Arctic compared to the Low Arctic and need to be considered.

The present data support the idea that, as habitats become increasingly mesic, the effects of even minimal mechanical disturbance tend to exert a greater control over vegetation composition than do factors such as moisture or pH. It appears in these cases that the disturbance gradient may, in fact, comprise a complex of underlying environmental gradients. For instance, increasing trampling intensity may be represented by a number of factors - increasing soil compaction and bulk density, decreasing infiltration rates, decreasing albedo, etc. Other important factors appeared to be the amount of vegetation initially destroyed or displaced and the life history characters of the surviving plants and proximal species in the undisturbed matrix (Section 4.2). In the case of non-mechanical disturbance, such as in drained peatlands at CR, it is clear that environmental factors such as pH, active layer depth and soil temperature are more closely correlated with the observed variations in vegetation composition. Increases in pH were significantly correlated both with the degree of drainage and with an increase in the frequencies of bryophytes normally associated with calcareous habitats. These results are notable in an area that is otherwise dominated by moderately acidic transitional poor fens.

The overall results indicate that the disturbed stands can be roughly classified into two categories: stands where the original vegetation has been entirely destroyed or removed; and, stands where some of the original vegetation has been left intact. In Chapter I, the classification of the disturbance regimes themselves was discussed. Each of these distinctions can be important in classifying the nature of disturbance. The nature of the impact, or the effect of the disturbance, can also be classified. Broad, but useful and generally accepted classifications would be spatial (direct vs. cumulative impacts) and temporal (short- vs. long-term impacts). Differentiation between spatial classes is fairly straightforward.

Distinguishing between temporal classes is perhaps more difficult, but I suggest that the criteria considered should include some combination of the lifespans of the affected plants, or portions of affected plants in the case of extensive clonal mats, and human or animal lifespans as well, where grazing habitat is a consideration. Impacts would then be important in terms of the numbers of generations over which they persist, a more useful yardstick than years alone. Years are certainly more concrete, but the data from this and other studies (Kevan 1971b; Bliss 1983; Ebersole & Webber 1983) indicate that few humans will live to see the natural regeneration of mesic tundra intensely disturbed. The best we can do in such cases is estimate, and generations seem to be a more logical means of estimation, though these can certainly be coupled with traditional estimates. Multivariate approaches to analyzing vegetation and environment are probably the best way to rapidly and holistically estimate the extent of community recovery at a given point in time.

4.2 Discussion of analyses of parameters not included in the ordinations

i. Abiotic factors

a. Annual and seasonal active layer development

The most significant ecological determinants for plant growth in arctic regions are snow melt and subsequent timing and thawing of the active layer (Sørensen 1941; Tieszen 1978). Snow melt procedure during the summer has an enormous impact on phytosociological differentiation within a given area as well as on reproductive success within species (Kudo 1991; Molau 1992). Flowering and seed development occur throughout the growing season in arctic plants, but most species reach anthesis within 2-5 weeks after snowmelt. The sequence of species flowering is thus generally related to time since snowmelt, which may vary by 2-4 weeks between years, or even longer where late-melting snowbanks occur (Shaver & Kummerow 1992). The snowmelt and thaw data from 1989 and 1990 have shown that the study site at CR was snow-free more than a week earlier in 1990 than 1989. The latter was a shorter and, overall, a cooler growing season. Despite these differences, the general pattern and maximum depth of thaw was quite similar among years between all natural and disturbed types. The maximum depth data from 1990 at TL, when compared with data collected by Barrett (1972) and Muc (1977), appear similar to the 'cooler' years (i.e. 1972) during which measurements were made for the IBP.

The short-term effects of vehicles on active layer depth in the High Arctic have been discussed elsewhere (Babb & Bliss 1974a). However, seasonal and long-term patterns of thaw have not been previously chronicled. Not surprisingly, thaw initiation and overall depth of thaw were earlier and greater, respectively, in multi-pass tracks where the organic mat and/or vegetative cover remained seriously reduced after up to two decades. The response of single-pass tracks was more variable, depending on whether a stand was within a water channel or a more mesic setting, although significant seasonal differences were detected between treatments and controls each year in each vegetation type.

The effects of trampling and altered hydrology on thaw in the region's sedge meadows have not previously been documented. Neither have they been documented for abandoned housepads. The present data have revealed annual patterns strongly associated with the level of initial impact even 21 yr after abandonement. In the early part of the growing season, for example, an increased rate of thaw was directly proportional to increased trampling intensity. These thaw patterns changed after 3-4 weeks in all disturbance zones or sites except the housepads, which were consistently deepest. Peatland drainage elicited different responses among areas downslope from ruts channelling spring runoff, depending on the local moisture regime. In water channels, thaw initiation was delayed and thaw depths were reduced for the first 3-4 weeks of the season in areas downslope from both single- and multi-pass tracks. Similar results were reported by Pessi (1958), who measured seasonal thaw over a number of years in drained and undrained Fennoscandian bogs. In the more mesic interfluves in this study, thaw was enhanced in downslope areas.

Thaw rate differences restricted to the early part of the growing season will be crucial for plants such as Eriophorum angustifolium and Arctagrostis latifolia ssp. latifolia, whose roots grow apace with the thawing front (Chapin et al. 1980; Callaghan et al. 1991). In drained water channels these plants, in general, will be at a disadvantage as their rooting systems experience a functionally reduced growing season. Those plants growing in otherwise equivalent but warmer, faster thawing soils will be at an advantage. Overall differences in depth, such as those recorded on the housepads and in multi-pass tracks, are more likely to be exploited by plants such as Alopecurus alpinus, which can send roots deeper than most species into relatively infertile and compact soils (Bell & Bliss 1978; Aleksandrova 1988; see also Section 4.2.ii.c).

b. Seasonal and diurnal soil temperature regimes

Patterns of surface and near surface temperatures and temperature fluxes were generally predictable and closely tied to thaw patterns. Soil temperatures and, in particular, temperature fluxes are also of critical importance for vegetation development. For example, in a series of transplant experiments Chapin (1974) showed that the capacity for phosphate absorption by such plants as Carex aquatilis (*sensu lato*), Dupontia fisheri (*sensu lato*) and Eriophorum angustifolium was negatively correlated with the soil temperature of the habitat of origin. Chapin found that species and races from thermally fluctuating environments achieved greater compensatory changes in the phosphate absorption rate through temperature acclimation than their counterparts in more stable environments. Chapin (1981) emphasized, however, that soil phosphate status was more important than soil temperature in determining phosphate absorption capacity, at least for C. aquatilis. Others have shown that freeze-thaw cycles result in the physical release of nutrients (Cheng et al. 1972; Summerfield & Rieley 1973; Jonasson & Sköld 1983).

In this study, mechanically disturbed soils demonstrated significantly greater fluxes of diurnal and seasonal soil temperature than did immediately adjacent undisturbed soils. An important implication is that if the vegetation cover is lightly damaged and the organic mat even lightly compressed, but not entirely destroyed, through accelerated decomposition its nutrients may become available for plant growth in greater quantities on disturbed ground than would otherwise be possible at this latitude. Other researchers have also demonstrated that growth and phenology of alpine tundra plants are more strongly controlled by soil temperature than by air temperature (Holway & Ward 1965; Bliss 1971; Kudo 1991). In this study, the dominant graminoids exhibited substantial differences in the number of inflorescences between natural, mechanically disturbed, and drained meadows (**Plate 3.18**).

In drained water channels, spot-checks of mid-season soil temperatures revealed areas downslope from multi-pass tracks to be significantly warmer than controls upslope. However, active layer profiles show that thaw is consistently delayed in these drained areas. These results are in general agreement with findings from northern Alberta peatlands, where the substrates of drained areas became warmed to above 0°C slightly later than adjacent undrained areas but maximum summer temperatures were higher in the drained site (Lieffers & Rothwell 1987). The same authors reported that the lowering of the water table and removal of excess water changed the physical properties of surface peat and concluded that, after thawing, drained substrates should therefore warm and cool faster, and have greater extreme surface temperatures than undrained substrates (Rothwell & Lieffers 1987).

c. Surface albedo

Analysis of airphotos revealed that several drained areas had higher albedos than upslope control areas. These differences were detectable late in the growing season within four years of the initial vehicle disturbance (**Plate 2.9**), and were visible over thousands of square meters, together constituting a set of serious cumulative impacts.

The effects of these changes in reflectance are both significant and persistent, as can be seen in the major anomalies in seasonal active layer development, soil moisture, soil temperature, and biotic effects in drained areas relative to control areas, even two decades after abandonment. Jeglum (1975) used airphotos to chronicle the effects of 23 years of drainage in a peatland in northern Ontario and reported similar effects. At CR, the area with the highest albedo by far is the chemical dumpsite below the former weather station. The white crust at this site expanded greatly in size during the 1960's (**Plates 2.8 and 2.9**) and showed no signs of breaking down during the course of this study.

d. Soil structure

Patterns of variation in soil structure were recorded in soil pits dug in each stand. Representative examples are presented here using close-up photographs of soil profiles as the basis for discussion. **Plate 2.6** is a profile typical of naturally occurring soils in a hygric meadow at CR and shows a marked separation of the organic mat, comprised mainly of shrub roots and fibric peat, from the unhorizoned mineral soils below. On the surface is a layer of litter and a dense, springy mat of bryophytes. Pits from beneath single-pass tracks and adjacent controls in another portion of the same meadow are seen in **Plate 4.1**. After 21 yr, the organic mat remains clearly compressed in the track. Although there has been little mixing of organic material into the mineral layer, the mineral layer is more firmly attached to the organic mat due to a pronounced increase in graminoid roots. The main structural difference between the mineral soils of the two areas is the significant increase in relative moisture beneath the tracks, and a concomitant reduction in bulk density.

Single-pass tracks perpendicular to local slope in an interfluve zone have resulted in a dramatic increase in the organic content of the mineral soils (**Plate 4.2**). This appears to be due to accelerated decomposition rather than cryoturbation. The increase is reflected in the soils analyses of Section 3.10.vii.b. Significant shifts in the concentrations of nutrients in plant tissues where also evident here, but did not appear tied to the extractable nutrients in the soils (Section 3.10.vii.a).

Soils beneath multi-pass tracks oriented parallel to the contours of local slope in a mesic meadow are seen in **Plate 4.3**. The naturally occurring mineral soils appear somewhat frost-churned, with a moderate amount of organic content and light mottling visible. The organic mat still peels away easily from the mineral layer. Water flows gently in these tracks in the early part of the growing season and the much grayer color of the tracked soils seems to indicate that some leaching of organics has taken place. All shrubs and almost all above-ground vegetation were eliminated on these tracks by the initial disturbance. However, the large, visible root of <u>Salix arctica</u> attests to the size of the individuals in the stand and the depths to which its roots penetrate.

A range of similar changes was evident in the disturbed soils of TL. **Plate 4.4** shows soils approximately 20 yr after a few passes of a heavy vehicle in a hygric frost-boil meadow with Gleysolic Turbic Cryosols and a slope of ≤1°. Although the layer of peat mosses typical of meadows at CR is lacking, the undisturbed soils are friable and display a similar lack of horizonation. The organic content of the disturbed soils is clearly increased. **Plate 4.5** shows soils from a more mesic frost-boil meadow, transitional between a granitic rock outcrop and a hummocky meadow, with more clearly mottled naturally occurring Gleysolic Turbic Cryosols. The multi-pass tracks through this stand comprise a series of large puddles with a surface of fairly organic, coarse mud. The standing water persists througout the growing season. A thin mat of Carex aquatilis var. stans binds the surface together, and its roots extend well into the mud.

Plate 4.6 is taken from multi-pass track through a mesic hummocky meadow and the undisturbed profile shows a Gleysolic Static Cryosol quite similar to those depicted for CR, with a fairly thick organic mat and little integration of the organic and mineral layers. The tracked soils appear the same except that the organic mat has been been completely removed and few bryophytes or vascular plants have recolonized. Slightly less mesic and more organic Gleysolic Static Cryosols with a well-developed organic mat are seen in **Plate 4.7.** A few passes of a heavy tracked vehicle have resulted in more saturated soils. In a wetter hummocky meadow, Gleysolic Static Cryosols are also present but exhibit a higher organic content (**Plate 4.8**). Multi-pass tracks remain saturated throughout the growing season, but otherwise appear quite similar to those in **Plate 4.7.**

Fibric Organo Cryosols occur in the wettest meadows at TL. **Plate 4.9** shows typical wet meadows soils and an attempted restoration of tracks which had been completely denuded of vegetation at the time of experimental sodding in 1972 (Barrett 1975). The only significant difference between the two soil blocks is the depth of the organic mat, which averaged 20 cm in the restored tracks vs. 13 cm in the naturally occurring soils. In cooler years the mineral soils in these meadows may remain frozen and inaccessible to roots. However, the fingerprints visible in the **Plate 4.9** mark an attempt to separate the main units and show that the organic and mineral layers are firmly bound together by a dense network of fine roots, mostly of Carex aquatilis var. stans. Naturally recovering soils in the wet meadows appeared similar to those of tracked soils seen in **Plate 4.5**; although generally with a better developed organic layer.

The effects of trampling on soils can be seen in **Plates 4.10 and 4.11** from CR. **Plate 4.10** is from a moderately trampled zone in a mesic meadow, which shows that the main effect of trampling is to level hummock-hollow microtopography at the surface. Soils beneath were significantly compacted. This was clear from the penetrometer and bulk density data in Chap. III, but overall hummock-hollow structure is still evident. Thus, the mineral soils beneath the former hummock at left are relatively dry and friable with minimal organic content. The soils beneath the former hollow at right remain moist, sticky and suffused with organic matter. Note that Sphagnum spp. have been completely displaced by Aulacomnium and other species in the bryophyte layer. Poa arctica is the dominant vascular species, but remnant individuals of Salix arctica mark the sides of the former hummock. In **Plate 4.11**, soils beneath the former housepad (with no materials added) are seen at left. The knife points to the interface between the mostly mineralized former organic mat and the extremely compacted mineral layer beneath and to roots of Alopecurus alpinus, which is the only species able to penetrate the mineral

Plate 4.1 - Soil profiles from single-pass track (right) and adjacent control (left) (**Stand 2**) in a hygric meadow at CR. Mosses (mostly Sphagnum spp.) are extremely compressed and soils are wetter with lower bulk densities on the track. Both profiles lack horizonation within the mineral layer, but the organic mat in the undisturbed profile separates easily from the mineral layer, which is relatively dry and friable. Photo date: 24 June 1990.

Plate 4.2 - Soil profiles from single-pass track (right) and adjacent control (left) in a mesic interfluve zone at CR (**Stand 15**). Bryophyte mat is compressed on track, as in previous plate, but there has been an increase in the organic content of the mineral layer, probably through increased decomposition. This is a common response of mesic tundra vegetation and soils to surface disturbances of this nature. Here, again, few roots penetrate the mineral layer and the organic mat peels away quite readily. Photo date: 25 June 1990.

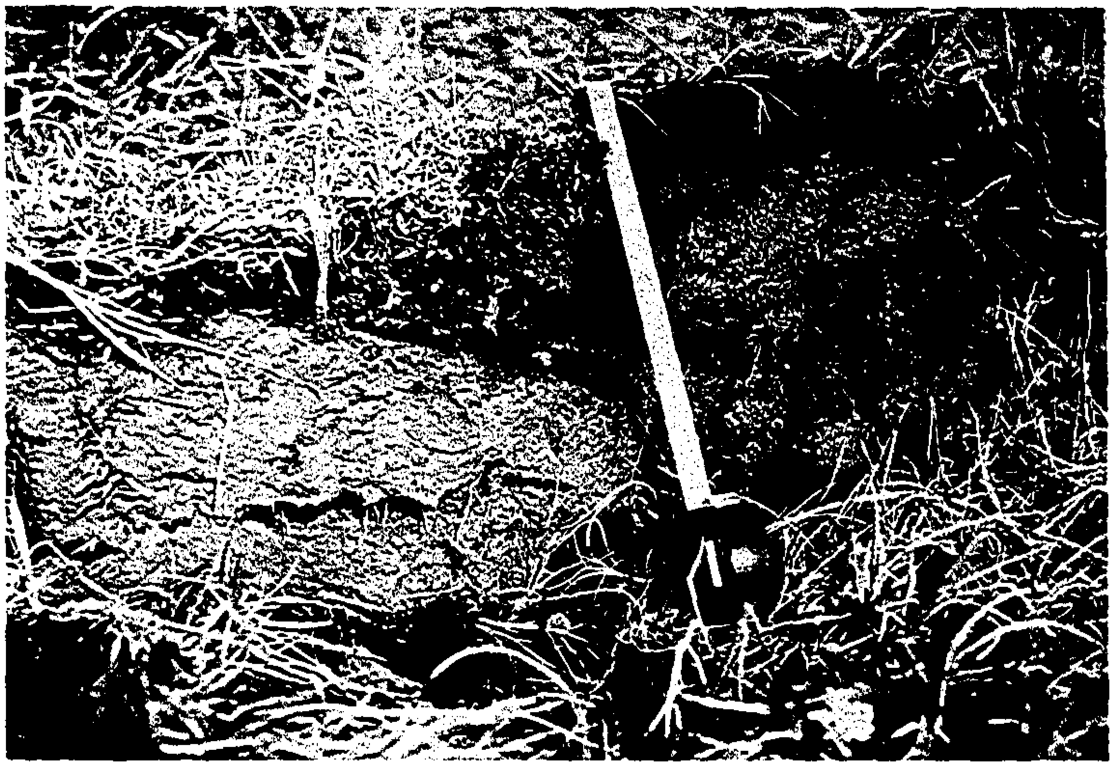
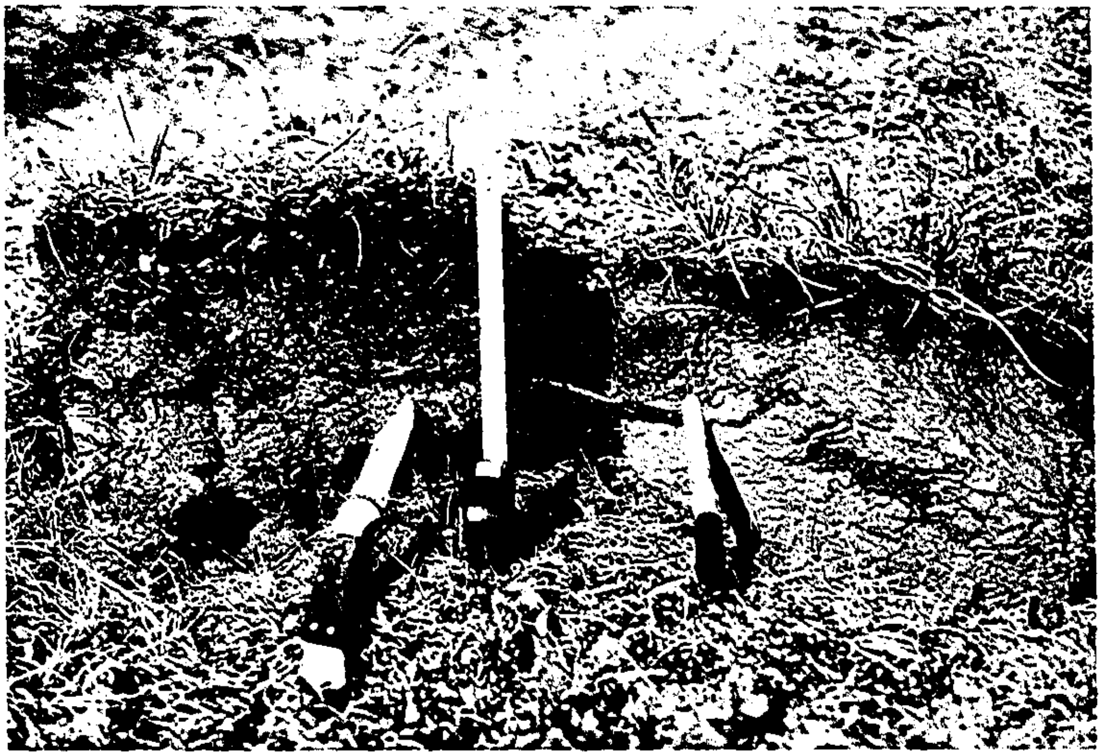


Plate 4.3 - Soil profiles from multi-pass track (right) and adjacent control (left) in a mesic hummocky meadow, one of the driest stands sampled, at CR (**Stand 9**). The undisturbed soils show signs of organic mixing through cryopturbation and are friable. The large Salix root, emerging from the undisturbed plug behind the tape and indicated by the pen, extended only to the base of the organic layer, from where it grew horizontally. As in the single-pass tracks, soil moisture was increased somewhat in the tracks relative to the controls, but soils beneath multi-pass tracks tended to be more compact with higher bulk densities than those beneath single-pass tracks. Photo date: 25 June 1990.

Plate 4.4 - Soil profiles from few-pass track (right) and adjacent control (left) in a hygric frost-boil meadow at TL (**Stand 2**). Organic mat is thin and poorly integrated on undisturbed soils, and absent or well integrated on disturbed soils. Vascular cover of mostly graminoids is also thin and roots are sparse but penetrate to depths of ≤20 cm. Undisturbed mineral soils are sandy and very stony, while disturbed soils are dark and peaty. Photo date: 6 August 1990.



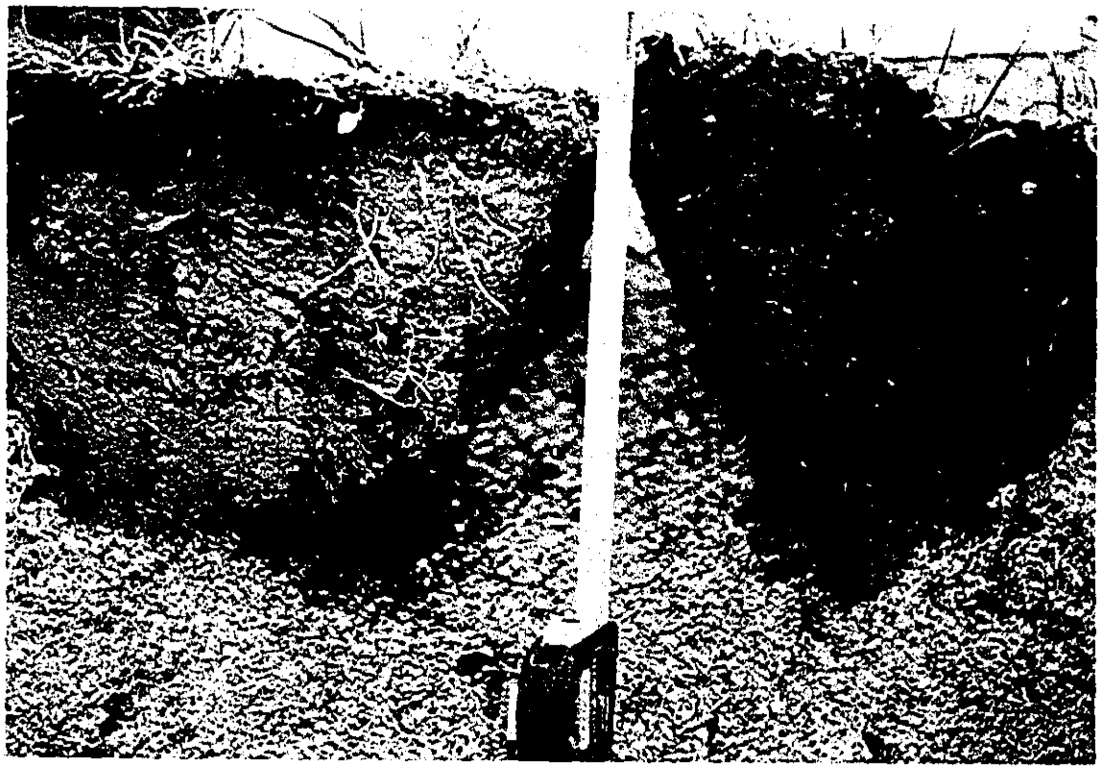


Plate 4.5 - Soil profiles from multi-pass track (right) and adjacent control (left) in a mesic frost-boil meadow at TL (**Stand 4**). Undisturbed soils are covered by a thick, dry bryophyte mat (Aulacomnium spp., Orthothecium chryseum, Tomenthypnum nitens, etc.) and are clearly frost-churned, with mottles of organic materials visible. The tracks have remained essentially large puddles with stony organic muds colonized only by Carex aquatilis var. stans and Ranunculus hyperboreus. No bryophytes were observed colonizing in the tracks. Photo date: 5 August 1990.

Plate 4.6 - Soil profiles from multi-pass track (left) and adjacent control (right) in a mesic hummocky meadow at TL (**Stand 6**). Both disturbed and undisturbed soils are fairly well-drained and friable. The only visible change in the disturbed profile is the almost complete lack of an organic layer. Bryophyte diversity and frequency are fairly high on the tracks, but cover is extremely thin. The natural vegetation in this stand corresponds almost precisely to Barrett's (1972) 'caricetosum membranacei' subassociation and the most successful colonist on the tracks in Carex membranacea, indicative of mesic conditions. Photo date: 5 August 1990.

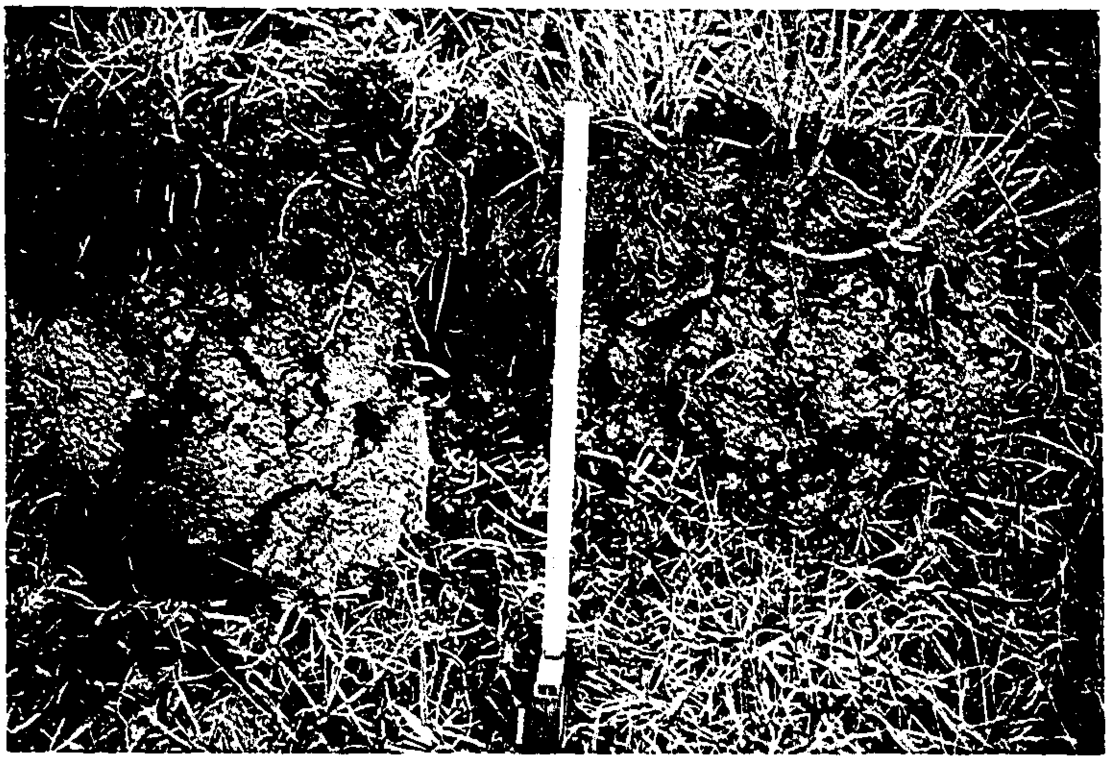


Plate 4.7 - Soil profiles from multi-pass track (right) and adjacent control (left) in a hygric hummocky meadow at TL (**Stand 7**). Undisturbed mineral soils are suffused with fine graminoid roots and slight leaching of organics is visible in the uppermost layer. Hummocks are generally much smaller at TL with the result that the depth of the organic mat is more homogeneous over larger areas. In this stand it is fairly thick (12-13 cm). The disturbed soils are clearly wetter and stonier and the surface layer of bryophytes appears mostly decomposed. Dominant vascular species on the tracks are Carex aquatilis var. stans and Arctagrostis latifolia and 'green belting' is evident from a distance. Photo date: 6 August 1990.

Plate 4.8 - Soil profiles from multi-pass track (right) and adjacent control (left) in a hygric hummocky meadow at TL (**Stand 1**). Undisturbed soils remain very moistm but not saturated, througout the growing season and are high in organics. Medium and fine graminoid roots penetrate to ≥22 cm. Disturbed soils remain saturated througout the growing season and have been colonized by Eriophorum angustifolium, Carex aquatilis var. stans and Ranunculus hyperboreus. Bryophyte cover in the tracks is patchy, mostly mats of Bryum pseudotriquetrum, Meesia triquetra and Drepanocladus spp. The previous organic mat appears to have decomposed. Photo date: 6 August 1990.

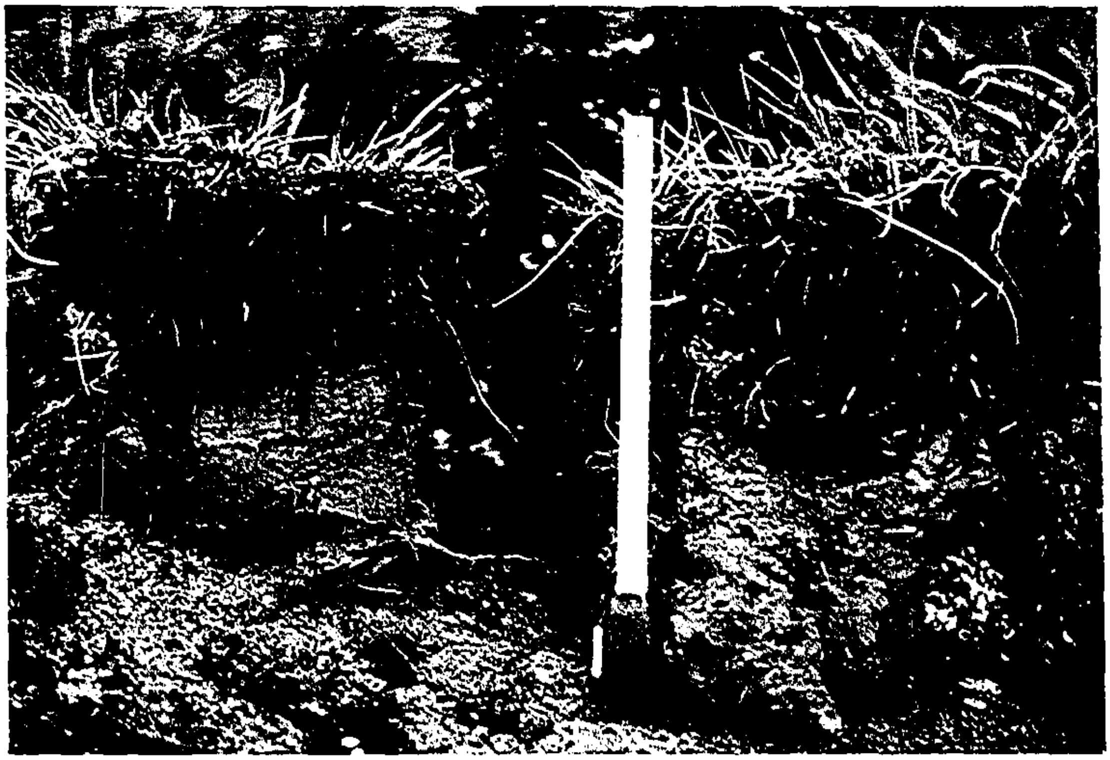


Plate 4.9 - Soil profiles from Barrett's (1975) attempted restoration of a multi-pass track (left) and its adjacent control (right) in a wet meadow at TL (**Stand 11**). The profiles differ little in appearance except for the significantly thicker organic mat on the track. As can be seen, most large and medium roots are restricted to the organic layer. Indentations from fingers show where I attempted to separate the mineral and organic layers. A key difference was that fine and medium roots were not as well integrated with the mineral layer on the track as they were in the control area. The active layer averaged only 30 cm here (including up to 20 cm of fibric peat), not much deeper than indicated by these profiles. As a result, many fine roots were found extending into permafrost, especially in the control area. Photo date: 5 August 1990.

Plate 4.10 - Soil profiles from moderately trampled zone in a mesic meadow at CR (**Stand 18**). Sphagnum spp. and microtopography have been eliminated, but former hummock (left) and hollow (right) zones are apparent from the underlying soil structure. All soils were significantly compacted from trampling. Sphagnum spp. have been replaced by Aulacomnium spp. and Poa arctica, which are relatively tolerant of trampling. These species comprise an extremely dense turf which is resistance to recolonization by the original species. Remnant populations of Salix spp. and sedges were of relatively limited extent in this zone, but tended to have high concentrations of tissue nutrients (Section 4.iii.a). Photo date: 27 June 1990.

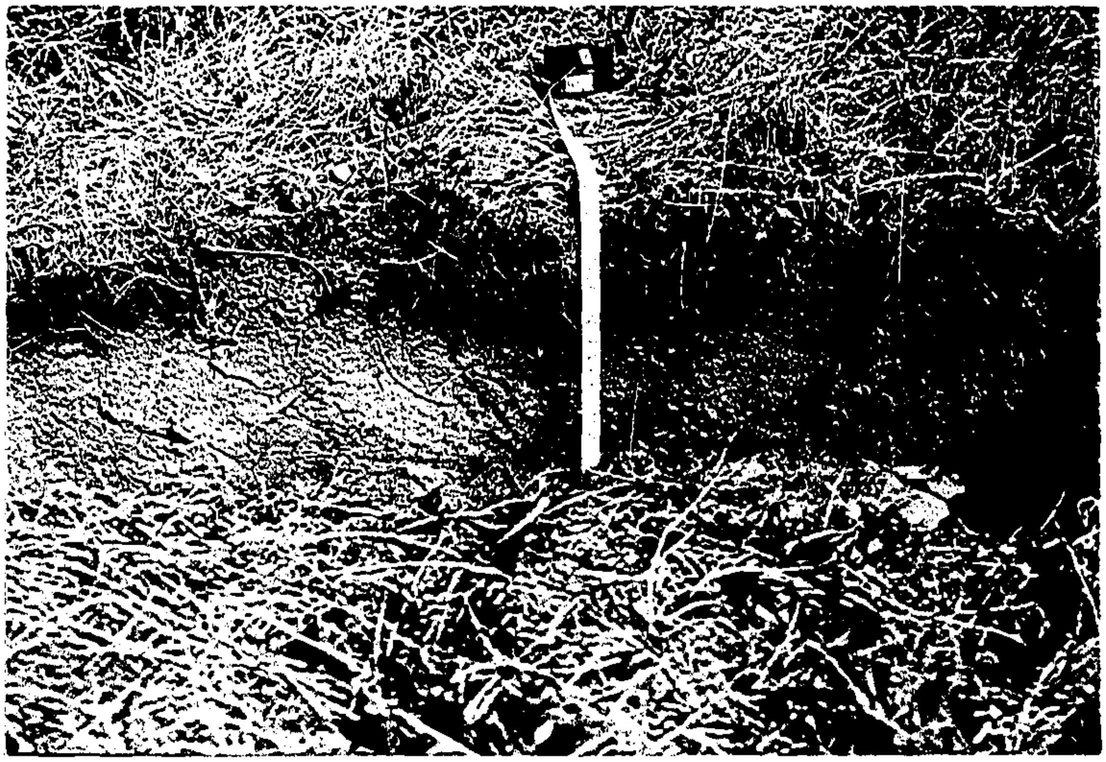
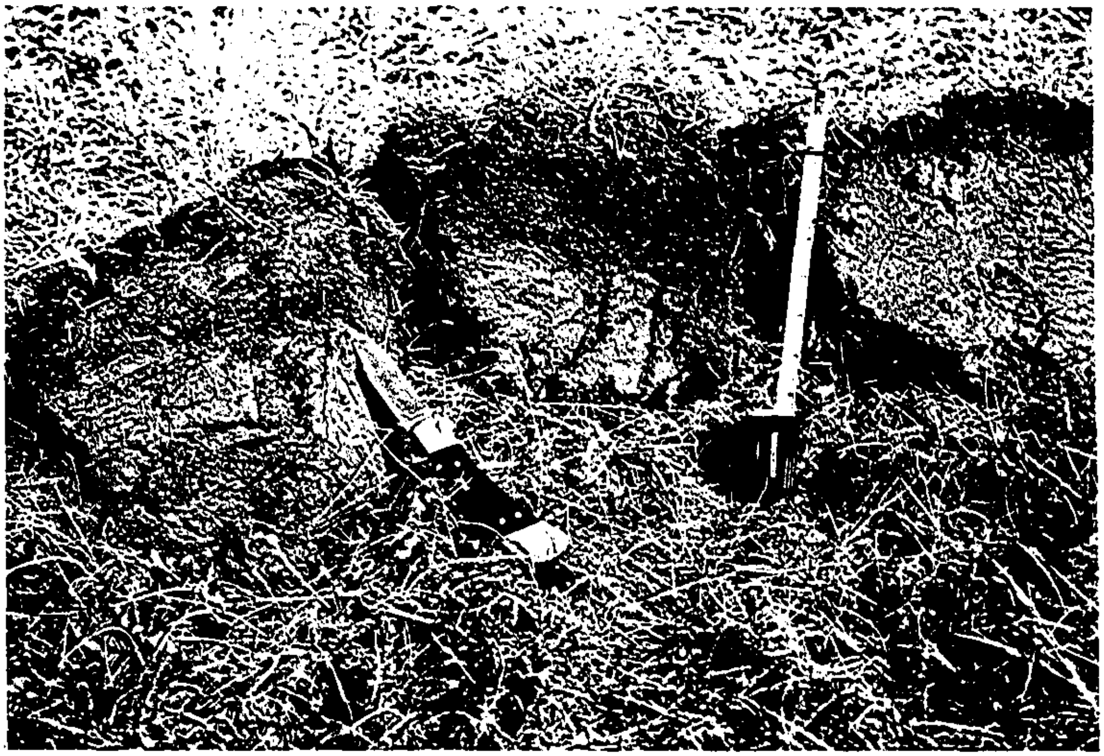


Plate 4.11 - Soil profiles from Housepad Type A (left) and adjacent trampled mesic meadows at CR (**Stand 18**). The housepad soils were exceedingly difficult to penetrate with a shovel and registered the highest penetrometer values and bulk densities (and lowest moisture values) of any soils sampled in this study. Still, roots of Alopecurus were common at depths of over 30 cm. Knife points to lower extent of mineralization from former organic layer. The profile at center is from a heavily trampled hummock top immediately adjacent to the pad. These mineral soils were also dry with few roots other than Alopecurus, but slightly less compacted and more friable. Note partial mineralization of lower organic layers. Lightly trampled soils, seen at right, are much less dense (**see Fig. 3.85**) and hold considerable moisture by comparison. Organic mat here is loose and most woody plants are intact. Salix roots are excluded from the mineral soils (seen crossing tape), although fine roots of Eriophorum angustifolium extend well into the mineral layer. Photo date: 27 June 1990.

Plate 4.12 - General aspect of Housepad Type B at CR showing prominence of discrete clones of Alopecurus alpinus on pad, comprised of successive layers of gravel and sand, and on adjacent heavily trampled ground. Photo date: 25 June 1988.



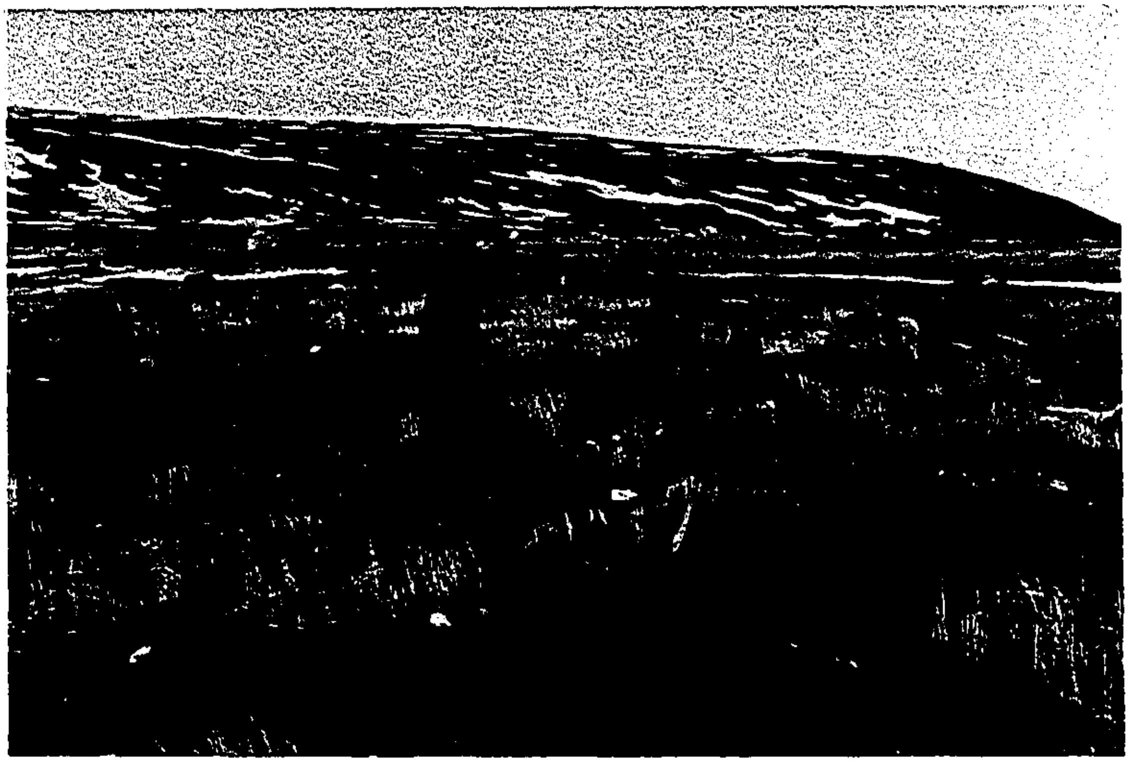
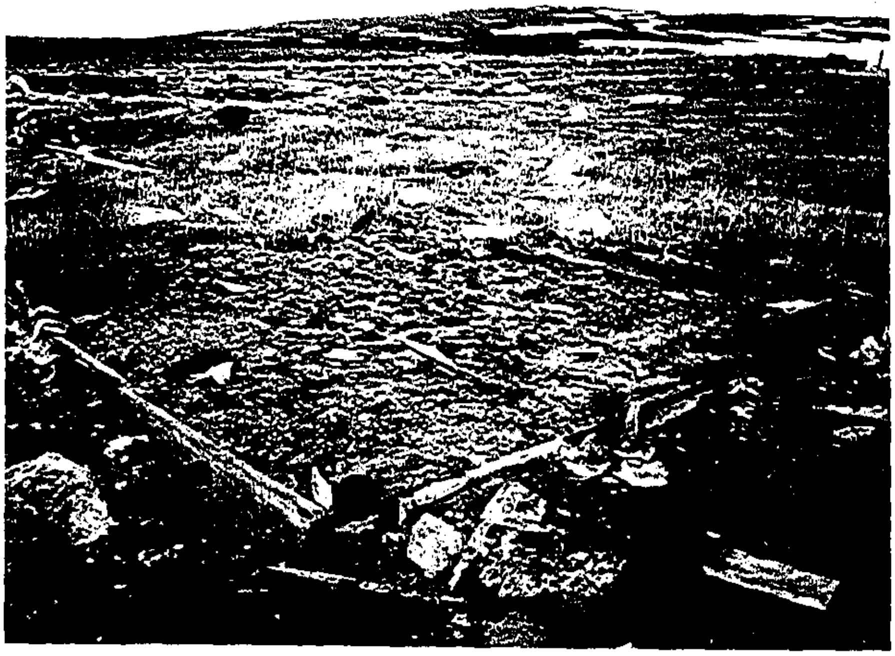


Plate 4.13 - General aspect of Housepad Type A at CR showing prominence of merging clones of Alopecurus alpinus on pad with no materials added, and on adjacent heavily trampled ground. Note high density of inflorescences, visible in foreground. By the end of the growing season, culm heights of ≥30 cm were common, as seen from last year's dead standing culms. Photo date: 15 July 1988.

Plate 4.14 - General aspect of Housepad Type C on beach ridge and adjacent trampled wet meadows at CR showing both discrete and merging clones of Alopecurus alpinus and caespitose graminoids (**see also Plate 4.16**). Foundation or base frame is still visible, into which sand and gravel were poured to create a level building surface. Moss tufts from grazing snow geese are visible in dark strip behind and to the right of pad, such as those seen in **Plate 3.15**. Photo date: 21 June 1989.



layer. A. alpinus roots penetrated to a depth of >30 cm. The dark layer at the surface is a thin veneer of ruderal bryophytes. The center plug is from the side of a heavily trampled former hummock. Here again, few roots penetrate into the compacted mineral layer and the organic mat peels away easily unless the site is vegetated by A. alpinus, which appears in discrete clonal patches throughout this and other similar zones (see **Plates 4.12, 4.13**). The plug at left is from a lightly trampled hummock top and shows a thin organic mat with few roots in the mineral layer. Salix spp. are common in this zone but the roots of this and other species are generally limited to the surface and very few penetrate the mineral layer.

Using a scanning electron microscope, it was determined that the 'soil', or rather whitish crust, on the slope below the former weather station was actually 100% aluminum oxides (Racine 1991, pers. comm.), the apparent by-product of mixing lithium hydrate to make hydrogen for launching weather balloons. The crust was extremely compact and resistant to digging and probing, although pits were dug to a depth of ≥30 cm. No plants were growing on the surface of the crust and the only plants colonizing the narrow ecotone bordering the adjacent meadows were Phippsia algida, Saxifraga rivularis, Desmatodon heimii, and an unidentifiable Bryum.

ii. Biotic factors

a. Biomass

Aboveground vascular biomass is one of the most important state variables in any ecosystem and changes in biomass are considered key components of response to disturbance (Whittaker 1975; Odum 1989). For example, it should be apparent from the data that the amount and composition of vegetation on a given patch have certain implications for moisture retention, surface reflectance, soil temperature and rate of active layer development within that patch. The interplay of these parameters will, in turn, determine to some extent the nature and rate of vegetation development within the patch. The amount of biomass aboveground may also be a key factor for vertebrate herbivores that graze and nest in the area, particularly small herbivores such as lemmings that regularly feed and nest at a scale in which spatial and temporal patchiness are important (Batzli et al. 1980).

Data on above-ground vascular standing crop within vehicle tracks indicated that total biomass was consistently reduced under each level of disturbance and that individual gains among surviving graminoids were rarely enough to offset losses among other species, particularly dwarf shrubs (Forbes 1992b). Conspicuous patterns of change in standing crop were evident under most of the other disturbance regimes surveyed as well and several of these reflected patterns reported from research in more temperate regions. For example, the biomass of aquatic graminoids in this study was consistently reduced in drained areas resulting from both single- and multi-pass tracks perpendicular to local slope. At least one study in the U.K. (Phillips 1954) has claimed that reduction of the moisture content of peat is the 'principle reason' for the eradication of Eriophorum angustifolium from grasslands there. In this study, standing crops of both E. angustifolium and Carex aquatilis var. stans were reduced by drainage, although the magnitude of change appeared linked to the original moisture regime within a zone, i.e. interfluve vs. water channel, as well as the extent of the altered hydrology. Sphagnum spp. and associates were eliminated by severe drainage, and species usually associated with more mesic, calcareous substrates have begun to replace them (**see Plate 3.6**).

It is well documented from research in temperate, boreal and subarctic regions, that peatland drainage can improve tree growth. Increased tree growth after drainage is attributed to improved substrate environment resulting from decreased water content, increased aeration, and higher substrate temperatures (Tamm 1951; Pessi 1958; Harris & Marshall 1963; Jeglum 1975; Lieffers & Rothwell 1987; Rothwell & Lieffers 1987). Temperate wetland drawdowns lasting longer than 1 year have allowed heath and other woody plant species to establish and attain considerable size (Ellenberg 1988; Luken 1990). However, where severe drawdown occurs in extremely nutrient limited boreal peatlands, total live biomass may not increase and may eventually decrease over time (Gorham 1991). After 21 yr, sustained drainage at CR had the effect of significantly increasing both foliar and woody biomass of *Salix arctica*. This is the dominant shrub present in the control area. These results are consistent with those cited above, although it is not certain whether, in the longer-term, total biomass will decline, as predicted by Gorham. Along with *S. arctica*, the biomass of the caespitose graminoid *Luzula nivalis* has increased significantly and is replacing the aquatic rhizomatous sedges. Numerous crustose and fruticose lichens were also colonizing the desiccated hummocks.

In trampled areas, the standing crops of individual species varied considerably according to trampling intensity. The two species comprising the bulk of the biomass on moderately and heavily trampled ground were *Poa arctica* and *Alopecurus alpinus*. There are few quantitative data on pedestrian trampling in the Arctic with which to compare these results. Studies of zoogenic disturbance both within and outside the Arctic have shown that, under continued grazing pressure, mosses and moncotyledons will often revegetate areas previously dominated by lichens (Palmer & Rouse 1945; Reimers 1977; Mack & Thompson 1982; Klein 1987). A problem with comparing the present data directly to such studies is the difficulty in partitioning the effects of actual foraging (i.e. direct clipping of shoots) from those of associated manuring and trampling (Mack & Thompson 1982; McNaughton 1986; Belsky 1987; Snaydon 1987; Jefferies et al. 1992).

The present data are unique in that the effects of the initial mechanical disturbance have been effectively isolated from enrichment through manuring and clipping from grazing. However, evidence of subsequent selective and sustained grazing and nest-building by lemmings was strong within moderately and heavily trampled vegetation at CR. It would thus be prudent to assume that such intensive grazing, manuring and redistribution of plant materials has affected succession and contributed in some ways to the current patterns of patch-level biomass distribution. Similar patterns of selective grazing and nesting were observed on both excavated and unexcavated Thule dwellings at TL and RB and some multi-pass vehicle tracks at TL. On the unexcavated Thule dwellings, cover of faeces from lemmings, hare, muskoxen and ptarmigan was substantial and significantly greater than that occurring on the adjacent beach ridge. As well, numerous culms of _Alopecurus alpinus_ and other species, including _Salix arctica_, showed evidence of grazing.

Quantitative comparisons of the observed patterns of manuring and foraging to patterns of biomass distribution were not possible, given the manner of data collection, the number of potential variables involved and the highly covariate nature of interactions between them. On the other hand, the concentration of patch-level herbivore activity casually observed at the three study sites is worth noting as tundra herbivores are known to affect productivity and compositional change at several scales, including that of the patch (Schultz 1964, 1969; Batzli et al. 1980; Jefferies et al. 1992). It should also be noted here that the patches with the strongest signs of herbivore activity were often the same patches where inflorescence density was greatest. This was particularly the case with A. alpinus on housepads at all three study sites and on heavily trampled ground at CR.

b. Species richness

Species richness has been related to many aspects of communities, including standing crop (Al-Mufti et al. 1977; Wheeler & Shaw 1991), pH (Grime 1973), level of disturbance (Connell 1978), life forms Grubb (1987), and age of the vegetation (Jha & Singh 1991). In this study, species richness in mechanically disturbed areas was significantly lower among the communities of surviving plants relative to controls. This is consistent with studies of locally catastrophic anthropogenic disturbance in more temperate regions where low germination rates combine with reduced habitat heterogeneity to decrease species richness (Denslow 1985). The observed floristic convergence among trampled communities in this study has been previously described for both tropical (Frenkel 1972) and temperate regions (Ellenberg 1988).

The fact that the trampled communities were so closely related to those of contemporary and prehistoric housepads points to the small number of suitable colonist species. Because the pool of colonists was so limited, stands characterized by these plants were usually poorer in species than both controls and remnant communities. Even in the wettest tracked meadows at TL, species richness (including non-vascular plants) often remained significantly reduced, despite the fact that vascular biomass had nearly recovered to pre-disturbance levels. In the undisturbed meadow communities at CR and TL, species richness generally corresponded to changes in microtopography and drainage such that more heterogeneous (i.e. hummocky), moderately well-drained sites provided the greatest number of microhabitats and were richest in species. Conversely, in more level and poorly-drained meadows or snow-bed sites, numbers of both vascular and bryophytic species were reduced. Other important factors may have included exposure and local soil nutrient gradients.

The primary reason for increasing species richness in excessively drained areas at CR may not have been because microtopography was increased, but rather because several common species of crustose and fruticose lichens had colonized the sides and tops of hummocks. Such microsites, more than likely, were too moist for habitat requirements of these lichens prior to drainage. It seems that few new vascular species are well suited to the warm, dry, less acidic conditions in the drained areas and the remnant populations of aquatics may soon become extinct there. Studies of temperate populations of Eriophorum angustifolium and Carex aquatilis have reported both plants unable to survive prolonged drainage (Phillips 1954b; Grootjans & van Tooren 1984; Wallace et al. 1992). The remaining Sphagnum associates and other bryophytes of moist habitats were also in apparent decline in drained areas at CR and, unless additional lichen species colonize these areas, species richness will probably level off and begin to decline in future years.

Beta diversity is defined as the degree of change in species diversity along a transect or between habitats (Magurran 1988). At the landscape level, beta diversity has increased at CR, since many of the ruderal plants are either colonists absent from the natural vegetation or those which do not occur at the same high densities found within anthropogenic patches. The disturbances were of variable intensity, but human activity ceased in all sample stands at approximately the same time. A spectrum of ages among disturbed patches affects structural and habitat diversity as well as overall species diversity (Hobbs & Huenneke 1992). However, overall differences in species composition among patches at CR and TL were more closely tied to the nature and intensity of the disturbance, than to time elapsed since abandonment.

c. Growth form

Support has increased for models of vegetation change that rely on species life histories (Noble & Slatyer 1980; Huston & Smith 1987). Plant growth form characteristics are believed by many to be particularly important in determining species distribution and abundance patterns under both natural and disturbed conditions (Grubb 1977; During 1979; Harper & Bell 1979; Barkman 1988; Shaver & Chapin 1991). The number of species within a growth form has been shown to vary predictably along naturally occurring environmental gradients in tundra ecosystems (Webber et al. 1980; French 1981). These groups of species often possess similar physiological traits (Tieszen et al. 1981). For example, within the life forms of tundra plants, lichens have the lowest concentrations of nitrogen, deciduous dwarf shrubs, monocotyledons and forbs have the highest, and evergreen dwarf shrubs are intermediate (Callaghan et al. 1991). The species which proved important in directing and responding to disturbance in this study were relatively few. Enough is now known about the population ecologies and life histories of most of these species that a brief discussion of their essential characteristics, particularly growth form, is warranted.

In clonal plants that spread horizontally by rhizomes, stolons, or roots, contrasting guerilla and phalanx growth forms can be identified (Lovett-Doust 1981). Modular clonal graminoids typically possess large systems of interconnected tillers. An example is Carex bigelowii, a species morphologically similar to Carex aquatilis var. stans in which tiller clumps may represent ≥27 yr of growth (Callaghan et al. 1991). The two dominant sedges in this study were of the guerilla growth form, at least in mechanically disturbed areas where extensive excavations were made (**Plates 3.12 and 3.13**). The persistence of C. aquatilis var. stans and Eriophorum angustifolium in trampled meadows and many heavily tracked stands indicates that the rhizomatous graminoid was the most resistant of all the vascular growth forms encountered. This resistance was attributed to the thick rhizomes, particularly in Carex, and the dense mats formed by both species. Others, working in heavily trampled temperate alpine meadows, have also reported high levels of resistance among communities dominated by this growth form (del Moral 1979; Grabherr 1982), as have Mack & Thompson (1982) in steppe grasslands, and Bliss (1979) in high arctic tundra.

The clonal growth form is an extremely important factor in determining the resistance and resilience of mechanically disturbed tundra graminoids. A primary reason for this is that mortality can effect modules individually, without necessarily causing death of whole genets. In a species with the guerilla growth habit, genets spread widely and may intermingle. A single lethal incident may remove modules of different genets but rarely all modules of a single genet (Sackville Hamilton et al. 1987). Disturbance is known to increase shoot turnover in many rhizomatous tundra graminoids

(Henry 1987). In response to the disturbances reported here, the guerilla growth form allowed daughter tillers to occupy space quite far apart from the parent tiller and to forage within patches where the organic mat was long since destroyed, where soil nutrient levels were generally high, competitors were absent and soil temperature fluxes and active layer depths were found to be extreme.

Similar patterns of establishment and spread have been reported for clonal graminoids in the Low Arctic by Chapin et al. (1980b). Research with low arctic populations of C. aquatilis has shown that shoots may not live >2 yr, but that the 'tiller clump' of roots, rhizomes and stem bases where they emerge successively may live up to 4 yr after aboveground growth ceases. Since individual rhizomatous tillers may live 4 to 7 yr, there is a total life of 'tiller clumps' of 5 to 8 yr (to 10 yr) (Shaver & Billings 1975). Carex, with 90% of its biomass below ground (Chapin 1980), invests proportionally more tissue in roots than do the other two species which were most abundant in multi-pass tracks (E. angustifolium and Dupontia fisheri ssp. psilosantha), and is most successful in nutrient-poor situations (Chapin et al. 1980b). In contrast to Dupontia and Carex, the longer-lived (from 5-8 yr) Eriophorum tillers lose rhizome connections and become physiologically independent within two or three years, although the root system of this species is replaced annually (Shaver & Billings 1975). Henry (1987) estimated shoot longevity in high arctic meadow populations of C. aquatilis var. stans and E. angustifolium to be 5-8 yr and 7-10 yr, respectively.

Another important clonal graminoid in this study was Alopecurus alpinus, a species which was absent in all of the 'undisturbed' meadows sampled, but was frequent, even dominant, under several anthropogenic disturbance regimes. Exceptions include single-pass tracks, peatland drainage, and chemical dumping. Bell & Bliss (1978) report that Alopecurus has 65% of its biomass below ground and rapidly elongating roots that can penetrate the soil to depths greater than many other arctic species (**Fig. 3.22**). Regardless of site conditions, the production of viable seed by high arctic populations of Alopecurus ostensibly occurs only in rare summers (Nosko 1984; Bliss 1991, pers. comm.), similar to the dominant sedges (Bell 1975; Bliss & Grulke 1988). Alopecurus is common on zoogenic and cryogenic disturbances, such as bird cliffs, animal burrows, and the active margins of ice-wedge polygons (Wiggins 1951; Eurola & Hakala 1977; Nosko 1984), and has long been associated with arctic archaeological sites (Porsild 1932; Polunin 1948).

Even if the maturing of seed is a rare event, the persistence of viable seed in the seed bank would help to explain the abundance of Alopecurus, Arctagrostis and Poa seedlings and the rapid dominance of these and several other species on the recently excavated Thule dwelling and the adjacent spoil heap at TL. The latter, which was not sampled quantitatively, was located on a nearby rock outcrop about 1.5 m above the beach, thus limiting dispersal to the site by heavy propagules. Nonetheless, within three years the entire patch of several square meters was suffused with robust individuals of Saxifraga cernua and Polygonum viviparum, both of which reproduce from rather heavy vegetative corms, bulblets, and bulbils. Such propagules are unlikely to have dispersed up to the ledge in large numbers in such a short period of time. Other abundant plants, such as Papaver radicatum, Cerastium and Stellaria, produce lighter and regularly viable seeds, but it seems unlikely that they would have so thoroughly colonized the site in such a short time. This interpretation indicates recruitment from a rich seed bank present in the highly organic soils of the Thule dwelling at the time of excavation.

Overall, A. alpinus occurred on a wide variety of substrates ranging

Plate 4.15 - Quadrat from Housepad Type A at CR showing extremely compact soils and minimal colonization by graminoids and forbs.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from loose, nutrient-poor sands and gravels (**Plate 4.14**), to extremely compacted soils (**Plate 4.15**), to organic muds (**Plate 3.1b**), to almost pure peat (**Plate 3.11**). Excavations on the most compact soils at CR revealed its roots penetrating to depths of almost 40 cm. The other growth forms present were mostly upright forbs (Papaver radicatum, Saxifraga spp.) and caespitose graminoids (Luzula nivalis, Phippsia algida, Juncus biglumis), whose roots penetrated to ≤5 cm. Even the matted forbs (Cerastium alpinum, Stellaria edwardsii) covered only small patches. The mats of A. alpinus were comprised of more or less discrete clones. However, its growth form allows the clones of A. alpinus to overlap and eventually to form closed mats (**Plate 4.13**), as its strong roots work to break up the brick-hard soils. The caespitose graminoids, on the other hand, may clump together somewhat but never form a true sod (Bliss 1979).

Almost as important as Alopecurus in this study were the grasses Poa arctica and P. alpigena var. colpodea, which are closely related and are both viviparous in the northern and eastern Canadian Arctic (Porsild & Cody 1980). Savile (1972) reported that P. arctica did not produce seed in a typical high arctic summer and did not even reach anthesis, yet he also noted that it formed substantial mats and postulated that it could persist this way even if seed were produced only once in 50 years. Lee & Harmer (1980) have speculated that vivipary may be an advantage in marginal arctic environments and noted that while seminiferous species may produce seed only in favorable years, viviparous species may produce an abundance of propagules annually.

Alopecurus and Poa spp. were codominants on trampled areas at CR and on Thule dwellings at TL and RB. Fredskild (1961) made intensive investigations of the former Eskimo settlement of Sermermiut in W.

Greenland and reported A. alpinus and P. arctica to be the dominant vascular species on the walls and floors of old dwellings. The swards occupying these dwellings appear floristically similar to the association described for a low arctic Thule camp in Canada by McCartney (1979). As with A. alpinus, P. arctica is a colonizer of numerous natural disturbances, including patterned ground, mudflows, bird cliffs, and overgrazed tundra (Palmer & Rouse 1945; Marr 1969; Lambert 1976; Odasz 1988). Wycherley (1953) and others (Lee & Harmer 1980) have noted that viviparous grasses require adequate moisture and that both bulbils and plantlets are limited by moisture stress. This might partially explain why, in the present study, A. alpinus was common on sands and gravels but Poa spp. were absent. It has long been known that intensive and continuous trampling is favorable to Poa spp. (Stillingfleet 1759). As a result, several members of the genus, along with numerous grasses with similar growth form, figure prominently in the treading floras defined by phytosociologists (Bates 1938; Davies 1938; Ellenberg 1988; Liddle 1991). It is notable that, after Alopecurus and Poa, two of the most frequently occurring plants on trampled ground were the viviparous Saxifraga cernua and Polygonum viviparum.

Of all the growth forms encountered, the prostrate dwarf shrubs, both deciduous and evergreen, were the least resistant to mechanical impact (Forbes 1992c). Unlike the rhizomatous graminoids, even a single-pass of a vehicle could be lethal for an individual, depending on whether the main stem was crushed or broken, or whether damage was restricted to peripheral branches. In the latter instance, death did not occur, but neither did the 'clipping' result in enhanced foliar growth, as has been observed in the Low Arctic. Despite its ability to produce abundant viable seed on an annual basis, seedlings of Salix arctica, the most common deciduous shrub, were rare and restricted to the driest microsites, evidence of the overall poor resilience of this growth form (Forbes 1992b).

Among lichens, there were definite patterns of response within the various growth forms. Only the foliose Peltigera aphthosa was able to resist low intensity mechanical disturbance, such as light-moderate trampling or a single passage of a vehicle. Grabherr (1982) and Bayfield et al. (1981) have reported on alpine lichens and their sensitivity to trampling. Grabherr found fruticose forms to be 'very sensitive' and crustose forms to be somewhat less so, but he did not mention foliose forms. Bayfield et al. indicate slight differences in sensitivity among various fruticose (Cladonia) species, but note that this variation is reduced or eliminated when the lichens are dry. This is the typical state of raised microsites in the High Arctic, particularly after snowmelt. Similar findings have been reported from studies of zoogenic and anthropogenic disturbance in both arctic and antarctic regions (Kightley & Smith 1976; Pegau 1970; Hoogesteger 1984; Kappen 1984). As with Salix arctica, the prospect for a natural return to predisturbance levels of cover/abundance among fruticose and crustose lichens appears unlikely on mechanically disturbed terrain as their microhabitats are often significantly reduced in extent or eradicated. On the other hand, lichens within these two growth forms have extensively colonized the drier microsites within the drained peatlands. Tamm (1951) also reported increases in cover/abundance of Cladonia spp. from peatland drainage in northern Sweden, as did Ellenberg (1988) in central Europe.

Several bryophytes on disturbed sites in this study were successful in resisting the initial impact, in invading disturbed vegetation, or both. Acrocarpous genera (Bryum, Ceratodon, Pohlia, Polytrichum) were most common on the drier sites at CR and where material was added, while pleurocarps tended to dominate wetter disturbances. Many of these species have been noted for their opportunistic nature elsewhere (see Leach 1931; Birse et al. 1957; Bliss & Cantlon 1957; Watson 1980). In many bryophytes, particularly at high latitudes, the maintenance of populations is almost entirely dependent on asexual propagation, which may facilitate rapid colonization following disturbance (During & van Tooren 1987; Longton 1988). It has been observed that a single bryophyte genotype may be capable of regenerating by several mechanisms (During 1979). Subsequently, it has been suggested that the ecological amplitudes of bryophytes are determined not only by genetic variability and phenotypic plasticity, but also by regenerative flexibility, which may be tied to growth form (Grime 1990). This was apparent in the present study, for example, on sites where the reproductive organs of acrocarps were able to remain above or quickly penetrate great quantities of added sand and gravel on housepads, whereas pleurocarps were unable to do so.

Experimental work with bryophytes in temperate, arctic, and alpine regions has demonstrated that both acrocarpous and pleurocarpous growth forms are capable of partial or complete vegetative regeneration from numerous parts such as from stem, leaf and/or branch fragments (Bayfield 1976; Miller & Ambrose 1976; Wilmott-Dear 1980; Poschold & Schrag 1990). Species tested include some naturally occurring and ruderal species which occurred at high frequencies in this study, such as Aulacomnium palustre, Bryum argenteum, Calliergon giganteum, C. stramineum, Campylium stellatum, Drepanocladus revolvens, Leptobryum pyriforme, Polytrichum commune, P. juniperinum and P. piliferum. Mechanical disturbance may therefore both create and disperse viable propagules and thus be beneficial to the establishment, maintenance and spread of these and other species. Indeed, many bryophyte species and growth forms may be favored by moderate levels of trampling (Liddle 1975; Studlar 1980).

Results from research with Sphagnum indicate that this genus is generally sensitive to impacts such as trampling, especially in comparison to the sedges and grasses with which it usually is found, and in comparison to other acrocarpous mosses, as well as pleurocarps (Bayfield 1971; Tachibana 1976; Rees & Tivy 1978; Moen 1990). Yet there certainly are differences in trampling resistance and resilience among species of Sphagnum (Tachibana 1976; Studlar 1985; Poschold & Pfahenhauer 1989). In this study, no species of Sphagnum remained on either trampled sites or multi-pass tracks at CR and there was no evidence of recolonization. In single-pass tracks, however, S. capillifolium var. tenellum remained in 75% of single-pass tracks while S. squarrosum was missing from 80% of the same tracks. This would seem to indicate the relative resistance of the former and possibly differences among their respective sections within the genus (Acutifolia and Squarrosa). McQueen (1990) comments on the stiffness of S. squarrosum, which may be a factor in its failure to resist even minimal vehicle traffic compared to S. capillifolium var. tenellum, which has thinner, more flexible stems.

Although sporophytes were not observed on either species in any of the stands, S. squarrosum was beginning to colonize single-pass tracks across a mesic interfluve where both species were absent in the natural vegetation (Stand 15). The tracks themselves were relatively moist and pH was significantly higher than in the control area. Colonization may have been by vegetative propagules, the viability of which was recently demonstrated for this species by Poschold & Pfahenhauer (1989). Poschold & Pfahenhauer also noted that both species can regenerate from trampling, although they do not specify what levels of trampling intensity were tested. Bayfield (1971) conducted a rigorous trampling tolerance experiment in the Scottish alpine within a wet Calluna heath with abundant Eriophorum angustifolium and Sphagnum rubellum (the inland equivalent of S. capillifolium var. tenellum, Crum 1988). He found that while E. angustifolium was singularly resistant compared to other heath plants, damage to Sphagnum was 'considerable', resulting in crushed or detached shoots, even at a 'low level' of trampling (80 walks).

In the context of drainage and associated moisture deficits, poikilohydric tundra plants are especially vulnerable (Savile 1972; Tenhunen et al. 1992). Among bryophytes, Sphagnum appears poorly adapted to withstand prolonged drought, but duration of desiccation is important and Sphagnum is generally resilient (Clymo 1973). Water table manipulations have revealed differences among species with regard to short-term drought and indicate that hollow species tend to suffer greater injury relative to hummock species subject to the same level of desiccation (Rydin 1985; Rydin & MacDonald 1985; Ellenberg 1988). Downslope drainage from single-pass vehicle tracks at CR clearly affected soil moisture, pH , surface albedo, and vascular cover and biomass.

Yet, while some Sphagnum associates were absent in these areas, the populations of Sphagnum appeared reasonably healthy after 20 yr (**Plate 3.2**). Below multi-pass tracks, however, populations of both species of Sphagnum appeared to have been extinct for some time in water channels and interfluve zones (**Plate 3.6**). Salonen (1990) observed the reinvasion of small amounts of Sphagnum into cut-over and drained peatlands in central Finland, but he also noted that heavy and/or long-lasting rainfalls were common and that the uppermost peat layers would remain saturated for many days or even weeks. Although fogs were not uncommon on the lowland at CR, the perennially dry summers of the region are likely to keep the drained areas dry after snowmelt and thus inhibit the reinvasion of Sphagnum and associated species. Evidence from northern Alaska indicates that occasional fogs may to be the key the maintenance of fruticose lichens (Lechowicz 1981), such as those observed invading the more severely desiccated areas. Among non-sphagnous bryophytes at CR, pleurocarpous forms were clearly less resistant to prolonged drought and most colonists in drained areas were acrocarps.

In summary, the growth forms of several of the dominant plants appear important in the context of the disturbances reported here. Growth forms present at the time of impact determined, at least in part, the extent to which mechanically disturbed communities were affected. Rhizomatous graminoids, for example, were highly resistant and resilient, while dwarf shrubs demonstrated little resistance and low resilience. Cryptogamic growth forms were also highly variable in their responses to trampling, tracking, and drainage. The data have shown that the remnant and colonist components of mechanically disturbed plant communities were dominated - in terms of cover and above-ground biomass - by long-lived clonal sedges and grasses. Harper & White (1974) point out that plants with clonal growth may never die and they cited several examples of extremely long-lived clones.

The absence of complete senescence in clonal species appears to be an adaptation for perpetual site occupation, a fact that makes clonal plants ideal candidates for the development of stable plant communities. Growth form and longevity, combined with vivipary, could help explain why the dense, matted graminoid swards which occupy housepads and trampled ground appear impervious to recolonization by the species originally displaced, and would also explain the persistence of these swards over hundreds of years, as appears to be the case on archaeological sites in this and other studies. As in more temperate regions, Sphagnum spp. have proven unable to withstand prolonged drought and in drained areas have been largely replaced by non-sphagnous acrocarps and fruticose and crustose lichens.

iii. Nutrient cycling - a combination of biotic and abiotic factors

The chemical composition of plants often provides information about the availability of plant nutrients in the soil that in many cases cannot be obtained from soil analyses. Despite generally poor soils, arctic plant species can have tissue concentrations of nitrogen and phosphorus that are twice those of temperate and even low arctic species (Dowding et al. 1981). Different tundra plant species and growth forms have different nutrient demands and different abilities to extract nutrients from the soil (Chapin 1980; Lechowicz & Shaver 1982; Chapin & Shaver 1985), which makes the choice of indicator species very important in studies of nutrition by foliar analysis.

Studies in Fennoscandia indicate that the variation in composition of evergreen species with age and season can be more complex than that of deciduous species. Thus, the timing of tissue sampling is also important (Tamm 1951). Other critical factors may include soil fertility and moisture, stand structure, and stand history (Auclair 1977). In northern Alaska, deciduous, evergreen, and graminoid species have been distinguished by growth form in a multivariate comparison of N, P, K, Ca and Mg concentrations. The authors reported that differences among growth forms in these plants were maintained both through the growing season and in response to fertilization (Shaver & Lechowicz 1985). Temporal and spatial changes in tissue nutrient content have serious implications for forage quality and the nutrition of tundra herbivores (Batzli et al. 1980). However, nutrient concentrations are clearly not the only factors involved in food preference (Jung et al. 1979; Chapin et al. 1980a).

According to Dowding et al. (1981), exchangeable and soluble pools of phosphorus and potassium are largest at snow melt in both arctic and alpine soils around the world. These elements progressively decrease in concentration through the growing season. Research in temperate grasslands, and arctic, alpine and subantarctic tundras, suggests that plant mineral content is often, but not always, correlated with local soil chemistry (Schultz 1969; Harner & Harper 1973; Walton & Smith 1979; Jonasson 1986; Kummerow et al. 1987; Chapin et al. 1988).

For tundra plants, in general, spring tissue is laden with minerals, while late summer and fall tissue is extremely low in nutrient content (Dowding et al. 1981; Svoboda 1992, pers. comm.). Muc (1977) conducted studies within sedge meadows at TL and found that, for Carex aquatilis var. stans, peak chemical levels developed by mid-season in aboveground (live and dead) tissue and in soil organic matter, but at the corresponding time interval, belowground (live and dead) tissue chemical levels were at their lowest. Similarly, Chapin et al. (1980a) reported that it was mid-July when the leaves of deciduous shrubs reached their maximum nitrogen content in northern Alaska. The present data were gathered near anthesis for all species except Salix arctica, which was post-anthesis, and it is assumed that these mid-season values represent approximate peak season tissue nutrient concentrations for the 1990 growing season at each study site.

In this study, differences among growth forms were often apparent, but certainly not as a rule. In single-pass vehicle tracks and drained areas, for example, rhizomatous sedges displayed similar patterns of change in their concentrations of N and P, but both differed markedly from the deciduous

Salix arctica with regard to these same nutrients. In contrast, changes in N and P content were quite similar for the grass Alopecurus alpinus and S. arctica between excavated and unexcavated Thule dwellings at TL. Within the rhizomatous sedges at TL, changes in N and P content were virtually opposite in response to similar minimal vehicle disturbance at CR. These differences may be linked to the contrasting minerotrophic/oligotrophic status of the sampled meadows at the two study sites.

Controlled fertilization experiments in oligotrophic low and high arctic sedge meadows have resulted in significant increases in above-ground standing crops of foliage and tissue nutrients in ≤2 yr (Henry et al. 1987; Kummerow et al. 1987; Chapin et al. 1988). Chapin & Shaver (1981) reported significant increases in biomass and tissue concentrations of N and P in Eriophorum angustifolium and Carex spp. after ≤3 yr in northern Alaska. Together these findings indicate that the changes recorded in this study were probably manifest within the first few years following the initial impacts.

The present data are unique with regard to the long time elapsed since the cessation of vehicle activity. Chapin & Shaver (1981) mentioned sampling stands of E. angustifolium from a single 25 yr old track, but did not report any tissue nutrient data from that site. The other tracks they sampled were all ≤7 yr old. They also reported on the effects of a roadway impoundment, where they found N and P concentrations in graminoid shoots to be generally higher than adjacent controls, but they did not sample the effects of drainage, nor any other nutrients. Many natural tundra disturbances, such as patterned ground, fire, herbivore trampling, grazing, nesting and manuring, have been shown to have significant effects on patterns of nutrient uptake (Schultz 1969; Wein & Bliss 1973; Smith 1978; Walton & Smith 1979; Batzli & Jung 1980). However, in some cases these effects have been highly ephemeral and have persisted for periods of ≤18 months (Wein & Bliss 1973; Walton & Smith 1979). A key difference appears to be where the soils are subject to perennial and/or structural changes, such as frost heave or compaction. Ice-wedge polygons, for example, may evolve only slowly over hundreds of years, but can have major affects on soil structure, microtopography and local hydrology (Lachenbruch 1962) which, in turn, have been shown to effect patterns of vegetation development and exploitation by herbivores (Fuller et al. 1975; Hjeljord 1975; Batzli et al. 1980). The present data are significant in that they have shown that similar changes can be induced virtually overnight, with as little as a single passage of a tracked vehicle, but that the effects are persistent for periods of ≥21 yr.

None of the effects measured in this study could be considered ephemeral since sampling took place 17 to 21 yr after major human activity had ceased. In some cases, however, the effects may no longer be directly linked to the initial impact. In single-pass vehicle tracks there was no evidence of animal activity and it would seem safe to assume that altered nutrient cycling is attributable to the compression and accelerated decomposition of the organic mat and vegetation and the subsequent release of available nutrients, as modelled by Chapin & Shaver (1981). In drained areas, on the other hand, the effects of disturbance have spread far from the point of initial impact, even when the event was limited to a single vehicle pass. These are considered cumulative impacts (Walker et al. 1987b), and have not previously been documented for the High Arctic. There was no evidence of animal activity in any of the drained areas.

It is well known that moisture stress can affect the carbon and nitrogen metabolism of plants. The effects vary by plant species, tissue type, the duration of stress, etc. Typically, however, total N gradually increases as stress intensifies (Mattson 1980). For tundra species, annual nutrient uptake shows a strong positive correlation with water availability, both within and among arctic ecosystems (Kielland & Chapin 1992). For example, after ordinating vegetation and edaphic features from mesic sites at Oumalik in northern Alaska, Ebersole (1985) concluded that 'the important controlling nutrient' was nitrogen. In contrast, phosphorus was found to be the controlling nutrient in ordinations done on Barrow vegetation, which is primarily wet meadow (Webber 1978), and fertilization studies have shown that phosphorus is a limiting factor in other wet sites in northern Alaska (Chapin & Shaver 1985). Within a given community, however, nutrient uptake is often highly individualistic (Lechowicz & Shaver 1982; Chapin & Shaver 1985b; Henry et al. 1987). Other potentially important factors are pH and, indirectly, soil temperature (Herbein & Neal 1990; Kielland & Chapin 1992). For instance, citing overall warmer temperatures in drained peatland soils, Lieffers (1988) concluded that surface rates of decomposition might be faster in drained sites relative to natural peatlands.

In response to concerns over the potential effects of so-called global warming, Kielland & Chapin (1992: 331) recently predicted that "a drying of wet tundra soils would probably increase overall nitrogen uptake and plant production". They also noted that "phosphorus availability responds quite differently to soil aeration than does nitrogen", and predicted that "increased aeration of now-saturated soils might increase soil redox potentials, thereby reducing phosphate solubility". The present data, being derived from former water channels and adjacent interfluves in an oligotrophic peatland, have provided a small-scale analogue for the 'drying of wet tundra soils'. The data are thus suitable for testing Kielland & Chapin's hypotheses, especially with long-term effects at the community level. In contrast to the predicted increase, N was significantly reduced in the two dominant rhizomatous graminoids (Carex aquatilis var. stans and Eriophorum angustifolium) and the dominant deciduous shrub (Salix arctica) growing in drained areas. Together these three species comprise almost 61% of the above-ground foliar biomass in the interfluves, and 90% in the water channels. It would thus seem reasonable to conclude that 'overall nitrogen uptake' has not increased in the plant communities of drained peatlands after two decades. Phosphorus concentrations demonstrated a different pattern, however, being significantly reduced in both Carex and Eriophorum, but not in Salix arctica. These findings indicate that, in the long-term at least, the rhizomatous graminoid growth form is more susceptible to soil desiccation than the dominant deciduous shrub and that Kielland & Chapin's generalization should perhaps be modified.

It would be helpful to have short-term data and data from other tundra sites for comparative purposes to determine if these responses are consistent with regard to species, growth form, and time since disturbance. In Fennoscandia, research with deciduous shrubs and trees has provided a great deal of evidence suggesting general deficiency in mineral nutrients on many drained mires (sources in Tamm 1951). Regarding the supply of N after draining, Tamm's own leaf data from two Betula spp. demonstrated significant reductions after 39 yr when compared to an adjacent undrained mire. Tamm reported even greater reductions in P content. He pointed out that birch leaves collected from the same area in two different years had very similar compositions. He reasoned that the good agreement between samples from the same patches in two different years, and the equally good agreement between similarly fertilized patches, lent support to the idea that differences in leaf composition may be a good guide to nutritional differences among patches. Tamm's results from Betula spp., demonstrating significant reductions in P after 39 yr, contrast with my results from Salix arctica, in which P was not reduced after 21 yr. Taken together, these findings would seem at first to indicate that responses to soil desiccation are more variable among deciduous shrubs than rhizomatous graminoids. However, data from differing species at the same site(s) would be needed to confirm this.

Although they were not sampled, drainage might also be expected to affect populations of soil invertebrates. At TL, nematodes were the main invertebrates contributing to energy flow (Procter 1977). During the IBP, it was determined that nematode numbers were consistently higher in well-drained tundra habitats compared to wet meadows (Procter 1977; MacLean 1981), leading me to conclude that long-term drainage of arctic wetlands could have the effect of increasing overall nematode densities. In support of this prediction is a recent report of the long-term (≥30 yr) effects of drainage in numerous temperate peatlands, in which Wasilewska (1992) found that drainage was always accompanied by increasing numbers of nematodes, especially in the group of phytophages, thus enhancing nutrient cycling. Lôhmus (1981), working in drained Estonian peatlands, partly attributed the enhanced decomposition of peat to the increased activity of the soil fauna.

Nutrient cycling within trampled areas is poorly understood since past studies have dealt mostly with soil compaction, erosional effects, plant cover and regeneration strategies (Monti & Mackintosh 1979; Marchand & Roach 1980; Emanuelsson 1984; Bayfield & Barrow 1985). Liddle (1991) recently noted that the interrelation between trampling and soil nutrient change is almost unknown. Neither are there data on the effects of pedestrian trampling on plant nutrient uptake. Although zoogenic trampling has certain effects in this regard (Leader-Williams et al. 1981; Archer & Tieszen 1986; Henry & Svoboda

1989), it is not directly analagous to pedestrian trampling for reasons mentioned earlier.

The present data reveal changes in soil nutrients and standing crops of tissue nutrients, in addition to above-ground biomass, which appear related to levels of pedestrian trampling intensity at CR. It was apparent that the mechanical disturbance led to rapid and significant increases in the cover/abundance of nutritious colonist graminoids such as Alopecurus alpinus, as well as long-term changes in the nutrition of the remnant species.

Together the higher biomass and nutrient concentrations have led to greater standing crops of foliar N, P, K, Ca and Mg on trampled ground and housepads relative to adjacent controls. This is important because the actual diet of animals depends not only upon preference, but also upon relative abundance (Batzli et al. 1980; Chapin et al. 1986). It was also apparent that grazing, nesting, and manuring by lemmings was localized in heavily trampled areas at CR, as was manuring on housepads colonized by Alopecurus and/or Salix at all three study sites. Others have reported selective grazing by lemmings, caribou, and snow geese on A. alpinus and other ruderal plants growing in abundance on natural disturbances such as ice-wedge polygons and drained thermokarst lakes (Hjeljord 1975; Batzli et al. 1980; Fox 1985; Ovenden 1986). Grime once noted (1979: 38) that "in habitats subject to severe environmental stress there is a general decline in palatability", and that "there is evidence that the palatability of vascular plants from unproductive or late-successional vegetation is lower than that of ruderal species". There is also strong circumstantial evidence that arctic microtine populations reach their highest densities in habitats with the highest-quality food (Batzli 1983; Batzli & Hentonnen 1990; Jefferies et al. 1992).

In addition to Alopecurus, the changes in the cycling of nutrients by the remnant species on trampled ground are potentially important since, the forage quality and palatability of dicots is generally superior; they have higher concentrations of nutrients and are more digestible than monocots (Chapin et al. 1975; Batzli & Cole 1979; Batzli & Jung 1980). At TL and other tundra sites, the collared lemming has been found to eat dicotyledons, particularly Salix spp. (Watson 1956; Fuller et al. 1975; Batzli & Pitelka 1983).

In this study, S. arctica growing on Thule dwellings exhibited significantly higher concentrations of all five nutrients sampled relative to adjacent controls. In a recent study in northern Alaska, a single independent variable, green biomass of the sedge Eriophorum angustifolium, explained 92% of the adjusted variance in tundra microtine abundance among eight different habitat types. The addition of a second significant variable, green biomass of other sedges (Carex aquatilis and C. bigelowii), increased the cumulative variance explained to 98% (Batzli & Lesieutre 1991). The authors concluded that E. angustifolium serves as an indicator species for the presence of tundra voles near Toolik Lake. At CR, many nutrients were present at significantly increased levels on trampled ground in S. arctica and E. angustifolium. These gains, coupled with dramatic increases in the cover and green biomass of Alopecurus, may serve as indicators of lemming presence, as observed anecdotally over the last several years in the vicinities of housepads and adjacent trampled areas.

There is strong evidence that some grazers (e.g. lemmings, hare, ptarmigan) feed selectively at fine temporal and spatial scales and are thus sensitive to differences in forage quality exhibited over distances of ≤1 m and may shift their feeding habitats several times during the growing season according to patchy trends in nutrient uptake within a given community

(Batzli et al. 1980; Chapin et al. 1980b; Batzli & Lesieutre 1992; McKendrick et al. 1992). According to Batzli et al. (1980), the propensity of lemmings to feed in polygon troughs and wet meadows more than in drier areas may be related to the higher nutrient status of graminoids in those areas. In support of Batzli's assertion are the results of Schultz (1969) in which the macronutrient status of northern Alaskan tundra vegetation was altered. By fertilizing heavily, Schultz increased the protein, calcium and phosphorus levels in graminoids well above those in nonfertilized areas. In 1968 there were about 75 winter nests/ha in the fertilized area and none in the control areas. The effect continued through 1971, although by then it was less dramatic, indicating the ephemeral nature of the treatment. These results suggest that, at least in some winters, reproductive performance of lemmings can be stimulated by improving vegetation quality (Batzli et al. 1980).

In summary, anthropogenic disturbances mimic important aspects of natural disturbance regimes. The former often alter soil structure and give rise to persistent swards of palatable forage species in which concentrations of macronutrients are high relative to adjacent controls. These spatial shifts in vegetation quality and quantity affect patterns of herbivore nesting and grazing. Feedback loops are apparent; once initiated, selective grazing has certain implications for vegetation structure and composition within a given patch. Under continued grazing pressure, mosses and moncotyledons tend to revegetate areas previously dominated by lichens and dwarf shrubs.

In this study, plant species characteristics within trampled areas and on housepads appear to have created positive feedbacks to patterns of nutrient cycling. In the long term, the nesting activities of herbivores may stimulate decomposition, while excretions may enrich soils, together increasing rates of mineral cycling and primary production in dominant deciduous shrubs and rhizomatous graminoids. The result has been to enhance nutrient availability within what was formerly a relatively low-nutrient habitat. The observed shifts appeared in some cases to be tied to levels of extractable soil nutrients.

Demonstrating such differences so long after disturbance fails to illuminate how additive or interactive effects among nutrient losses and/or gains may have determined the pathways by which these populations arrived at their present nutrient status and levels of production. Nevertheless, the anomalies appear tied to low-levels of impact (i.e. single-pass vehicle tracks where the organic mat was retained), serving as a caution that destruction of the organic mat not be used as the most important yardstick in gauging the intensity of an impact, as was recommended by Shaver et al. (1983). The measured effects of humans on plant macronutrient status appear persistent for periods of up to 21 yr, in the cases of mechanical disturbance and drainage, and appeared to be highly persistent on archaeological sites where organics were transported to the patches.

Altered slope hydrology afforded the chance to address recent predictions regarding the drying of wet tundra soils and its potential effects on nutrient uptake. Concentrations of many nutrients were substantially reduced in the leaves of the dominant species. In contrast to the expectations of Mattson (1980) and Kielland & Chapin (1992), N content of plants was significantly reduced in areas drained for ≥21 yr. Leaf concentrations of P were reduced in rhizomatous graminoids growing in drained areas, but not in Salix, thus contrasting with the assertions of Kielland & Chapin and the findings of Tamm (1951) for Fennoscandian Betula spp. These alterations, despite the often low level of the initial impact, were detected in areas far from the point of initial impact and thus indicate the spatial breadth of the cumulative impacts.

4.3 Synthesis

i. Restatement of original hypotheses

Hypothesis One. Unassisted or natural 'recovery' within the plant communities of anthropogenic patches will, depending on the nature, intensity and age of the original disturbance, exhibit characteristic patterns of species composition, vegetation cover and biomass differentiable from corresponding patterns of adjacent undisturbed ground.

Hypothesis Two. Comparable high arctic plant communities that have experienced similar disturbance events are marked by comparable recovery sequences among both vegetation and soils.

Hypothesis Three. Excessive soil compaction is a key factor associated with the spread of the adjoining flora into anthropogenic habitats.

Hypothesis Four. The spatial and temporal 'signatures' of the plant associations of the various disturbances will be best distinguished by their non-vascular floristics.

Hypothesis One:

With regard to the first hypothesis, the results of the multivariate analyses have shown that the anthropogenic patches surveyed did indeed exhibit characteristic patterns of species composition and cover. Most of the patches were distinguishable from each other, and from the background matrix, according to the nature and intensity of the level of disturbance. Age was less important and the plant communities of vehicle tracks that were only three yr old were floristically similar to tracks that were ca. 20 yr old, although vascular biomass was lower in the former. In both ordinations and numerical classifications, unexcavated Thule dwellings at TL and lightly trampled mesic meadows at CR were similar despite dramatic differences in the nature of disturbance, soil structure and chemistry, and geography. These results also reflect the depauperate nature of the regional flora and the limited number of growth forms suitable for colonizing surface disturbances. Total vascular biomass was consistently reduced in vehicle tracks relative to controls (Forbes 1992b), but was increased in trampled areas relative to controls. Recently abandoned housepads had lower total biomass and species richness than adjacent sedge meadows, but biomass and species richness were increased on recently excavated Thule dwellings compared to adjacent beach ridges at TL, reflecting recruitment from the seed bank and colonization by a number of ruderal cryptogams. Total biomass on unexcavated Thule dwellings did not differ significantly from controls.

Responses to prolonged drought coroborrated patterns reported from temperate and subarctic regions in which obligate aquatics have become locally extinct and have been largely replaced, to some extent, by vascular and non-vascular species indicative of more mesic conditions. In more xeric drained areas the result was a significant increase in species richness. In water channel zones formerly dominated by aquatics, total biomass has shown a net loss, while in interfluve zones, the enhanced growth of previously dominant dwarf shrubs has contributed to a net gain in total biomass.

Patterns of cover and biomass of individual species and growth forms were also examined. Rhizomatous graminoids present at the time of the initial impact, particularly sedges, were resilient to mechanical disturbances and comprised the bulk of the biomass and cover in trampled and tracked areas up to 21 yr after activity had ceased. Dwarf evergreen and deciduous shrubs were consistently reduced under these disturbance regimes, as were fruticose and crustose lichens. Acrocarpous and pleurocarpous bryophytes exhibited different degrees of resistance and resilience and these were largely predictable based on the intensity of disturbance and the local moisture regime. The foliose lichen Peltigera aphthosa was common in both trampled and tracked areas.

Hypothesis Two:

Comparable recovery sequences were recognized, as asserted by the second hypothesis, although the sequences themselves were rather limited dynamically. Both geographic and local variation among sequences appeared linked to the degree of disturbance of the organic mat, the exposure of mineral soils, and the nature of the substrate (calcareous vs. siliceous). Mechanical disturbances which left the organic mat intact tended to reduce microtopography and habitat heterogeneity, leading to floristic convergence among patches. Similarly disturbed patches on different islands were most readily differentiated on the basis of their bryofloras, which reflected marked geobotanical variation (minerotrophic vs. oligotrophic). Remnant vascular floras among these patches are small and virtually identical.

Colonization by seedlings of the dominant dwarf shrub was limited to mesic microsites found only in a few single-pass tracks at CR, thus limiting the number of potential sequences in naturally recovering patches. However, recruitment from the seed bank was extensive in places where the organic mat was manipulated, including the excavated Thule dwelling and Barrett's (1975) restoration treatment with sods of bryophytes. Such recruitment led to several surpises, including the relatively rare germination of Alopecurus, Arctagrostis, Poa and Eriophorum scheuchzeri.

The sequences of vegetation change on the excavated dwelling appears to be more variable and less predictable than the other patches with remnant floras, responding to the initial floristics (Egler 1954; Wilson et al. 1992). However, if the adjacent unexcavated dwellings are any indication, the fast-growing but persistent grasses (Poa and Alopecurus) and the slow-growing Salix arctica will eventually dominate the patch, as they have at TL, RB, and on similarly vegetated trampled meadows at CR.

Another factor affecting sequences of change appeared to be surface texture. Species richness was greater on well-drained housepads with rough surfaces (i.e. sand/gravel) relative to smooth, compacted surfaces. The latter were dominated by one rhizomatous grass (Alopecurus) and one viviparous forb (Saxifraga cernua). The vegetation of the former comprised a diverse mix of mostly caespitose graminoids and matted and erect forbs. The eventual structure and compostion of the 'rough' surfaced housepads is less predictable, given the apparently random nature of colonization and the great number of successfully established species. However, it is certain neither smooth nor rough housepads appear to be returning to their predisturbance composition.

Hypothesis Three:

The third hypothesis, which predicted that excessive soil compaction would be an important limiting factor, was based on reports in the literature of the influence of compaction on the recovery of vegetation and soils from vehicular and pedestrian traffic. After two decades, the effect of single-pass vehicle tracks in mesic meadows has been to reduce soil compaction and bulk densities. In wet meadows compaction was unchanged by any level of vehicle traffic. Soil compaction was positively correlated with increasing trampling intensity in mesic meadows, but less so in wet meadows. Bulk densities were moderately high in the soils of multi-pass tracks through mesic meadows, due to the continued use of the vehicle after the removal of the organic layer.

Rhizomes and roots of the dominant graminoids were able to exploit both loosened (single-pass) and moderately compacted (multi-pass) soils. However, severely compacted and bared soils were extensively colonized by only two vascular species, and were dominated by only one of these (Alopecurus), indicating that extreme compaction was a factor in the initial colonization of these patches. On heavily compacted soils, the persistence of the dense sward of Alopecurus may indicate that competition is equally or more important than soil compaction after the initial colonization of ruderal species. On moderately compacted and trampled soils, Alopecurus was replaced by Poa arctica as the dominant species. The extent of the latter appears to have been tied more to the resistance of the growth form to continuous trampling, and its viviparous mode of reproduction, than to compaction *per se*. Here, again, the absence of seedlings within the dense sward suggests that competition was of greater importance than soil compaction in limiting recolonization of the patches by the original species.

Hypothesis Four:

Hypothesis Four predicted that variations in cryptogamic floristics within and among the different lowlands would be more important than vascular floristics in differentiating among the vegetation 'signatures' characterizing the numerous disturbance regimes. Although cryptogamic floristics have only rarely been included in the classification of high arctic plant communities, and never in the context of anthropogenic disturbance, there is considerable evidence that the most important factor affecting the geographic and local distribution of arctic and alpine bryophyte assemblages is substrate type (Steere 1978; Vitt & Horton 1979; Vitt et al. 1987). Some common lichens, too, can be reliable indicators of substrate conditions, even at local scales (Walker 1989). In this study, absent, remnant, and colonizing bryophytes all tended to reflect quite accurately the chemical and moisture conditions within a given patch at the time of sampling.

Cryptogamic colonists were usually present only at low levels of cover/abundance, but often at high enough frequencies to reflect subtle yet significant changes in factors such as soil pH over very short gradients (≤50 cm). These fine scale patterns of establishment are comparable to those observed on natural tundra disturbances which similarly affect substrate chemistry, resulting in small, calcareous patches within otherwise acidic meadow-heaths (Jonasson & Sköld 1983; Jonasson 1986). The removal of cryptogamic species from both sets of multivariate analyses consistently led to poor separation of patches within and among different lowlands which were structurally and floristically quite dissimilar, i.e. meadows with and without Sphagnum hummocks. Cryptogams were more reliable geographic and ecological (patch-level) indicators than vascular plants alone (Forbes 1992d).

CHAPTER V. OVERVIEW AND CONCLUSIONS

5.1 Contributions to patch dynamics theory

i. Evidence in support of the generalizations outlined by Pickett & White and others

The results of this study are in accord with several generalizations in the literature of patch dynamics (Pickett & White 1985). The bases for some of the diversity of interpretations within the field of patch dynamics are often scale-dependent phenomena, while others relate more to the use of different reference ecosystems. Much of the current literature is derived from natural disturbance regimes examined within four ecoregions; marine, temperate forests, tropical forests, and grasslands. Theories and models derived from temperate and tropical systems need to be tested within the Arctic. There is also a lack of analyses from patchy anthropogenic disturbance regimes and it is not yet certain if these require methodological or theoretical separation from natural disturbances.

According to Forman (1981), based on work in the forests of New Jersey, small patches tend to be more dissimilar in community composition from one another than are large patches. Connell & Keough (1985), working in marine subtidal habitats, suggested that the larger the disturbance, the less predictable the postdisturbance composition. These and other contrasting generalizations derived from studies of temperate systems illustrate the importance of scale in different ecosystems. What constitutes a 'small' patch needs to be established.

In this study, the patches derived directly from human activity have ranged in size from strips ≤50 cm across to trampled areas covering hundreds of square meters. In comparison to other studies of direct impacts on tundra, based mostly in the Low Arctic, the present disturbances have resulted in patches of generally small spatial scale (Babb & Bliss 1974a; Smith & James 1979; Lawson 1986; Walker et al. 1986). However, the cumulative impacts of altered hydrology and chemical dumping reported here have spread the effects of disturbance over large portions of the landscape and it is debatable whether they should still be considered as 'patches'. If so, they are best considered as 'large' patches.

Within a given patch, the level of direct anthropogenic disturbance measured ranged from none, in naturally occurring stands, to maximum, in stands where all above and below ground living vegetation were killed or displaced by the initial impact. Examples of the latter would be each of the three types of contemporary housepads surveyed, as well as some of the multi-pass vehicle tracks where the organic mat and all shoots, rhizomes, and roots were destroyed. A range of cumulative impacts was also observed, but only chemical dumping has resulted in the complete elimination of the vegetation and the organic mat.

The above definition of maximum disturbance follows from the designation of arctic ecosystems as 'root-biased' systems (**Fig. 1.4**) (Bell & Bliss 1978; Chapin et al. 1980b; Callaghan et al. 1991), so that a disturbance which leaves roots or rhizomes intact cannot be considered as 'maximum'. The present data have demonstrated, however, that non-destruction of the root-mat is not necessarily a guarantee against significant and essentially permanent change to both vegetation and soils within a patch, although the likelihood of such change clearly increases with the frequency and intensity of disturbance.

With regard to the concept of 'intermediate disturbance', and its effects on species richness and biomass, the present data offer some useful insights. Briefly, the intermediate disturbance hypothesis states that disturbed patches will host a local 'succession' of species during their post-disturbance recovery, or what has also been referred to as gap-phase or microsuccession (Watt 1947; Grubb 1977; Pickett 1980; Denslow 1985). Thus, according to Fox (1981), in areas sufficiently large to contain several patches, the vegetation at intermediate levels of disturbance would contain a relatively equable mixture of differently aged patches in various stages of recovery. The result is a relatively even mixture and greater variety of species (including early- and late-successional plants).

Tests generally follow one of two approaches: (1) verifying predicted species diversity/disturbance relationships at a 'macroscopic' scale, or (2) demonstrating microsuccessional dynamics at the patch scale. In general, calculations of plant species diversity are affected by both the number of species per unit area (species richness or species density) and the evenness of their relative abundances. Limitations of the present data set for truly robust tests of the hypothesis stem from, among other things, the lack of a single definition of diversity (Magurran 1988), and the difficulty of obtaining accurate estimates of individual plant abundances in tundra vegetation. On the other hand, simple species richness and dominance measures are invariably informative (ibid). Biomass is another state variable which has often been related to both species richness and level of disturbance (Wheeler & Giller 1982; Vermeer & Berendse 1983; Fox 1985; Moore & Keddy 1989).

With regard to vehicle disturbance, I have shown that even a single passage was adequate to produce a significant reduction in species richness and biomass in mesic, hummocky meadows at CR (Forbes 1992b). Single- and few-passes through more hydric, hummock-free meadows at TL produced similar responses. Not surprisingly, the same state variables were further reduced on both islands by multi-pass tracks which registered the defined maximum level of disturbance. The end result is that neither species richness nor biomass had increased at any level of disturbance in any of the different meadow types after ≤21 yr. Evidence from controlled, short-term studies at TL by Babb & Bliss (1974a), combined with my own short-term observations from a known number of passes (Forbes 1992b), indicate that the present data have not failed to represent increases which immediately post-dated the cessation of activity. It is clear that vehicle disturbance almost invariably reduces both species richness and biomass within high arctic tundra, and that these reductions are more persistent than similar impacts in the Low Arctic (Hernandez 1973; Ebersole 1985).

A more complete disturbance gradient is represented by the different levels of trampling surveyed in a mesic, hummocky meadow at CR. Yet here again species richness was significantly reduced at each level of disturbance **(Fig. 3.18)**. The relationship between species richness and total standing crop is seen in **Fig. 3.19**. While it is apparent that species richness was highest at moderate levels of total biomass, it was illustrated earlier that this was not true for live foliar biomass only. In this case, total biomass was highest under the heavy trampling regime (**Fig. 3.15b**), but species richness was extremely low (**Figs. 3.14a, 3.18** and **3.19**).

It seems that for these types of mechanical impacts an intermediate level of disturbance does not maximize species richness at the scale of the patch. A contributing factor appears to be the lack of differentiation between early- and late-successional species which, in turn, is certainly related to the depauperate regional flora and the widespread failure of sexual reproduction among potential colonizers. By comparsion, short- and long-term observations in the Low Arctic and Subarctic have reported seedlings of up to 35 species of shrubs, herbs, and graminoids colonizing similarly disturbed patches (Hernandez 1973; Kershaw 1983; Ebersole 1985; Bishop & Chapin 1989). Analyses by Ebersole (1989) in northern Alaska determined that some important early colonists, such as Arctagrostis latifolia, Poa arctica, and many others, were not present in the seed bank at the time of disturbance and were able to disperse into the patches from other areas.

Regardless of the colonization mode of the species occurring on the disturbed patches at all three study sites, vegetative maintenance and spread enable the observed clonal grasses to coalesce into dense swards. These swards appear able to resist the establishment of other species and may provide evidence of competitive exclusion. However, the relationship between disturbance frequency and the maintenance species richness does not appear to fit Huston's (1979) generalization, mainly because most of the mechanical disturbances in this study - at any frequency - resulted in outright reductions in species richness which susbsequently fail to match the levels of controls.

Pickett & White assert that species richness may be reduced in systems experiencing a 'severe disturbance regime' but having low resource bases and/or high levels of environmental stress. It appears that, at least partly, it is the synergistic effect of having both poor soils and severe climatic conditions within high arctic ecosystems that allows even minimal, infrequent impacts to result in significant reductions in species richness. Perhaps more important, as discussed earlier, is the small flora and the limited number of regeneration niches (Grubb 1977) within it.

In situations where species richness has increased over time, such as excessively drained peatlands, it is difficult to translate soil desiccation into frequency. Huston's (1979) and other generalizations by Pickett & White (1985) therefore seem better suited to testing the effects of mechanical disturbances. One of the generalizations by Pickett & White unsupported by the present data is the role of the root mat in what is clearly a 'root biased' system. They contend (1985: 380) that "above-substrate disturbances will alter resource availability most in 'shoot-biased systems but little in 'root-biased' systems. Furthermore, disturbance of insufficient intensity to open the root mat in root-biased systems will have little impact on species coexistence in those systems".

Data from the trampling gradient have revealed steep gradients in macronutrient status among the dominant species, as measured by peak-season foliar analysis, even on lightly and moderately trampled ground where the root mat withstood ≤6 yr of trampling. Soil nutrient analyses revealed similar patterns of response, as did biomass, species richness, and the range of growth forms present. The high cover/abundance of Poa arctica on moderately and lightly trampled ground, where the original root mat was compressed but not opened, is important. It indicates that a common, relatively low-intensity disturbance, which does not result in a rupturing of the root mat, can have long-term consequences for species coexistence. Both Carex aquatilis var. stans and Eriophorum angustifolium still persist in these trampled zones, but only at low cover/abundance values.

In discussing the interactions between two separated patches of the same forest community type, Forman (1981) observed that the transfer of energy and nutrients between such patches, in general, appeared insignificant. However, he also observed that animals, particularly specialists, may forage from patch to patch and that patches thus play an important role in feeding ranges. Clearly this is an issue of scale. At the scale of the individual tundra lowland, both anthropogenic and naturally disturbed patches in this study were invariably richest in terms of plant production for select species and were perennially preferred grazing sites. The repeated use of these patches leaves what amounts to substantial, if extremely local, loadings of nutrients through the deposition of excreta, nesting materials, and other organics, i.e. carcasses.

Studies from tundra meadows and other communities have demonstrated that even moderate grazing can affect several aspects of patch dynamics such as productivity, nutrient cyling, seed banks, and community structure (Fuller et al. 1975; Batzli 1978; Batzli et al. 1980; Henry & Svoboda 1989; Huntly 1991). The evidence in the case of tundra patches does not support the first part of Forman's generalization, since energy transfer among patches, in the form of redistribution of nutrients, did appear to be significant. The reason it was significant was that patches were favored sites for feeding by several species, and for nesting by lemmings.

In summary, rupturing of the root mat is not a precondition for long-term changes in species richness, biomass, and nutrient cycling within the root-biased plant communities of the High Arctic. The role of seed dispersal is generally less of a factor in the structure and composition of high arctic communities, relative to their low arctic counterparts, because germination rates tend to be low. In the context of anthropogenic disturbance, low germination rates combine with reduced habitat heterogeneity and a limited number of growth forms to decrease species richness within patches.

However, recruitment from the seed bank has shown that species which rarely produce viable seed (Alopecurus, Poa spp.) can still be pioneers and may even form dense, homogeneous and persistent swards into which other plants have difficulty establishing.

The plants which occupy the patches are generally long-lived and individual clonal graminoids which have the potential to cover large portions of the patches. The turfs which cover the unexcavated Thule dwellings have probably not changed appreciably in composition in many years, perhaps centuries. The great numbers of large individuals of Salix arctica attest to this stability and the patches shows no signs of shifting toward the adjacent beach ridge assemblage. Given the quantity of peat beneath these patches, there appears little reason they should change in this direction. Neither are the patches resulting from contemporary houses at CR being invaded by species from the adjacent natural vegetation, although here the peat has been removed, buried or severely compressed. In each case the substrate on which the prior community grew no longer exists in its original form. As long as this is the case, there is little reason to expect a return to previous site conditions on a 'human' time scale.

The patches observed at all three study sites were usually at least partially comprised of species absent in the control areas, and have had the net effect of increasing landscape heterogeneity. This was true despite the fact that the patches were almost always poorer in species than the natural matrix within which they occurred, including those subject to an intermediate level of disturbance. Species richness was highest at moderate levels of total biomass, but not for live foliar biomass only, in which case biomass was highest on heavily trampled ground dominated by Alopecurus.

In mechanically disturbed patches of several types, both the colonists and remnant species appeared to be favored for grazing, while the snow-covered areas adjacent to grazed housepads at CR appeared to be favored winter nesting sites for lemmings. Together the housepads and trampled areas have formed a network of patches in which nutrient cycling has been enhanced relative to adjacent controls, even though plant cover is often incomplete on the housepads themselves. Evidence of animal activity was absent from drained areas, but many of the same state variables were significantly altered over large areas resulting in cumulative impacts of much greater proportions than the original impacts.

ii. Contributions to arctic successional theory

a. Evidence in support of the models of arctic vegetation change presented by Svoboda & Henry, Chapin & Shaver, and Walker et al.

Svoboda & Henry's (1987) model

As with patch dynamics, much of the theory pertaining to vegetation change in the Arctic has been derived from observations of natural phenomena and has usually relied on the substitution of 'space for time' (*sensu* Likens 1989) to explain successional changes that were presumed to be extremely slow. However, it has now been several decades since the first large-scale human impacts arrived in the North American Low Arctic and Subarctic (Lawson et al. 1978; Lawson 1982; Kershaw 1983; Ebersole 1985). In the last few years, retrospective studies have led some authors to construct references tables of natural analogues for a variety of anthropogenic disturbances (Walker et al. 1987a; Walker & Walker 1991). There has been no such attempt at long-term synthesis in the High Arctic, not least because large-scale impacts associated with exploratory drilling were not apparent until the early 1970's (Smith & James 1979; French 1980; Bliss & Grulke 1988). However, tracked vehicles had arrived by the mid-1950's and were responsible for significant local damage (Kevan 1971b). Similar impacts have been manifest by many other small-scale anthropogenic disturbance regimes before and since then. As a result, it has remained unclear whether long-term responses to anthropogenic surface disturbance fit existing models of vegetation change derived from studies in the Low Arctic (Chapin & Shaver 1981; Walker et al. 1987a) **(Figs. 1.5 and 1.6)**, and/or the model created specifically for the High Arctic by Svoboda & Henry (1987) **(Fig. 1.7)**.

The basis of the model devised by Svoboda & Henry is the observation that the polar deserts and semi-deserts of the High Arctic comprise 'marginal' environments in which colonizing populations of vascular plants rarely progress beyond the initial invasion phase of succession and that the maintenance of such populations is often tenuous at best. These marginal populations are thus invariably comprised of discrete individuals of pioneer species which fail to compete with one another and depend largely on their individualistic strategies for survival. Competition is equated with an 'ecological warming up' of the system, in which a critical mass of standing crop is attained, leading to habitat improvement, enhanced recruitment, and the eventual replacement of the initial colonists. They argue that with increasing latitude and environmental severity, succession generally shifts from species replacement to species establishment and survival.

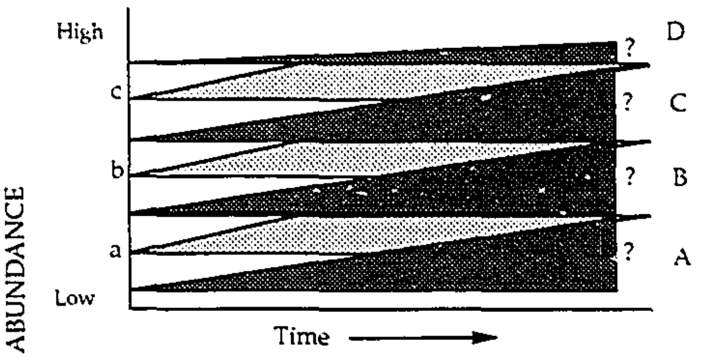
In this study, indicators of high levels of environmental stress were observed on housepads, which comprise marginal environments for primary plant establishment *sensu* Svoboda & Henry. Large, open patches attest to the failure of species to colonize completely either the relatively sterile sands and gravels (**Plate 4.14**) or the extremely compact tundra soils (**Plate 4.13**) after 21 yr. Although numerous caespitose graminoids and forbs were present, excavations revealed that they were generally discrete individuals (**Plate 4.15**) and competitive interaction was not a factor, except in those cases where the grass tufts came into contact with expanding clones of Alopecurus or one another (**Plate 3.7**). In drained areas, where soil desiccation has been severe, populations of many species have become locally extinct or are dying out. However, the successful replacement of these aquatic species by new colonists, and the significant increase in cover/abundance and biomass of Salix spp., indicate that these are not truly marginal environments.

The pattern of colonization in multi-pass tracks subject to the maximum level of disturbance indicates that these sites may also approach marginal environments. After two decades the sole vascular colonists in some of the more hygric places were the foraging tillers of Carex and Eriophorum, which had clearly penetrated from the adjacent control areas and were not established from seed. The sustained presence of even minimal moisture through much of the growing season and patchy bryophyte cover may preclude the characterization of these patches as marginal. Colonization of well-drained tracks, however, tended to follow the pattern observed on housepads where caespitose grasses and forbs had established from seed or viviparous propagules. These were typically small individuals (≤2.5 cm across) of plants such as Phippsia algida and Saxifraga spp., and were separated by distances of ≥20 cm, thus failing to interact competitively. In keeping with the observations of Svoboda & Henry, lichens were absent and bryophytes (i.e. Ditrichum flexicaule) were much less important in terms of cover. When present, bryophytes were generally restricted to the immediate vicinity of the larger tufts. This indicates that their successful establishment was contingent upon the prior existence of the vascular plants, rather than vice versa, and that they were unable to spread without the protection afforded by the larger plants. As on the housepads, seedlings of Alopecurus, where they have become established, appear to be spreading faster than any of the other colonists.

Together these patterns of establishment and spread indicate that housepads and well-drained multi-pass tracks should be considered high resistance environments characterized by directional, non-replacement succession in the model of Svoboda & Henry. Vegetation change in more hygric multi-pass tracks, and under other anthropogenic disturbance regimes, conforms to variations on the 'high resistance' model which are seen in **Fig. 4.1.** All of these pathways emphasize the central role played by initial floristics (Egler 1954) since, although in some cases propagules were lacking at the cessation of human activity, a so-called primary succession, it is the initial colonists which have clearly directed the course of vegetation change.

The present data do not appear to follow the sequencing depicted by directional replacement model for low resistance environments by Svoboda & Henry. On the contrary, the unexcavated Thule pads indicate that, in some cases, the pioneers may persist and the succession may stagnate at a given stage, a feature of non-directional, non-replacement change in extreme environments. Similar 'stagnant successions' have been reported for natural disturbances in extreme environments in the Fennoscandian alpine (Muller 1952; Matthews & Whittaker 1987). Rigorous floristic sampling of a cross-section of a number of younger archaeological sites in the High Arctic would help to confirm this for the region. However, the plant associations for the

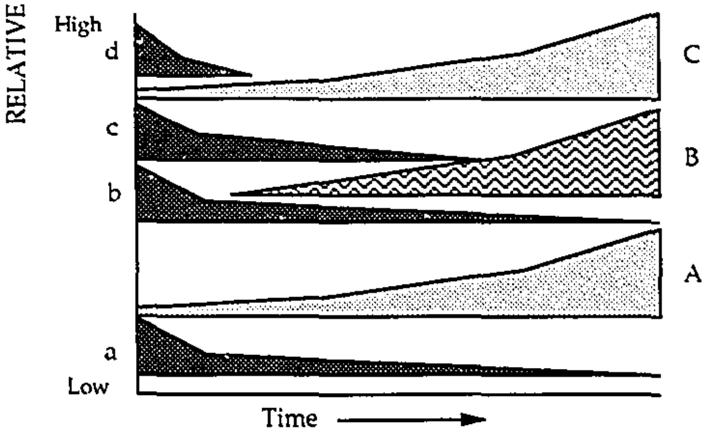
Fig. 5.1 - Synthetic diagram of vegetation change in various anthropogenic patches at CR and TL



Excavated Thule dwelling

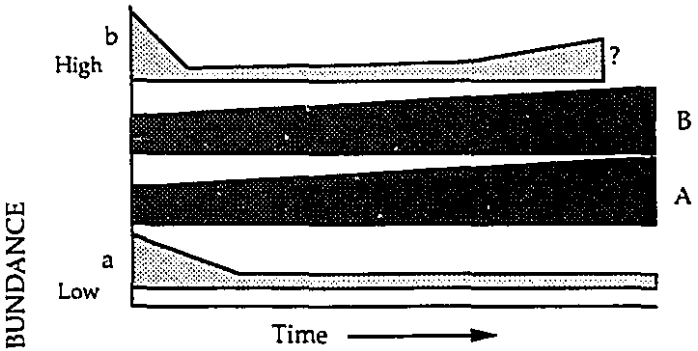
Characteristic species

A= Alo alp; B= Poa spp.;
C= Sal arc;
D= Various ruderal bryophytes
a= Pap rad, Sax spp.;
b= Cer alp, Ste spp.;
c= Various ruderal bryophytes



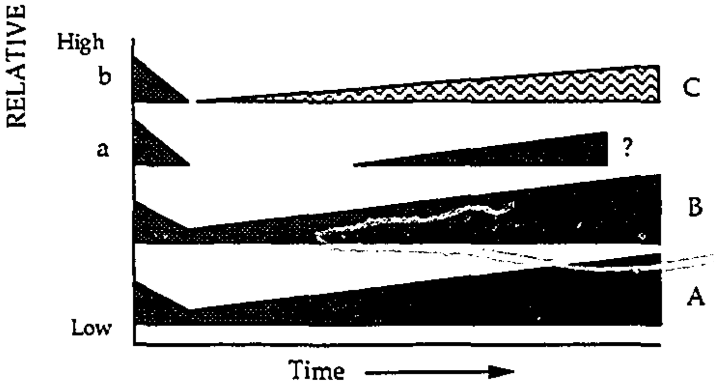
Moderate trampling in mesic Sphagnum meadow

A=Poa spp.; B= Alo alp;
C= Aul spp.
a= Car aqu; b= Eri ang;
c= Sal spp.; d= Sph spp.



Single-pass vehicle tracks

A= Car aqu; B= Eri ang
a= Sph spp.; b= Sal spp.



Multi-pass vehicle tracks (hygric)

A= Car aqu; B= Eri ang;
C= Various ruderal bryophytes
a= Sal spp.; b= Sph spp.

▇ and ▒ = Species occurring in the initial flora

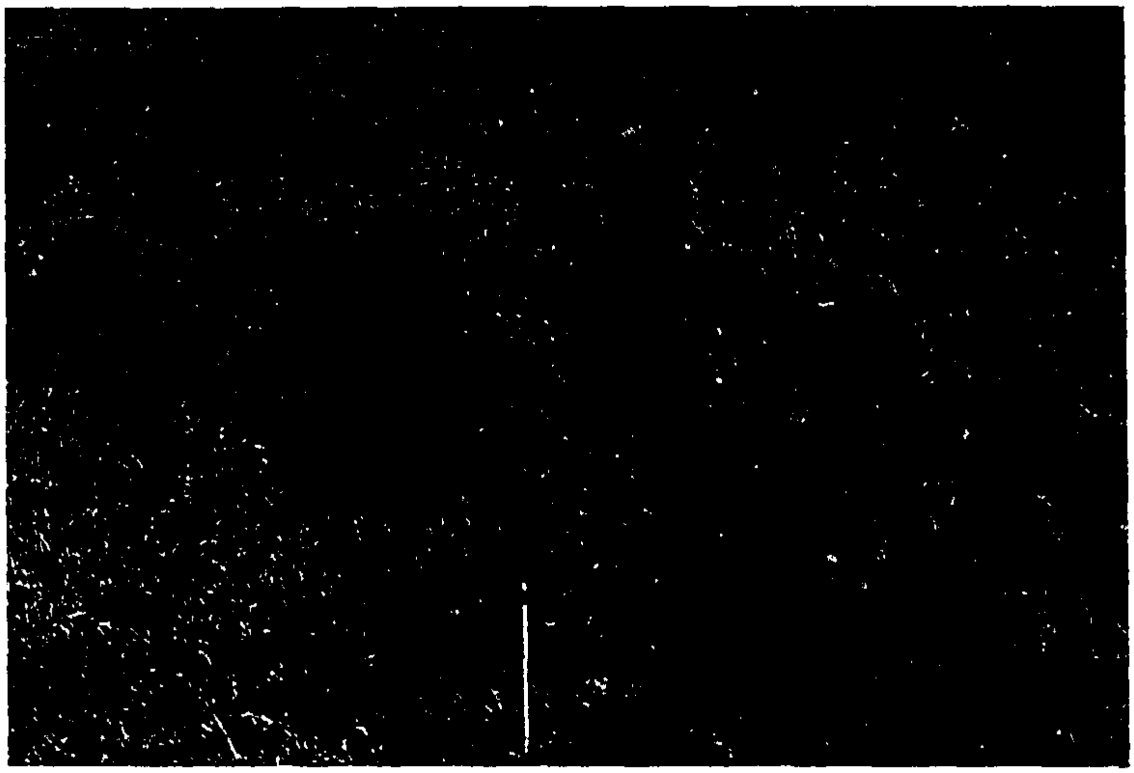
▨ = Colonists not occurring in the initial flora ? = Projected changes few North American low arctic sites represented in the literature appear strikingly similar to those reported here (Fredskild 1961; McCartney 1979; Daniëls 1992, pers. comm.). The implication is that clonal rhizomatous graminoids and Salix, both long-lived, are present from the beginning and once they assume dominance, as discussed earlier, further colonization is inhibited. In warmer regions, such as the Aleutians (Bank 1953), the flora, the number of growth forms, and the number of potential associations and successional pathways become much richer.

Chapin & Shaver's (1981) model

Studies of vehicular disturbance in mesic low arctic and subarctic tundra have often noted increases in vascular plant productivity (Hernandez 1973; Wein & Bliss 1973; Chapin & Shaver 1981). The prominence of green vegetation, and a reduction in dead standing crop, result in what Abele et al. (1984) have termed the 'green belt' effect (**Plate 3.9**). This response is common but certainly not ubiquitous, since many tracks are much more cryptic in their appearance (**Plates 5.1** and **5.2**), if not in terms of their composition and production. The actual physiological linkages between vehicle traffic and increased plant productivity are complex. Low arctic studies have found enhanced productivity to be associated with various substrate changes, such as increases in soil bulk density (Gersper & Challinor 1975), radiation absorption, soil temperature and thaw depth (Bliss & Wein 1972; Hernandez 1973; Haag & Bliss 1974; Chapin & Shaver 1981), and nutrient availability (Challinor & Gersper 1975; Chapin & Shaver 1981; Herbein & Neal 1990). Based primarily on short-term (<10 yr) studies in northern Alaska, Chapin & Shaver produced a graphic model to explain in a general manner the causal

Plate 5.1 - General aspect of multi-pass tracks in hydric-hygric meadow at TL, barely visible after nearly two decades (**Stand 3**). Stake marks center of berm between two tracks. Minimal green belting is evident. Note muskoxen grazing in background. Photo date: 24 July 1989.

Plate 5.2 - General aspect of multi-pass tracks in hygric hummocky meadow at TL, barely visible after nearly two decades with only minimal green belting (**Stand 7**). Stake marks center of berm between two tracks. If not for the shadows from the berms, the tracks would appear to blend in completely. However, species richness and biomass were significantly reduced in the tracks, primarily because of the absence of woody species, although biomass of graminoids was increased. Photo date: 24 July 1989.



relationships leading to increased productivity (**Fig. 1.5**). Similar models have been presented elsewhere (Webber et al. 1980). Since the present data have revealed that biomass was invariably reduced in both young (3 yr) and old (ca. 20 yr) tracks in the High Arctic (Forbes 1992b), it is worth considering the reason(s) behind this difference.

Of the factors listed by Chapin & Shaver which were measured in this study, many match the direction of change indicated by them. To begin, the immediate effect of all tracks was decreased vegetative cover, although increased bulk density was not a factor on single-pass tracks. Soil temperatures were significantly increased in all multi-pass tracks in mesic meadows, while differences were insignificant in wet meadows and in some single-pass tracks in mesic meadows.

Patterns for depth of thaw generally corresponded to those of soil temperature. Root growth was not measured, nor were 'available' soil nutrients, though extractable nutrients were higher in single and multi-pass tracks through mesic meadows at CR. Leaf macronutrient status was higher for some nutrients in some species in patches relative to controls. Shoot densities for some species appeared increased and flowering density was significantly higher for Eriophorum angustifolium in some multi-pass tracks (**Plate 3.18**). Species composition was altered in virtually every case. Photosynthesis was not measured. Compared to controls, greater biomass was measured for select species (i.e. rhizomatous graminoids). However, these gains were rarely enough to match or surpass predisturbance levels of biomass, even in the wettest meadows at TL where above-ground biomass of Eriophorum angustifolium remained significantly reduced.

Although nutrient concentrations tend to be higher in the tissues of high arctic plants compared to the low arctic (Dowding et al. 1981), overall biomass is generally reduced with increasing latitude, even in structurally similar lowland meadow communities with somewhat ameliorated mesoclimatic conditions (Wielgolaski et al. 1981). It may be that, in the absence of seedlings on disturbed mesic substrates, the nutrients available from the decaying organic mat have been exploited by the remnant species by default, thus contributing to elevated graminoid biomass and overall standing crops of macronutrients.

Total standing crop was reported to increase in six out of eight mesic and wet vehicle tracks surveyed by Chapin & Shaver. These findings contrast sharply with the present data from Devon and Baffin Islands. The differences are at least partly related to the failure of dicotyledons to colonize even small bare patches in the High Arctic. Most of the few seedlings of Salix arctica observed were limited to the tops of remnant mesic hummocks in single-pass tracks. No seedlings of other woody dicots were observed. Both foliar and woody tissues of dicots were major components of the undisturbed standing crop, particularly in hummocky meadows.

Biomass levels among sedges were somewhat greater for Carex spp. and Eriophorum angustifolium at TL relative to the communities sampled by Chapin & Shaver. However, the highest total standing crops measured in tracks in this study were generally less, often considerably so, than those reported by Chapin & Shaver. In several cases, according to their data, the biomass of E. angustifolium alone was three- to seven-fold greater than the highest levels measured in this study. Thus, despite significant increases in tracked areas, the gains in biomass among rhizomatous graminoids in this study have consistently failed to match levels reported by Chapin & Shaver in the Low Arctic and used for their model. In addition, the widespread failure of woody plants of any kind to regenerate is a hallmark of the tracks observed in this study and is a factor of great importance in both the short- and long-term.

The protracted responses of both monocots and dicots to disturbance are consistent with the general levels of natural productivity and the reproductive ecologies of the species involved in the sense that these have previously been shown to vary with bioclimatic zonation. Together these aspects of natural reponse to vehicle disturbance explain why the present data do not fit the model of Chapin & Shaver as it pertains to community productivity. On the other hand, the individual gains of the rhizomatous sedges do appear to match the model, even if the magnitude of the increases was not as great. The implication is that the regenerative capacity of high arctic meadows is significantly diminished compared to their low arctic counterparts, at least in the context of vehicle tracks (Forbes 1992b).

The model of Walker et al. (1987a)

Walker et al. have devised a general graphic model (**Fig. 1.6**) to identify successional pathways of natural and assisted regeneration of vascular vegetation based on data from a number of studies in northern Alaska and adjacent low arctic Canada. Central to each of their successional responses is the concept of 'recovery', characterized by them (Walker et al. 1987a: 6) as ". . . the process by which an ecosystem achieves relative biological and physical stability following a disturbance. The final stage of recovery is a healthy, functioning ecosystem that can maintain a steady-state equilibrium over a few decades . . . Although recovery may involve several successive steps, it does not necessarily result in a climatic climax (*sensu* Clements 1928) or even a plant community similar to one that previously existed . . . Complete recovery occurs only when the ecosystem has regained its original productivity and species composition". Despite a lack of consensus on what constitute 'steady-state' and 'climax' in arctic tundra, the model has appeal because it provides ancillary information with which to differentiate each of the various responses.

Most of the patches in the present study comprise variations of 'negative functional recovery' as defined by Walker et al., except for the Thule dwellings and the restored vehicle tracks, which are examples of 'positive functional recovery', and the chemical dump, which shows no recovery. In each case the resilience threshold of the community appears to have been exceeded, although the restoration attempt has been largely successful in restoring much of the original plant cover, if not the predisturbance levels of biomass and species richness.

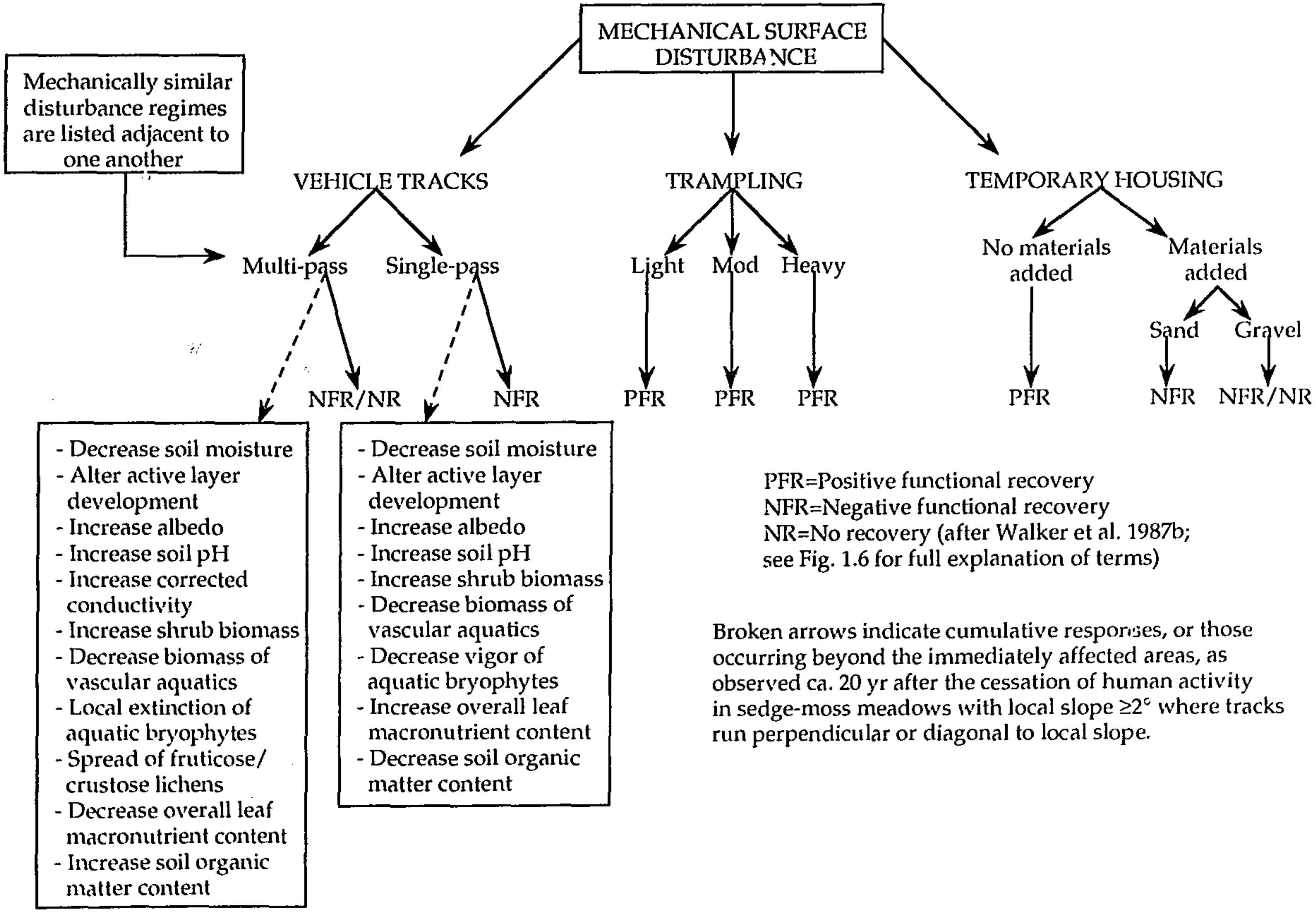
The treading communities do not necessarily fit into a single category. Although some moderately and heavily trampled meadows exhibited greater biomass than the original communities, the species compositions differed dramatically and the displaced species did not appear to be recolonizing the patches, indicating that the resilience threshold had indeed been exceeded. In these patches, as on palaeo and contemporary housepads, multi-pass tracks, and sites of chemical dumping, the vegetation may have no chance of returning to its original state. As the soils data have shown, this is at least partly because the set of conditions leading to the original community no longer exists (Webber & Ives 1978; Komárková & Webber 1978). In drained areas, it is not certain that a restoration of the original slope hydrology would lead to a return of the original community.

What is remarkable about the disturbances in this study is that even the lowest levels of impact appear to have exceeded the resilience threshold in each of the communities investigated, at least on a human time scale. In single-pass tracks, for example, the original community has failed to regenerate and vascular biomass remains significantly reduced. On lightly trampled ground total biomass was unchanged, but species composition was different from the original community. In contrast, patchy disturbances in the Low Arctic are often colonized by seedlings of many of the original species (e.g Eriophorum vaginatum, Salix spp.) and may quickly equal or exceed the original level of productivity at a site. In addition, both restoration attempts and natural successions in these more complex communities have come close to recreating the original vegetation in some cases (Hernandez 1973; Chapin & Chapin 1980; Chapin & Shaver 1981; Ebersole 1989; McGraw & Vavreck 1989; McKendrick 1991).

As with the previous model, the present data indicate the greatly reduced potential for natural and assisted recovery in the High Arctic compared to the Low Arctic and that resilience to human impact is minimal in all but the wettest lowland plant communities. Although each of the models presented emphasizes the biotic components of vegetation change, the impacts reported here have demonstrated the importance of disturbance to the abiotic environment. The relationships between some of the disturbances and their associated pathways of vegetation and environmental change are seen in **Fig. 4.2.** Cumulative impacts are emphasized because at this time they represent the most significant spatial changes with respect to scale of impact: scale of response.

Fig. 5.2 - Synthetic diagram of vegetation and environmental responses to various anthropogenic disturbance regimes, with emphasis on cumulative impacts. Environmental impacts resulting from pedestrian trampling and housepads are not treated here because of the highly temporal and variable nature the responses. For example, the airphoto analysis (see **Plate 2.10**) has shown that, within the first few years after deconstruction, the housepads remained virtually devoid of vegetation cover. As a result, those with added material, such as sand and gravel, had an especially high albedo. Those with organic soils and no materials added had a lower albedo. Later (see **Plate 2.7**), as the sand/gravel pads were colonized by even the thinnest veneer of vegetation, their albedo was decreased. As the present data have revealed, soil temperatures, active layer depth, and soil pH were significantly higher on all pads and trampled meadows compared to adjacent undisturbed ground, while soil moisture was much lower. However, it is not certain that each of these anomalies dates from the cessation of human activity. It is highly probable, for instance, that soil temperature regimes changed considerably with the colonization of sandy housepads.

PATHWAYS OF NATURAL RECOVERY FOLLOWING ANTHROPOGENIC DISTURBANCE



PFR=Positive functional recovery
NFR=Negative functional recovery
NR=No recovery (after Walker et al. 1987b; see Fig. 1.6 for full explanation of terms)

Broken arrows indicate cumulative responses, or those occurring beyond the immediately affected areas, as observed ca. 20 yr after the cessation of human activity in sedge-moss meadows with local slope ≥2° where tracks run perpendicular or diagonal to local slope.

5.2 Original contributions

The present study makes several original contributions to knowledge. Of these, the following three are considered the most important.

(1) The study provides empirical testing on a regional scale of three separate graphic models of arctic vegetation change. These include (a) the model of Chapin & Shaver (1981), which is empirically derived from mostly short-term (≤7 yr) studies in low and subarctic Alaskan sites. It specifically addresses the effects of vehicle tracks on tundra plant productivity; (b) a more general model of disturbance and vegetation response, also developed in northern Alaska, presented by Walker et al. (1987); (c) the model of Svoboda & Henry (1987), which sets out hypotheses about the driving forces and resistances which direct succession in marginal high arctic environments. The latter model had not previously been applied to anthropogenic disturbance.

The data have allowed local and biogeographic adjustment of all three models. In agreement with the Svoboda & Henry model (1987), the evidence indicates that life history characteristics are perhaps the most crucial factors in determining the nature of vegetation change within high arctic tundra. In particular, species' growth form appeared critical in directing the spatial and temporal responses of lowland plant communities to anthropogenic disturbance.

(2) The present study also provides detailed data on long-term responses at the community level. Most terrestrial communities and ecosystems are naturally patchy. However, even small-scale changes

superimposed on the existing mosaic through human agency may result in structural and functional systemic changes at the level of the landscape. The study provides compelling evidence that anthropogenic heterogeneity, manifest within the first few years following disturbance, may persist for decades or even centuries. For certain cumulative impacts, the leap from scale-of-impact to scale-of-response may encompass several orders of magnitude.

(3) Last, the study provides unique data on nutrient cycling in the context of anthropogenic disturbance. Nutrient cycling is an important aspect of patch dynamics. The nutrient status and standing crop of the dominant plants determines, in part, the degree to which patches become sites of intensive grazing by vertebrate herbivores.

The data demonstrate that even small patches (≤50 cm across), lightly disturbed by humans, may undergo fundamental edaphic and vegetational changes which appear augmented and perennated by intensive animal activity. That these effects are detectable ≥21 years after the cessation of human activity is cause for concern in a region where coastal lowlands and other comparably productive landscapes comprise ≤3% of the total land area.

The findings have challenged some generally accepted tenets of patch theory, such as the intermediate disturbance hypothesis and the defining criteria for disturbance in root-biased systems, at least in the context of mechanical disturbance. On the other hand, the findings also affirm the importance of patches in the feeding ranges of vertebrate herbivores, as suggested by Forman (1981).

5.3 Conclusions

The coastal lowlands of CR, TL and RB have afforded an excellent opportunity to study natural tundra responses to a wide range of anthropogenic disturbances of known age which are common throughout the High Arctic. This study significantly increases the information base of arctic disturbance ecology by addressing a greater variety of small-scale impacts than appear in the literature. That these impacts were much older than have previously been investigated is important in a region with plant communities dominated by long-lived perennials and where continuous permafrost is an important limiting factor. By employing complete floristic surveys and multivariate analyses to compare geobotanically contrasting sites within one of the region's largest single bioclimatic zones, the present data provide the level of detail needed to properly assess the ecological consequences and the potential for long-term recovery within the most productive meadow habitats over a sizable portion of the Canadian High Arctic. These data will be important in the planning of developments of different types.

The investigated disturbance regimes included (1) vehicle traffic, (2) peatlands drained as a result of (1) in sloped wetlands, (3) attempted restorations of (1), (4) pedestrian trampling, (5) different types of temporary (i.e. low-tech) housing construction, (6) unexcavated and recently excavated Thule archaeological sites (unexcavated sites were recently dated at ≈800 yr since occupation, Helmer 1991), and (7) chemical dumping. At the time of sampling, the contemporary disturbances ranged in age from 3 to 21 yr. Of these, only vehicle tracks and chemical dumping (drilling fluids) had previously been investigated in any detail within the region (Kevan 1971b;

Babb 1972b; Babb & Bliss 1974a; Barrett 1975; Addison & Bell 1976; Smith & James 1979; French 1980), but these studies were mostly limited to changes in vascular plant cover and thaw depth for periods of one to 11 yr.

TWINSPAN differentiated between naturally occurring meadow vegetation on Baffin and Devon Islands. These two data sets were further split into distinct groups representing gradients of relative moisture and microtopography. A total of 20 floristically similar noda were identified and the results were corroborated by DECORANA ordinations. In the first such application in the High Arctic, anthropogenically disturbed vegetation was classified by TWINSPAN into 41 noda. The noda were separated with remarkable accuracy by disturbance regime with little difference apparent between similarly disturbed patches of different ages.

Unexcavated Thule dwellings on Devon Island were found to be floristically similar to lightly trampled meadows on Baffin Island, indicating the limited number of ruderal species within the flora and demonstrating their abililty to form dense, persistent swards. Although the data had to be broken into subsets to yield interpretable ordination biplots, the results consistently corroborated the TWINSPAN classification through numerous random and calculated splits of the data.

Data subsets were subject to multivariate analysis of vegetation-environment relationships with CANOCO, the first application of this widely-used tool to problems of high arctic disturbance ecology. Although the results did not always explain the majority of compositional variation among patches, this was expected given the great number of potential interactions and the wide range of disturbance regimes surveyed. However, of the suite of eight environmental variables, several of these were important in various data subsets.

Some variables, such as slope, may have explained a large proportion of the variation in the natural vegetation, but clearly contained information from a range of complex environmental factors such as exposure, snow depth, and albedo. In mesic habitats, the effects of even minimal mechanical disturbance tended to exert a greater control over vegetation composition than factors such as moisture or soil pH. In such cases the disturbance gradient seemed to represent another complex of environmental gradients. In drained peatlands, moisture was less closely correlated with the observed variations in vegetation composition than factors such as pH, active layer depth and soil temperature.

With or without mechanical disturbance, increases in soil pH were significantly correlated with an increase in the frequencies of bryophytes normally associated with calcareous habitats, a pattern observed in natural disturbances which affect substrate chemistry (Jonasson 1986). Ebersole (1985) felt that the assemblage of plants on a recently disturbed site gives a less precise indication of the environment at that site than the community on a site that has been disturbed for 'some time'. Apparently, two decades was enough time for at least some cryptogamic colonists of narrow ecological amplitude to establish on the disturbances reported here. The present data have also indicated that age since abandonment is less important than the intensity of the initial impact and that ruderal colonists of wide ecological amplitude, particularly vascular plants, may persist indefinitely.

In addition to multivariate analyses, univariate analyses have addressed a range of biotic and abiotic features, such as substrate thermal characteristics, surface albedo, community productivity and nutrition, herbivore manuring, and changes in the abundances of various plant growth forms. From the perspective of patch dynamics, the data have provided insights from the previously unaddressed but ecologically important tundra ecoregion (*sensu* Bailey & Hogg 1986), and have demonstrated the importance of cumulative impacts. The data have allowed the most concrete test to date of Svoboda & Henry's (1987) model relating to succession in marginal arctic environment, as well as allowing tests of two models treating pathways of vegetation change following anthropogenic disturbance which had previously been applied only in the Low Arctic.

Based on the present data and the existing literature, it is possible to recognize geographic variation and similarities in tundra responses to disturbance between the High Arctic and the Low Arctic. In considering the above three models, it is now clear that there are stark differences between these two regions with respect to human impact and tundra recovery. This reveals that there is a geography of natural tundra recovery. There was little evidence from the present data that natural recovery occurs on a human time scale, despite a lack of thermal erosion typical of low arctic sites with more prevalent ice-rich permafrost.

Total biomass, species richness, and sexual reproduction were dramatically reduced in both natural and disturbed communities in this study compared to low arctic sites reported in the literature. In general, the observed patterns of vegetation change fit more closely the model of directional, non-replacement succession for high resistance environments (i.e. polar semi-deserts) than the directional, replacement succession hypothesized for the Low Arctic by Svoboda & Henry. Unlike the Low Arctic, increases in productivity within patches of any kind were rare and were largely due to colonizing species which were unimportant or absent in the original communities.

Vegetation and soil changes in vehicle tracks were often similar to those modelled for the Low Arctic by Chapin & Shaver, but the magnitude of change was invariably reduced, and community productivity did not increase as it did in northern Alaska. Responses to drainage were variable depending on local slope hydrology prior to disturbance, but the general effect of eliminating aquatics and stimulating the growth of shrubs and lichens was similar to that reported for subarctic regions. With some exceptions, most of the patches fit the description of 'negative functional recovery' defined by Walker et al.

As in the Low Arctic, herbivores appeared to play an important role in the redistribution of nutrients and responded favorably to patchy disturbances which increased plant productivity and nutrition. However, the effects which were noted as being relatively ephemeral in the Low Arctic have continued to be significant after 21 yr in the High Arctic. This difference may be partly due to slower nutrient turnover in the latter region, as well as edaphic changes (i.e. compaction) which were not factors in the fertilization experiments of Schultz (1969), for example.

It was also possible to recognize geographic variation and similarities among tundra responses to disturbance within the High Arctic. The multivariate analyses demonstrated the considerable ecological amplitudes of many of the vascular plants in coastal lowlands, most of which were included in Henry's (1992) 'core group' of meadow species in the northern and central Queen Elizabeth Islands. However, cryptogams, particularly bryophytes, were critical in the geographic differentiation of the various lowlands.

Cryptogams were also essential to characterizing patchy variations in vegetation composition along disturbance gradients within each lowland and responded to subtle changes in soil moisture and chemistry. The high frequencies and narrow ecological amplitudes of bryophytes, in particular, were largely responsible for the success of TWINSPAN and DECORANA in differentiating among both natural and anthropogenic plant communities.

While there was considerable variation among disturbance responses in different vegetation types, even in the wettest meadows anthropogenic patches were distinguishable in classification and ordination analyses. Such separation was evident even where biomass had come close to matching that of controls, as was the case in sites of naturally recovering and restored wet meadows. The level of detail achieved in these analyses illustrates that monitoring of floristic responses to human impact is possible at the community or patch scale and readily applicable to more geographic multivariate comparisons among widely disjunct study sites. This was done with meso-scale environmental data during the IBP (French 1981).

The importance of species' life histories was demonstrated through excavations and an analysis of the numbers of growth forms present within each patch. These results corroborate Svoboda & Henry's view of the overriding importance of population life history characteristics in the High Arctic. Even with a lack of sexual propagation, initial floristics (*sensu* Egler 1954) appeared critical in determining the composition of patches of all types, including those characterized by remnant floras and ruderal colonists.

Beyond initial floristics, the role of lemmings and other herbivores seemed to be critical in directing vegetation change on several patches, particularly those characterized by ruderal graminoids such as Alopecurus. It appeared that locally intense grazing, nesting, and excretions were factors in maintaining the dense swards of graminoids which dominated these patches. While it is certain that human impact provides the initial kick, triggering 'succession', herbivores seem to play an important role in the community-level response and may contribute to the inability of a given patch to return to its original state.

Despite evidence and assertions that natural disturbances often provide valid analogues for anthropogenic disturbances (McKendrick 1981; Racine & Johnson 1988; Walker et al. 1987a; Walker & Walker 1991), the floristic data supported this only in the most general sense. The floras of several natural disturbances were investigated at CR, TL, and other sites (**Appendix 62**).

Noticeably absent were observations of trails from large herbivores such as caribou, which do not reach high population densities in the archipelago. However, during a recent visit to Yamal Peninsula in northwest Siberia I had the opportunity to survey trails made from the concentrated trampling of several thousand head of reindeer in hummocky meadows of similar composition and structure to those in this study. The trails were identical in appearance to those reported for caribou habitat in northern Alaska by Racine & Johnson (1988). However, the actual impacts on vegetation and soils were more similar to those resulting from ATC's (cf. Racine & Johnson; Holt & Bay 1983; Bay & Holt 1985), and were not analagous to the vehicles in this study.

Of the natural disturbances observed, none exhibited vegetation cover analagous in composition or structure to the pedestrian trampled meadows, housepads, vehicle tracks, or the chemical dump. The drained peatlands were in transition to more mesic-xeric assemblages. Yet, while these appeared somewhat similar floristically to drier, naturally occurring communities, it is not certain that the human-initiated edaphic/thermal changes and nutrient cycles have natural analogues.

In general, the long-term data gathered here support short-term predictions (Kevan 1971a, b; Babb & Bliss 1974a, b) that high arctic sites are more susceptible to anthropogenic disturbance with a substantially reduced potential for either compositional recovery or functional recovery (return to original productivity). The ability to extrapolate results from the present study to other sites in the Canadian Arctic Archipelago will depend on general physiography and climate, as well as local substrate conditions and plant communities.

Physiographically, climatically, and geobotanically, CR is representative of the lowlands of eastern Baffin and adjacent Bylot Island (Polunin 1948; Maxwell 1980; Sempels 1982; Edlund 1987). The results from CR will be most applicable to other gently sloping (2-5°) lowlands on fairly fine-grained and moderately well-drained siliceous substrates with enough moisture from melting snow or other sources for hummocky, oligotrophic peatlands to develop. In addition, the snow patches sampled at CR (local slope 0-1.5°) will be representative of many such sites in the Baffin region with an open, non-hummocky plant cover and mildly acidic, poorly developed soils which dry out rather quickly after the snow disappears. The housepads with materials added along the coast at CR are probably representative of any such temporary structures along the beaches and beach ridges of Baffin and other islands. The chemical dumpsite is representative of several abandoned and still-active units of the 'Joint Arctic Weather Stations' scattered throughout Baffin and the Queen Elizabeth Islands (Stossel 1991, pers. comm.).

TL is bioclimatically similar to CR (Edlund 1987), but physiographically and geobotanically it is more representative of adjacent lowlands on northern Devon Island and other lowlands in the central and eastern Queen Elizabeth Islands (Bliss 1977; Sheard & Geale 1983a, b; Henry 1987, 1990). The results from the meadows at TL will be applicable to other sites with moderately poor to poorly drained fine-grained soils ranging from mildly alkaline to circumneutral and with a mean July air temperature of ca. 4°C. The remains of the Thule winter dwellings at TL and RB are similar in terms of general structure and age to others in the study area and elsewhere in the region (Schlederman 1976; Sclederman & Nash 1977; Helmer 1991).

The composition and productivity of beach ridge plant communities within a single lowland such as TL have been shown to vary with regard to age (Svoboda 1977). However, several studies have demonstrated that the plant communities found on the calcareous cobble substrates which commonly occur in the central and eastern portion of the northern islands tend to be dominated by similar groups of species within each life form (Steere 1951; Schofield & Cody 1955; Arkay 1972; Kuc 1973; Svoboda 1977; Thomson 1982; Sheard & Geale 1983a).

The disturbances reported here are generally of small spatial scale compared to full-scale industrial development. However, the data are unambiguous in demonstrating that even low-intensity, circumscribed anthropogenic patches can result in community-level changes which are long-lasting on the scale of the plant, animal, and human populations involved. Even minimal disturbances have the ability to spread far beyond the point of initial impact.

Despite evidence that many of these patches are not recovering to predisturbance levels of composition, cover, and productivity, at least some have proven extremely dynamic by encouraging locally intense herbivore activity which has, in turn, resulted in a pattern of nutrient redistribution which did not exist before. That these patterns persist after more than two decades sets them apart from their low arctic counterparts, where pulse loadings of nutrients into local communities have proved ephemeral by comparison. Only the wettest meadows show signs of returning to the original communities, yet even these have not fully recovered. Recovery of the original plant communities is ultimately dependent on the recovery of the soils, many of which have experienced substantial structural changes. It is unlikely that the more mesic patches will recover in the foreseeable future without assistance.

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APPENDIX 1A

LIST OF VASCULAR PLANTS (52 taxa) COLLECTED AT CLYDE RIVER with abbreviations used in all multivariate analyses and floristic tables

Nomenclature follows Porsild & Cody (1980) except where noted.

Alo alp - Alopecurus alpinus
Arc lat - Arctagrostis latifolia ssp. latifolia
Car bel - Cardamine belladifolia
Car aqu - Carex aquatilis var. stans *
Car big - C. bigelowii *
Car mem - C. membranacea
Car mis - C. misandra
Cas tet - Cassiope tetragona
Cer alp - Cerastium alpinum
Coc off - Cochlearia officinalis ssp. groenlandica
Dra lac - Draba lactea
Dra niv - D. nivalis
Dry int - Dryas integrifolia
Dup fis - Dupontia fisheri ssp. psilosantha
Emp nig - Empetrum nigrum ssp. hermaphroditum
Epi lat - Epilobium latifolium
Eri ang - Eriophorum angustifolium
Eri sch - E. scheuchzeri
Eut edw - Eutrema edwardsii
Fes bra - Festuca brachyphylla
Hie alp - Hierochloë alpina
Junc big - Juncus biglumis
Luz con - Luzula confusa
Luz niv - L. nivalis
Lyc sel - Lycopodium selago
Min rub - Minuartia rubella
Oxy dig - Oxyria digyna
Pap rad - Papaver radicatum
Ped hir - Pedicularis hirsuta
Phi alg - Phippsia algida
Pleu sab - Pleuropogon sabineii
Poa arc - Poa arctica
Pol viv - Polygonum viviparum
Pyr gra - Pyrola grandiflora
Puc lan - Puccinellia langeana
Puc phr - P. phryganodes
Ran niv - Ranunculus nivalis
Ran pyg - R. pygmaeus
Sal arc - Salix arctica

Sal her -	S. herbacea
Sal ret -	S. reticulata
Sax cer -	Saxifraga cernua
Sax fol -	S. foliolosa
Sax opp -	S. oppositifolia
Sax niv -	S. nivalis
Sax riv -	S. rivularis
Sil ura -	Silene uralensis (Rupr.) Bocquet (Melandrium apetalum)
Sil aca -	S. acaulis ssp. acaulis
Ste edw -	Stellaria edwardsii
Ste hum -	S. humifusa
Ste lon -	S. longipes
Tar lac -	Taraxacum lacerum
Vac uli -	Vaccinium uliginosum

* These two sedges are widespread circumpolar members of the Acutae section of the Cyperaceae. They are taxonomically complex and have a reputation for hybridization within the study area and in many other regions (Polunin 1940; Duman & Kryszczuk 1958; Faulkner 1973; Standley 1985). My own collections and observations were similar to those of Drury (1962) on Bylot Island. Some of the material appeared transitional between the two taxa, but the character types for each were generally well-differentiated by habitat. Both occupied turfy tundra. However, *Carex aquatilis* var. *stans* was generally better developed on wetter, moderately acidic substrates, while *C. bigelowii* was common in more mesic-xeric, mildly acidic substrates. The latter habitat was rarely included in the stands surveyed and the vast majority of the material sampled was *C. aquatilis* var. *stans*.

APPENDIX 1B

LIST OF VASCULAR PLANTS (51 taxa) COLLECTED AT TRUELOVE LOWLAND
Abbreviations as above except where noted

	Alopecurus alpinus
	Arctagrostis latifolia ssp. latifolia
Bra tho -	Braya thorild-wulfii
	Cardamine belladifolia
	Carex aquatilis var. stans
	C. bigelowii
	C. membranacea
	C. misandra
Car nar -	C. nardina
	Cassiope tetragona
	Cerastium alpinum
	Cochlearia officinalis ssp. groenlandica

Dra cor - Draba corymbosa
D. lactea
Dryas integrifolia
Dupontia fisheri ssp. psilosantha
Eriophorum angustifolium
E. scheuchzeri
Eri tri - E. triste
Equ arv - Equisetum arvense
Eutrema edwardsii
Juncus biglumis
Luzula confusa
L. nivalis
Min bif - Minuartia biflora
M. rubella
Oxyria digyna
Papaver radicatum
Ped arc - Pedicularis arctica
Ped cap - P. capitata
Ped lan - P. lanata
Ped sud - P. sudetica
Phippsia algida
Poa abb - Poa abbreviata
P. arctica
Polygonum viviparum
Ran hyp - Ranunculus hyperboreus
Sag niv - Sagina nivalis (Lindbl.) Fries
Salix arctica
S. reticulata
Sax cae - Saxifraga caespitosa
S. cernua
S. foliolosa
Sax hir - S. hirculus var. propinqua
S. nivalis
S. oppositifolia
S. rivularis
Silene uralensis (Rupr.) Bocquet (Melandrium apetalum)
Stellaria longipes
Tar phy - Taraxacum phytmatocarpum
Tri spi - Trisetum spicatum

APPENDIX 1C

LIST OF VASCULAR PLANTS (10 taxa) COLLECTED AT RESOLUTE BAY
Abbreviations as above except where noted

Alopecurus alpinus
Cerastium alpinum
Draba corymbosa
Juncus biglumis
Papaver radicatum
Poa alp - Poa alpigena var. colpodea
Salix arctica
Saxifraga cernua
S. oppositifolia
Stellaria longipes

APPENDIX 2A

LIST OF BRYOPHYTES (51 taxa) COLLECTED AT CLYDE RIVER

Nomenclature for mosses follows Vitt (1975) except where otherwise noted and *, which follow Steere (1978). Sphagnaceae follow Crum (1986). Hepaticae follow Schuster & Damsholt (1974).

Aul acu - Aulacomnium acuminatum
Aul pal - A. palustre
Aul tur - A. turgidum
Bar ith - Bartramia ithyphylla
Bli acu - Blindia acuta
Bra gro - Brachythecium groenlandicum *
Bra sal - B. salebrosum *
Bra tur - B. turgidum
Bry spp - Bryum spp.
Bry arc - B. argenteum
Bry cal - B. calophyllum *
Bry cry - B. cryophyllum
Bry pse - B. pseudotriquetrum
Cal sar - Calliergon sarmentosum
Cal str - C. stramineum
Cer pur - Ceratodon purpureus
Cir cir - Cirriphyllum cirrosum
Con tet - Conostomum tetragonum
Des hei - Desmatodon heimii var. arctica
Dic ang - Dicranum angustum
Dic elo - D. elongatum
Dic spa - D. spadiceum *
Dit fle - Ditrichum flexicaule
Dre bad - Drepanocladus badius *
Dre rev - D. revolvens
Dre unc - D. uncinatus
Hyl spl - Hylocomium splendens
Hyp bam - Hypnum bambergeri
Iso pul - Isopterigium pulchellum
Mee uli - Meesia uliginosa *
Onc wah - Oncophorus wahlenbergii
Phi fon - Philonotis fontana var. pumila
Pla med - Plagiomnium medium ssp. curvatulum *
Poh spp - Pohlia spp.
Poh and - P. andrewsii Shaw
Poh nut - P. nutans
Pog alp - Polytrichastrum alpinum
Pol com - Polytrichum commune *

Pol hyp - P. hyperboreum *
Pol jun - P. juniperinum
Pol pil - P. piliferum
Psi cav - Psilopilum cavifolium
Sph cap - Sphagnum capillifolium var. tenellum
Sph squ - S. squarrosum
Tom nit - Tomenthypnum nitens
Tor nor - Tortula norvegica *
Ana min - Anastrophyllum minutum
Ane pin - Aneura pinguis
Mar arc - Marsupella arctica
Pti cil - Ptilidium ciliare
Tri qui - Tritomaria quinquedentata

APPENDIX 2B

LIST OF BRYOPHYTES (55 taxa) COLLECTED AT TRUELOVE LOWLAND
Abbreviations as above except where noted

Aulacomnium acuminatum
A. palustre
A. turgidum
Brachythecium sp.
Bra col - B. collinum var. subjulaceum Pfeff.
B. groenlandicum *
Bryum spp.
B. argenteum
B. calophyllum *
B. cryophyllum
B. pseudotriquetrum
Cal gig - Calliergon giganteum
C. stramineum
Cam arc - Campylium arcticum
Cat nig - Catoscopium nigritum
Cin arc - Cinclidium arcticum
Cin lat - C. latifolium
Cirriphyllum cirrosum
Desmatodon heimii var. arctica
Des leu - D. leucostoma
Dicranum angustum
D. elongatum
Dis spp - Distichium spp. ¥
Ditrichum flexicaule
Dre bre - Drepanocladus brevifolius
D. revolvens
D. uncinatus

Enc alp -	Encalypta alpina
Enc rha -	E. rhaptocarpa
	Hylocomium splendens
	Hypnum bambergeri
Hyp rev -	H. revolutum
Lep pyr -	Leptobryum pyriforme
	Meesia uliginosa *
Mee tri -	M. triquetra
Mni lyc -	Mnium lycopodioides *
Myu jul -	Myurella julacea
Myu ten -	M. tenerrima
Ort chr -	Orthothecium chryseum
Ort spec -	O. speciosum
	Philonotis fontana var. pumila
Pla ell -	Plagiomnium ellipticum
	P. medium ssp. curvatulum *
Poh cru -	Pohlia cruda
	P. nutans
	Polytrichastrum alpinum
	P. juniperinum
Rac lan -	Racomitrium lanuginosum
Sco tur -	Scorpidium turgescens
Sel pol -	Seligeria polaris
Spl vas -	Splachnum vasculosum var. heterophyllum
Tim aus -	Timmia austriaca
Tim sib -	T. sibirica Lindb. & Arnell
	Tomenthypnum nitens
Tor arc -	Tortella arctica *
Tor fra -	T. fragilis
Tor rur -	Tortula ruralis
Voi hyp -	Voitia hyperborea
	Anastrophyllum minutum
	Aneura pinguis
Ar fen -	Arnellia fennica
Ble tri -	Blepharastoma tricophyllum
Lop rut -	Lophozia rutheana
Lop ven -	L. ventricosa
Tri qui -	Tritomaria quinquedentata

¥ In the Arctic, *Distichium* cannot be named without sporophytes, but 90% of the specimens sampled were probably *D. capillaceum* (Vitt 1990, pers. comm.).

APPENDIX 2C

LIST OF MOSSES (7 taxa) COLLECTED AT RESOLUTE BAY
Abbreviations as above

Bryum spp.
Cirriphyllum cirrosum
Distichium spp.
Ditrichum flexicaule
Drepanocladus uncinatus
Orthothecium chryseum
Tortula ruralis

APPENDIX 3A

LIST OF LICHENS (12 taxa) COLLECTED AT CLYDE RIVER

Nomenclature follows Thomson (1990).

Ale nig - Alectoria nigricans
Ale och - A. ochroleuca
Cet niv - Cetraria nivalis
Cal mit - Cladina mitis
Cla coc - Cladonia coccifera
Cla gra - C. gracilis var. gracilis
Cla ple - C. pleurota
Col spp - Collema spp.
Dac arc - Dactylina arctica
Och spp - Ochrolechia spp.
Pel aph - Peltigera aphthosa
Tha sub - Thamnolia subuliformis

APPENDIX 3B

LIST OF LICHENS (13 taxa) COLLECTED AT TRUELOVE LOWLAND
Abbreviations as above except where noted

Alectoria nigricans
Bry cha - Bryoria chalybeiformis
Bue spp - Buellia spp.
Cal tor - Caloplaca tornöensis
Cet del - Cetraria delisei
Cet niv - C. nivalis
Hyp sub - Hypogymnia subobscura
Lec epi - Lecanora epibryon
Och fri - Ochrolechia frigida

Par omp -	Parmelia omphalodes
	Peltigera aphthosa
Rhi geo -	Rhizocarpon geographicum
	Thamnolia subuliformis

APPENDIX 3C

LIST OF LICHENS (6 taxa) COLLECTED AT RESOLUTE BAY
Abbreviations as above except where noted

	Alectoria nigricans
Cet cuc -	Cetraria cucullata
Cet isl -	C. islandica
	C. tilesii
	Lecanora epibryon
	Thamnolia subuliformis

APPENDIX 4

LIST OF ALGAE COLLECTED

Microspora crassior (Hansg.) Hazen (Truelove Lowland)
Monostroma grevillei (Thur.) Wittr.¥ (Clyde River)
Nostoc commune Vauch. (Truelove Lowand and Clyde River)
Oedogonium sp. Link (Truelove Lowland)

¥ This is a marine form and was collected several hundred meters from shore (elevation ca. 18 m) in a wet hollow. Dansereau (1954: 338) remarked on this phenomenon on Bray Island, observing that "the tides wash up impressive quantities of large marine algae. These are stranded at the upper tide level, dry very readily and are blown inland to be deposited on the surface of all the plant communities".

APPENDIX 9

Technical data for aerial photography

Roll No.	Frame No.	Study Site	Year	Scale
VRR 2102	18	CR	1960	1:5000
A21157	157	CR	1969	1:6000
A23500	46	CR	1973	1:6000
A26392	47	CR	1983	1:20000
A16683	63	TL	1959	1:60000
A22541	139, 178, 191 231, 243	TL	1971	1:5000

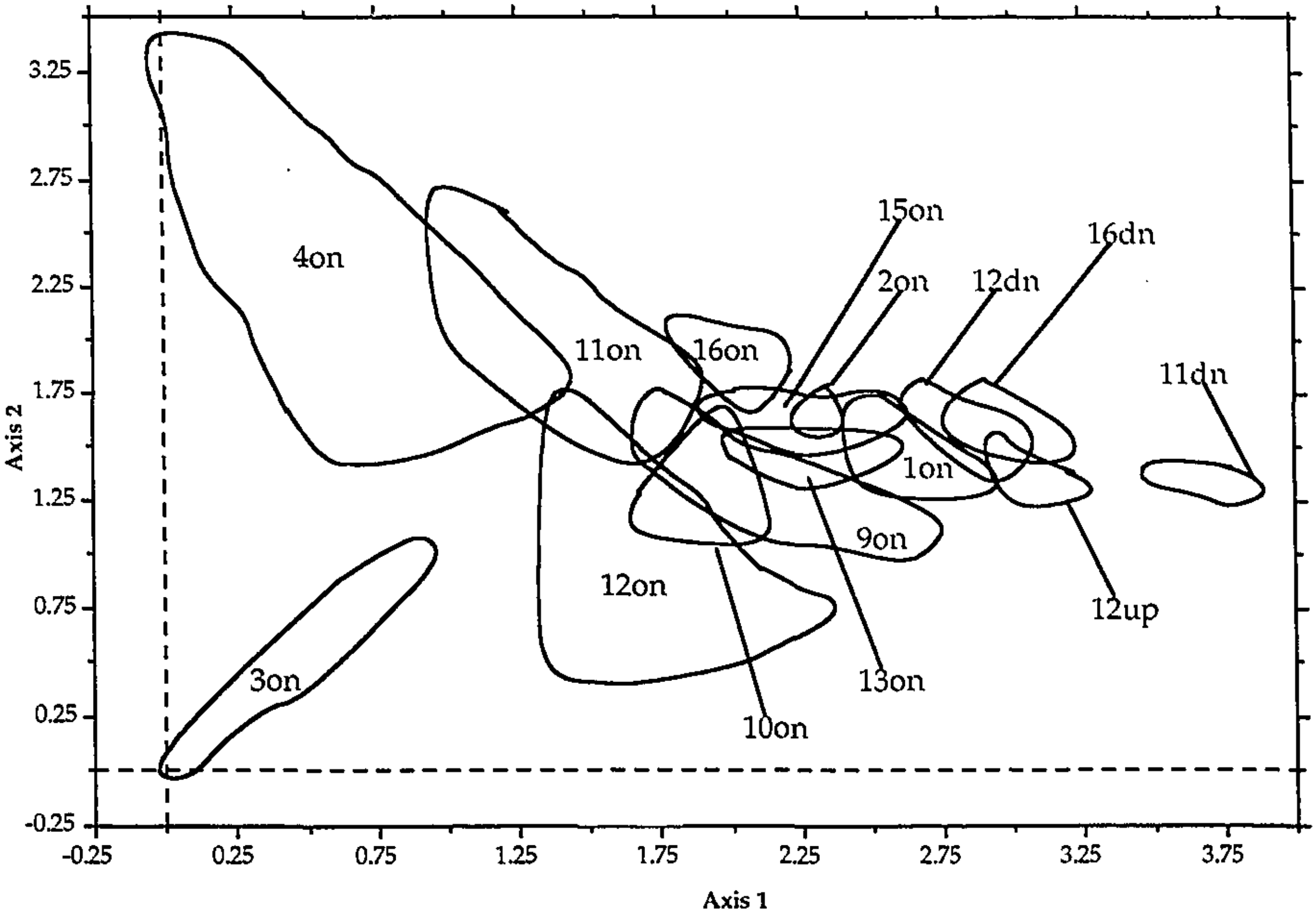
All contact prints and enlargements were obtained from the National Airphoto Library in Ottawa.

APPENDIX 10

Sample DCA ordination biplot of vehicle tracks and drained peatlands at CR

Appendix 10 combines all stands from CR representing tracked vehicle disturbance, as well as downslope stands affected by hydrological changes imposed by the tracks. Eigenvalues for all four axes are signifcantly increased, particularly the first two (0.500 and 0.369) (**Appendix 14a**), indicating that a substantially greater amount of variance is accounted for by these axes compared to the biplot of natural vegetation (**Fig. 3.4, Table 3.3a**). The gradient lengths along these two axes also increase, to 3.766 and 3.361. Stands 3 and 4 at the left margin of the biplot have almost no species in common with the drained peatlands (Stands 11dn, 12up, 12 dn) at the right margin. The primary gradient appears to be one of increasing organic mat depth from left to right. All stands occupying the periphery of the biplot are characterized by colonists which do not exist in the adjacent natural vegetation and should be considered intensely disturbed. These include single- (Stands 3, 4) and multi-pass (Stands 11on, 12on) tracks where the organic mat has been completely removed, or where it remains (Stands 11dn, 12up, 12dn) but the desiccated peat mosses are dead or dying and being invaded by new species (e.g. Drepanocladus badius, Isopterygium pulchellum and many lichens).

Stands clustered at the center are characterized by an impoverished 'remnant' flora, that is to say a subset of the original plants on the various sites. Most striking is the floristic convergence represented by the proximity and even overlap among Stands 9on, 10on (multi-pass tracks) and 15on, 16on (single-pass tracks). In the biplot of natural vegetation these stands showed great intra- and inter-stand variation. Their convergence is attributed to the removal of lichens and many or all peat mosses. That the components of the remnant vegetation are so similar among the two different levels of impact is significant and are discussed in Chapter V.

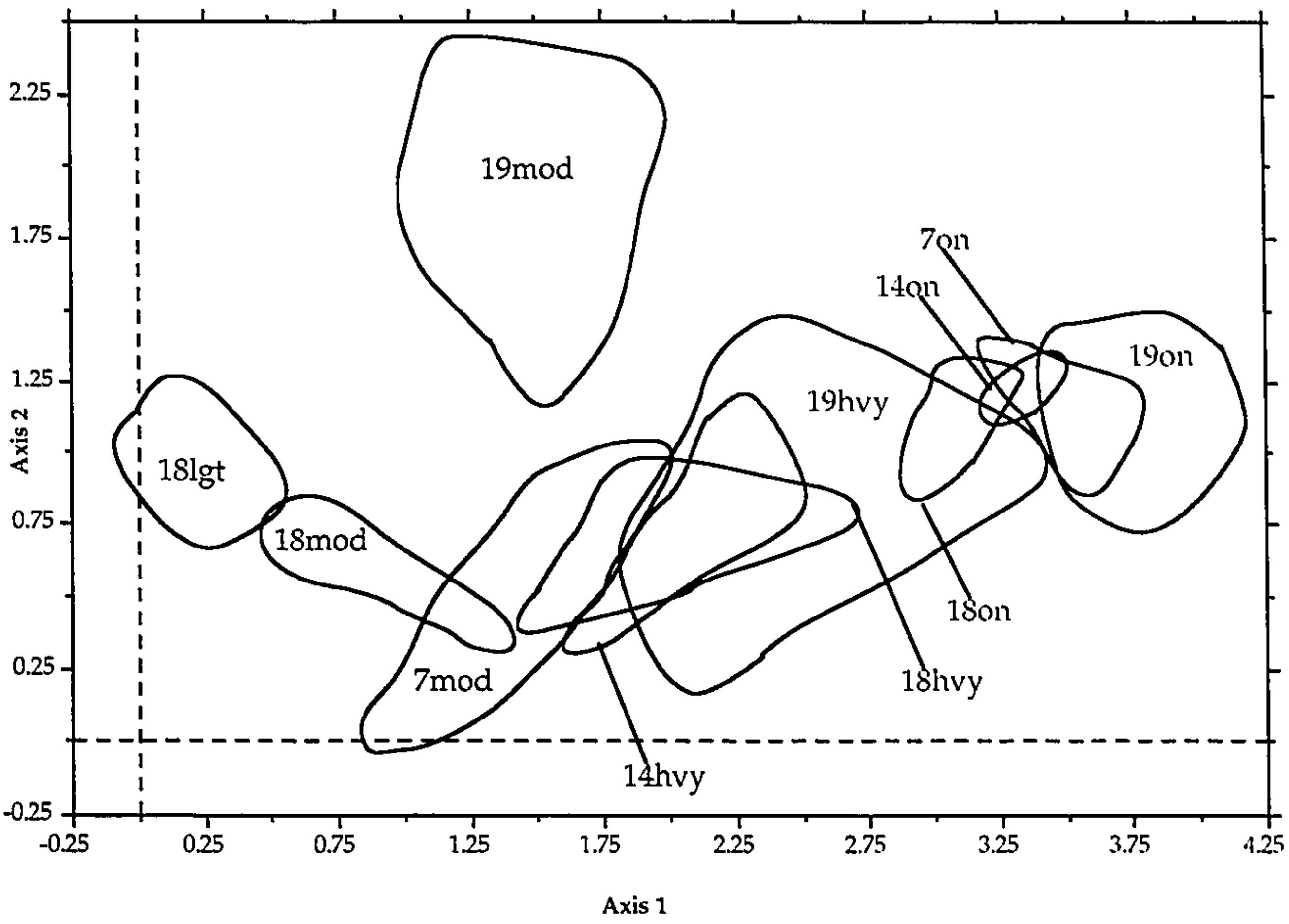


3.25
2.75
2.25
1.75
1.25
0.75
0.25
-0.25
Axis 2
-0.25
0.25
0.75
1.25
1.75
2.25
2.75
3.25
3.75
Axis 1
4on
3on
11on
16on
15on
2on
12dn
16dn
11dn
1on
9on
12on
12up
13on
10on

APPENDIX 11

Sample DCA ordination biplot of abandoned contemporary housepads and adjacent pedestrian trampled ground at CR

The primary axis in **Appendix 11** is a strong gradient (eigenvalue = 0.603) which appears to be correlated to increasing disturbance intensity, ranging from lightly trampled meadows on the left (18lgt) to heavily trampled ground and former housepads on beach ridges. Species turnover is complete along this axis with an estimated gradient length of 4.120 s.d. (**Appendix 14b**). The second axis, which seems to be one of decreasing moisture from top to bottom, is less clearly defined (eigenvalue = 0.302) and not as long (2.405 s.d.). Stand 19mod is by far the wettest and is closest to Stand 7mod, with which it shares Dupontia fisheri ssp. psilosantha and Carex aquatilis var. stans among abundant hydric-hygric graminoids. The least trampled vegetation which comprises Stands 18lgt and 18mod is a closed turf and retains a reasonable cover of woody plants (e.g. Salix arctica, S. herbacea). However, the more heavily disturbed stands have an open cover of ruderal grasses, forbs and bryophytes with no woody plants. The stands at the far right (7on, 14on, 19on) include housing foundations for which sand and gravel were added. No materials were added to the housepad in Stand 18on, nor any of the trampled stands. The relatively high eigenvalue (0.225) and long gradient (3.160) of the third axis (not shown) is apparently the result of extreme outliers (Juncus biglumis, Oxyria digyna), as suggested by Økland (1990c), which is not the case with the first two axes.

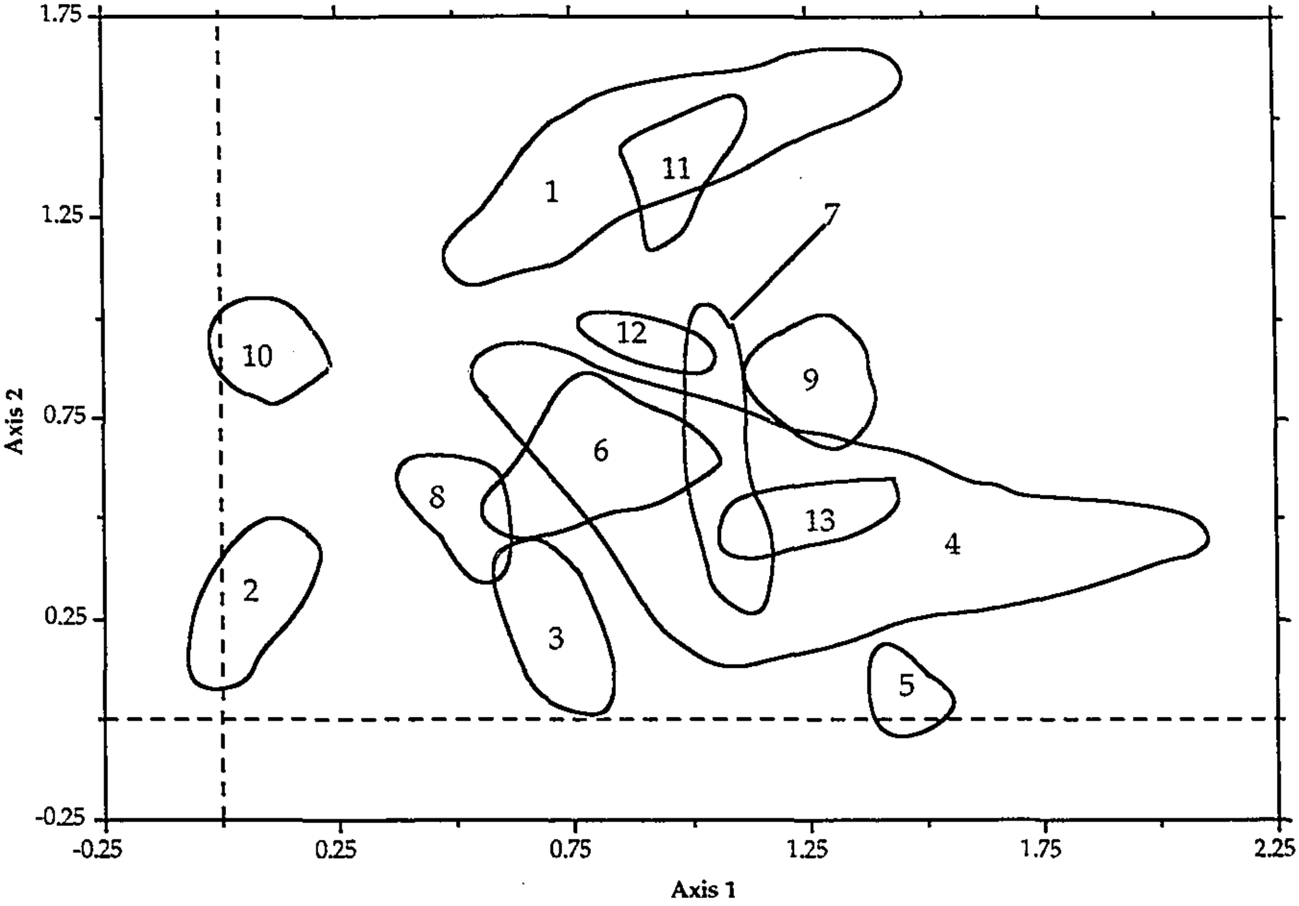

19mod
7on
14on
19on
19hvy
18lgt
18mod
18on
7mod
18hvy
14hvy
2.25
1.75
1.25
0.75
0.25
-0.25
-0.25
0.25
0.75
1.25
1.75
2.25
2.75
3.25
3.75
4.25
Axis 2
Axis 1

APPENDIX 12

Sample DCA ordination biplot of vehicle tracks at TL

Relative to the natural vegetation at TL, ordination of the tracked stands (**Appendix 12**) exhibits noticeable, if minor, change in that the stands are even more clustered than before. Eigenvalues along the first two axes remain similar at 0.233 and 0.141 (**Appendix 14c**). Estimated gradient lengths for these axes are slightly reduced (2.071, 1.613), which indicates a floristic convergence among stands. In support of this conclusion, the number of active species in the disturbed vegetation ordination is reduced to 39 from 51 in the natural vegetation. The most interesting differences lie in the arrangement of the individual stands in the biplot.

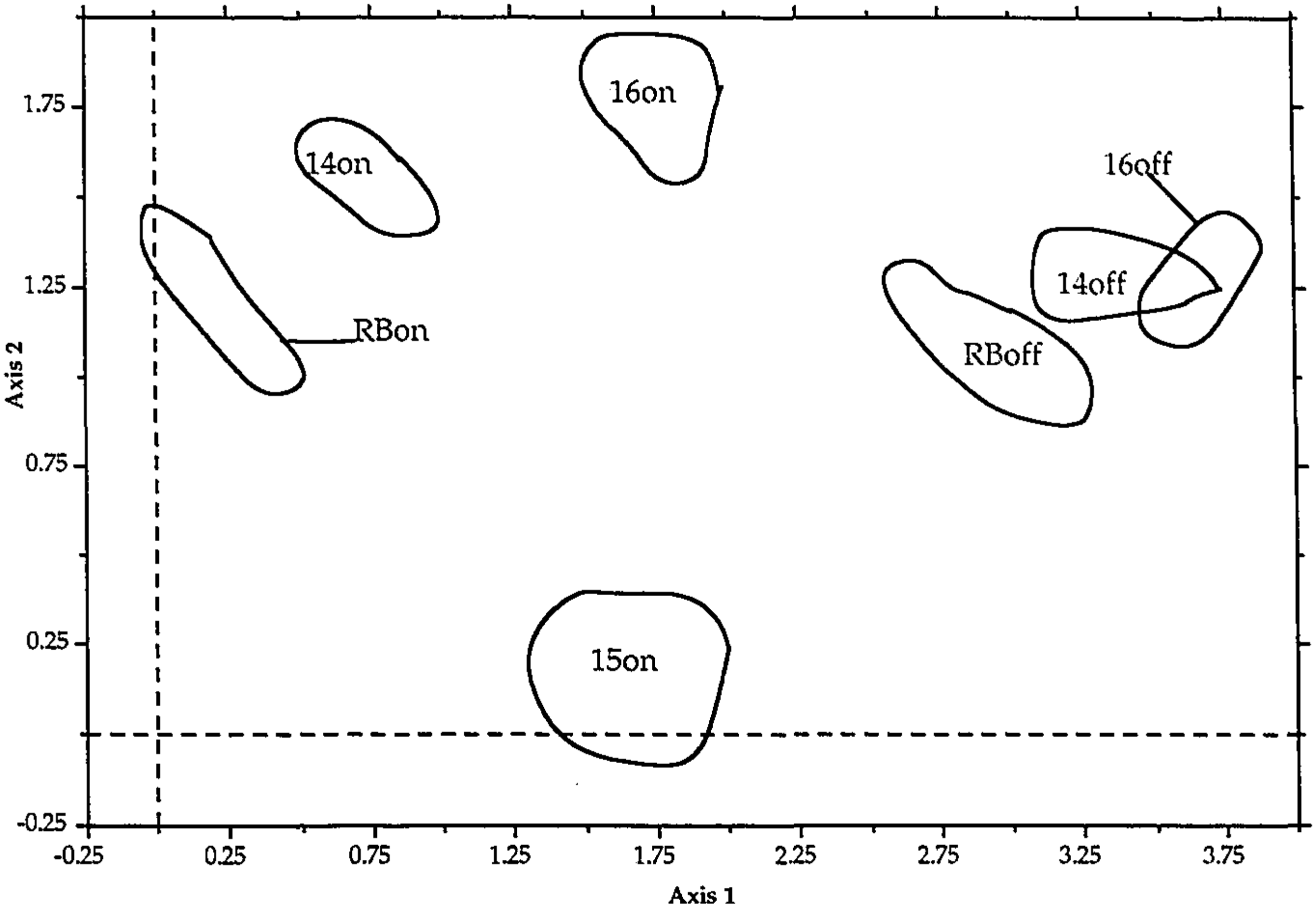
The first axis still appears to be a gradient of increasing moisture from left to right. However, whereas Stand 4off occupied the extreme left margin of the biplot of natural vegetation, Stand 4on has switched to the extreme right hand side in the disturbed biplot. The undisturbed stand comprises one of the most mesic, hummocky meadows sampled and is transitional between a granitic outcrop and a wet meadow. The tracks dissecting this stand are among the most used and rutted, thus retaining standing water thoughout the entire growing season, and are characterized by emergent aquatics (i.e. Ranunculus hyperboreus). Conversely, whereas the hummocky meadow represented by Stand 10off occupied the approximate center of the first axis, Stand 10on has sustained only minimal usage (few passes). As a result, it has had reductions among but few of its cover of 'hummock' species (e.g. Salix arctica, Tomenthypnum nitens) and has moved to the far left, being relatively mesic now compared to the rest of the tracks. As discussed in the classification analysis, only a few tracks are characterized by colonists (i.e. Seligeria polaris) and most are characterized by remnants of the adjacent, natural vegetation.


1.75
1.25
0.75
0.25
-0.25
-0.25
0.25
0.75
1.25
1.75
2.25
Axis 1
Axis 2
1
2
3
4
5
6
7
8
9
10
11
12
13

APPENDIX 13

Sample DCA ordination biplot of Thule dwellings and beach ridges at TL and RB

The biplot of Thule dwellings and beach ridges (**Appendix 13**) reveals a strong primary gradient (eigenvalue = 0.640) and an almost complete differentiation in species composition between the extremes (estimated gradient length = 3.824) (**Appendix 14d**). The beach ridges of both TL and RB are clustered at the far right and are relatively similar. There is far more variation among the Thule dwellings, even among unexcavated dwellings at TL which are only meters apart (T15on, T16on). Axis I corresponds roughly to intensity of disturbance although T14on, the most intensely disturbed stand, does not occupy the end of the gradient. The number of active species (77) is twice that in the meadows, with many more ruderal plants (e.g Alopecurus alpinus, Leptobryum pyriforme, etc.) figuring prominently on the dwellings. Some vascular plants (e.g. Carex aquatilis var. stans, Juncus biglumis) are near omnipresent and occur at various frequencies in both meadows and on dwellings, contributing to the high species richness of the latter. Salix arctica occurs in both of these vegetation types and on beach ridges as well, displaying probably the widest ecological amplitude of all. The second axis is more poorly defined (eigenvalue = 0.239) and shorter with much lower species turnover (estimated length = 1.899). Its endpoints appear to be based on the variations in moisture. Subtle differences in species composition differentiate the moist Stand T15on from the only slightly more mesic Stand T16on.



16on
14on
16off
RBon
14off
RBoff
15on
1.75
1.25
0.75
0.25
-0.25
Axis 2
-0.25
0.25
0.75
1.25
1.75
2.25
2.75
3.25
3.75
Axis 1

APPENDIX 14

Summary tables for detrended correspondence analyses

A. Vehicle tracks and drained peatlands at CR

	Axes				
	1	2	3	4	
Eigenvalues	0.500	0.369	0.175	0.139	
Lengths of gradient	3.766	3.361	2.438	3.041	
Cumulative percentage variance of species data	12.5	21.6	26.0	29.5	
Sum of all unconstrained eigenvalues					4.017

B. Housepads and trampled ground at CR

	Axes				
	1	2	3	4	
Eigenvalues	0.603	0.302	0.225	0.118	
Lengths of gradient	4.120	2.405	3.160	2.350	
Cumulative percentage variance of species data	16.1	24.2	30.2	33.3	
Sum of all unconstrained eigenvalues					3.742

C. Vehicle tracks at TL

	Axes				
	1	2	3	4	
Eigenvalues	0.233	0.141	0.099	0.062	
Lengths of gradient	2.071	1.613	1.847	1.270	
Cumulative percentage variance of species data	15.4	24.7	31.2	35.3	
Sum of all unconstrained eigenvalues					1.515

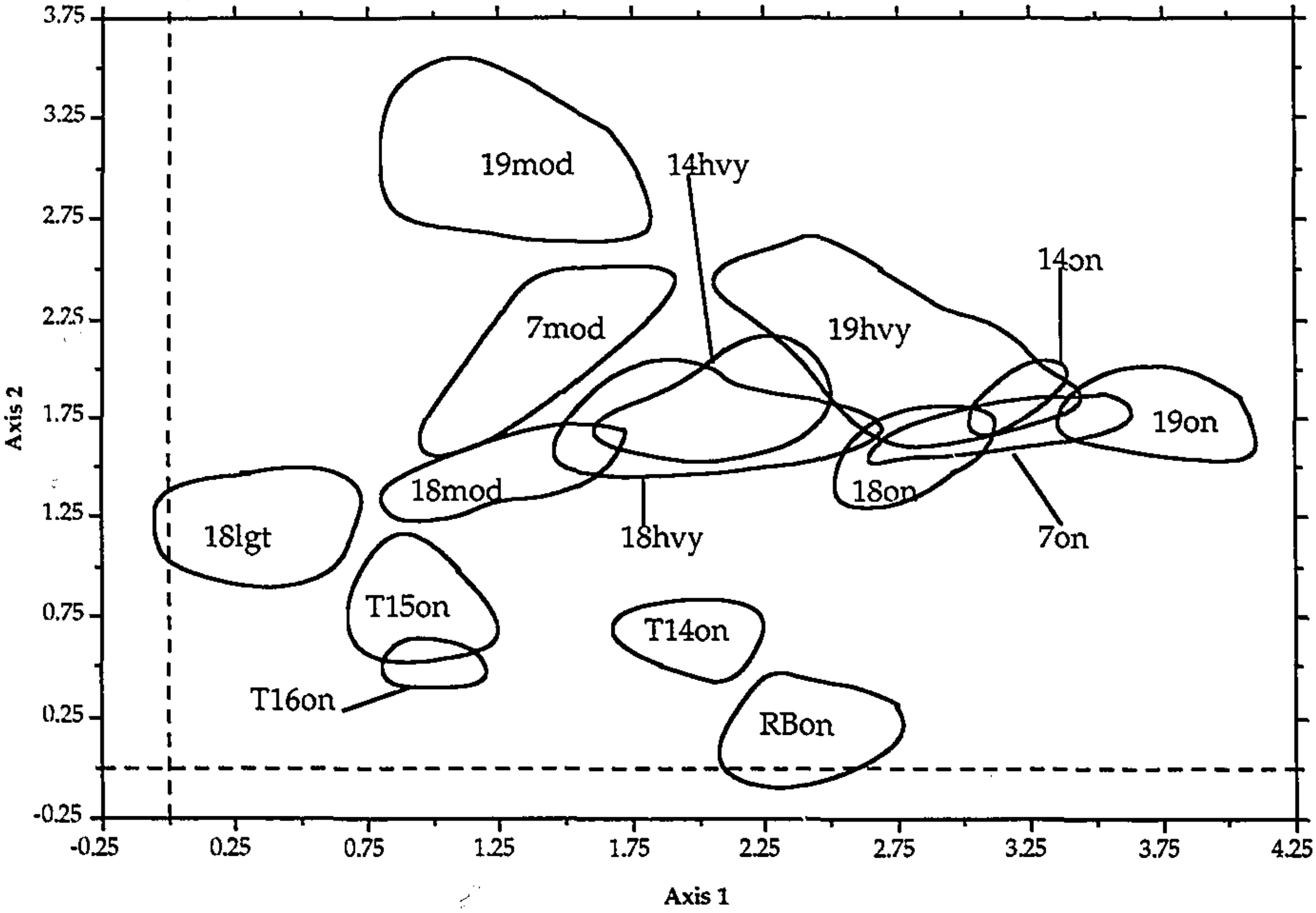
D. Thule dwellings and beach ridges at TL and RB

	Axes				
	1	2	3	4	
Eigenvalues	0.640	0.239	0.108	0.059	
Lengths of gradient	3.824	1.899	1.838	1.472	
Cumulative percentage variance of species data	24.7	33.9	38.1	40.3	
Sum of all unconstrained eigenvalues					2.593

APPENDIX 15

Sample DCA ordination biplot of Thule dwellings, abandoned 'contemporary' housepads and adjacent pedestrian trampled ground at CR, TL, and RB

Ordination of the combined Thule dwellings, beach ridges, contemporary housepads, and trampled stands (**not shown**) revealed strong local and geographic affinities among the vegetation types of all but the beach ridge stands. These outliers were removed and the new ordination resulted in the biplot seen in **Appendix 15**, in which these relationships are still apparent but with greater continuity among samples along gradients. As at CR, the first axis appears strongly linked with disturbance intensity (eigenvalue = 0.528), increasing from left to right. The second axis (eigenvalue = 0.405) seems to be one of decreasing moisture from top to bottom. Estimated gradient lengths are for the first two axes are 4.051 and 3.503 respectively and species turnover is high in both cases (**Appendix 19a**). As in the combined TWINSPAN analysis of all disturbed stands, the vegetation of the two unexcavated Thule dwellings from TL (Stands T15on, T16on) is closest to the lightly trampled meadow from CR (Stand 18lgt). Similarly, Stand 19on appears on the far right (dry) end of the gradient, while Stand 18lgt occupies the far left (moist) end, as they do within their respective portions of the TWINSPAN dendrogram.



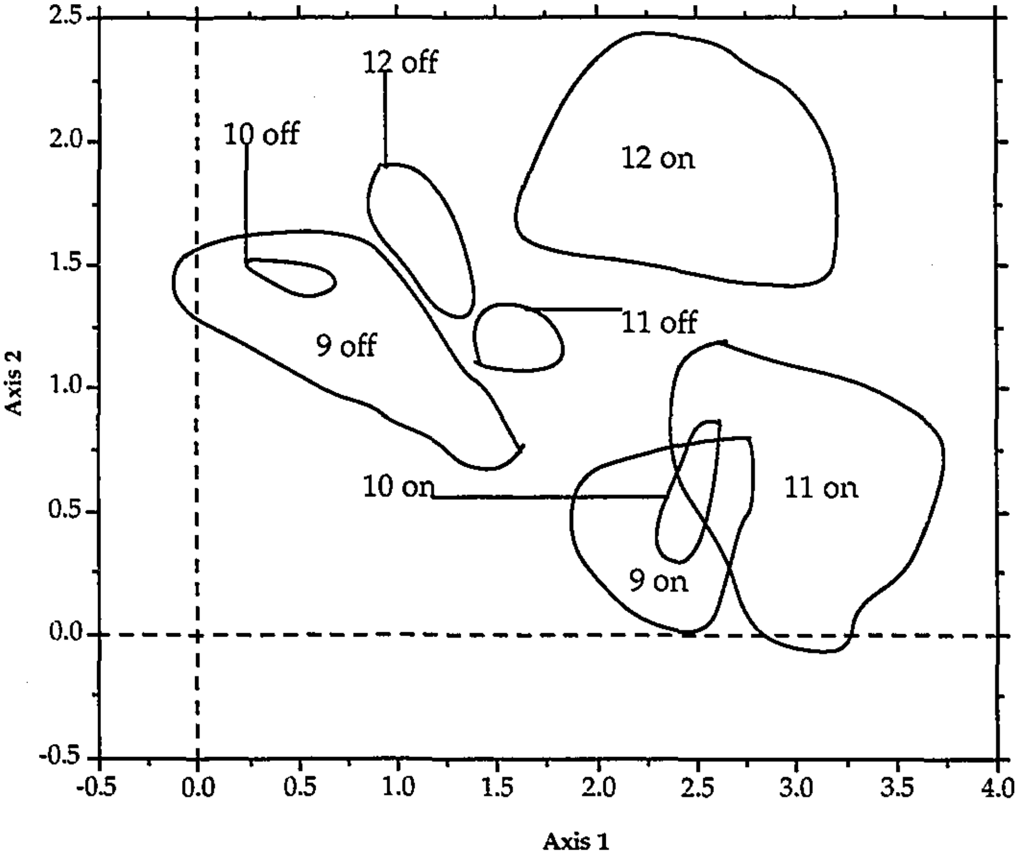
19mod
14hvy
14on
7mod
19hvy
19on
18mod
18on
18lgt
18hvy
7on
T15on
T14on
T16on
RBon
Axis 2
Axis 1
3.75
3.25
2.75
2.25
1.75
1.25
0.75
0.25
-0.25
0.25
0.75
1.25
1.75
2.25
2.75
3.25
3.75
4.25

APPENDIX 16

Sample DCA ordination biplot of multi-pass vehicle tracks and adjacent controls at CR

When ordinated with their adjacent controls (**Appendix 16**), most of the multi-pass tracks at CR exhibit an apparent increase in intra-patch compositional heterogeneity. Species turnover is high along the first axis (3.646 s.d.) and all the stands appear as discontinuous from their controls (**Appendix 19b**). Note that the composition of Stand 11 has shifted toward that of Stands 9 and 10 after impact. Stand 12, on the other hand, retains its dissimilar composition. A key difference between untracked and tracked vegetation is the virtual lack of Sphagnum spp. and woody plants in the latter.

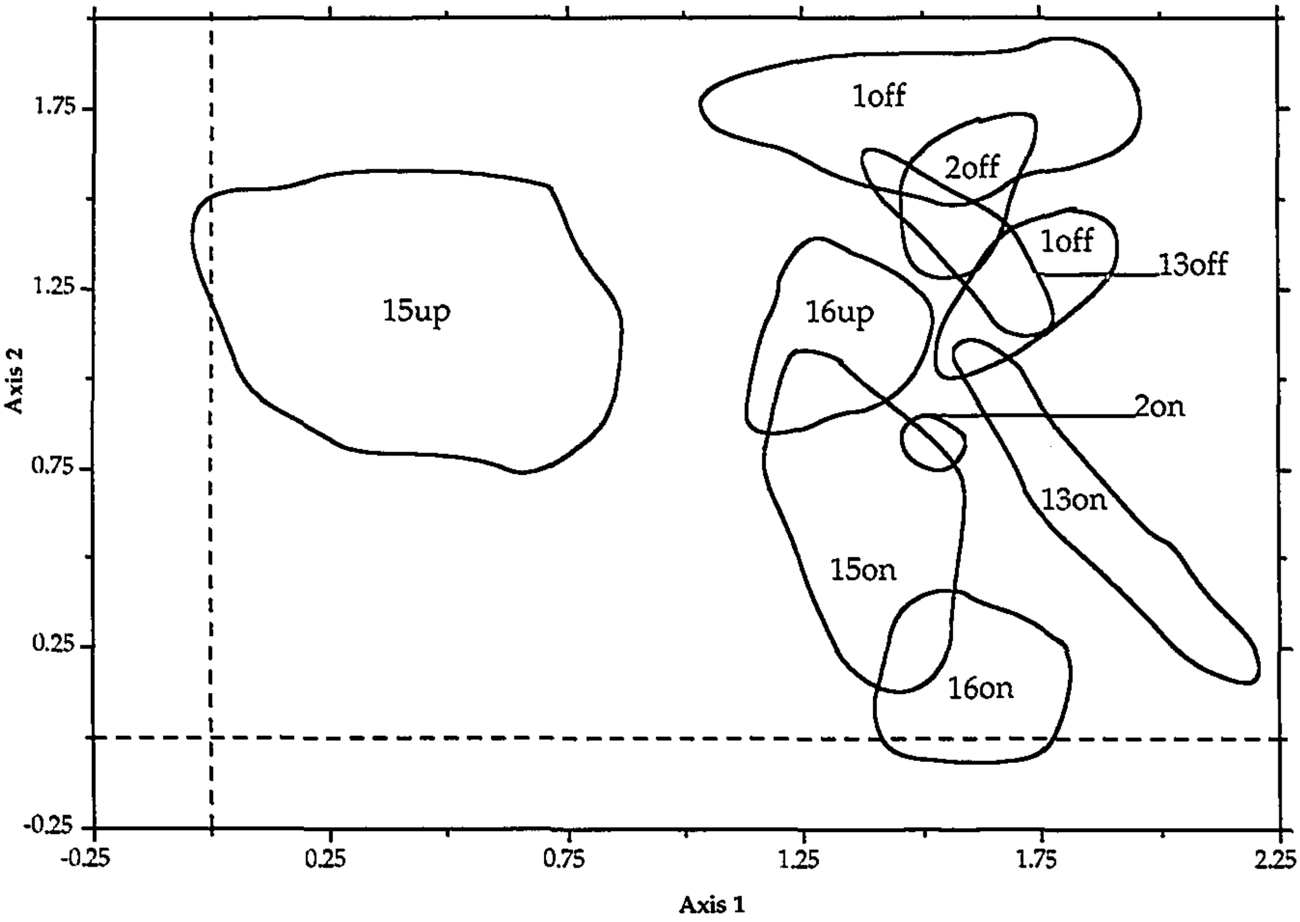
NOTE: The DCA ordination of tracked stands and adjacent controls at TL (**not shown**) resulted in a triplot which was too crowded for meaningful interpretation. This was attributed to the high density of samples and species, the virtual lack of colonists, and the similarity of the vegetation among both disturbed and natural stands. The most salient feature of the vegetation was the conspicuous absence of colonists to differentiate among the stands, indicating the prevalence of remnant floras within these patches.


12 off
10 off
12 on
11 off
9 off
10 on
11 on
9 on
Axis 2
Axis 1
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
-0.5
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0

APPENDIX 17

Sample DCA ordination biplot of single-pass vehicle tracks and adjacent controls at CR

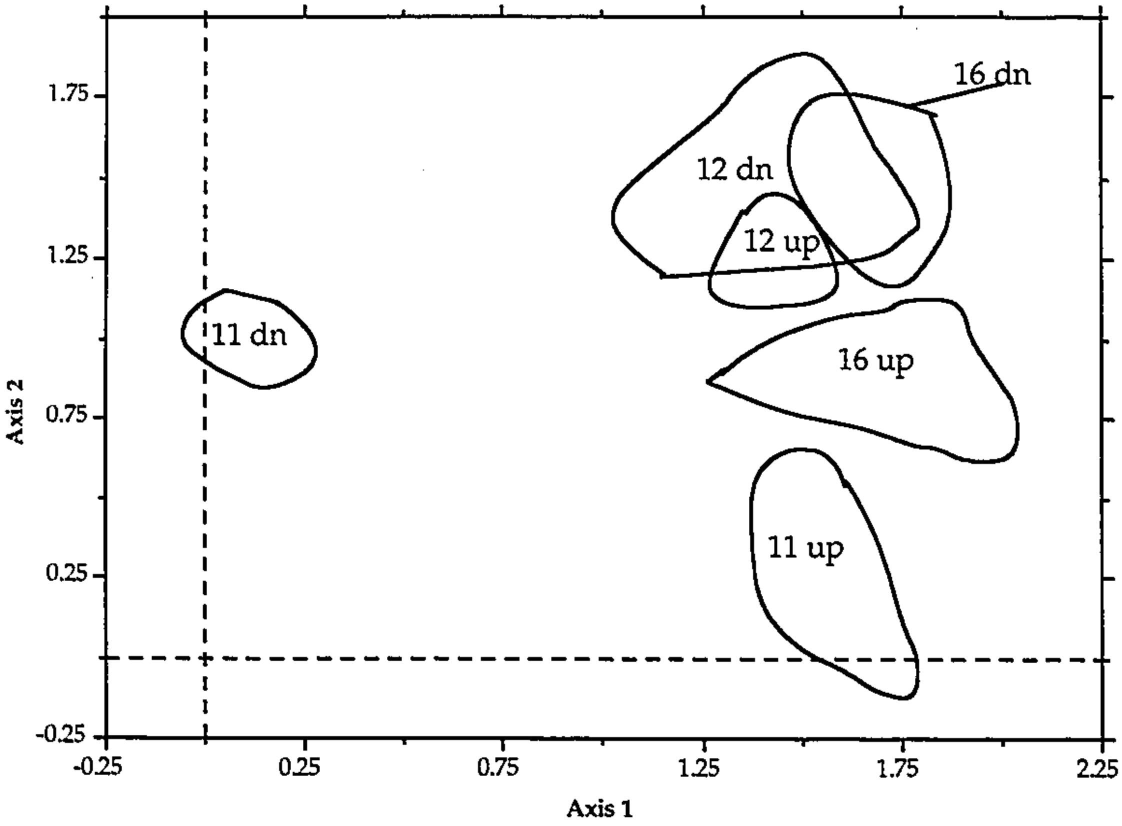
Compared to the multi-pass tracks, species composition among stands is little changed between single-pass tracks and adjacent controls (gradient lengths 2.154 and 1.898 for axes I and II) (**Appendices 17 and 19c**). The greatest change is that exhibited in the water channel (Stand 16) and on the adjacent interfluve (Stand 15), both of which had several species of lichens on the drier hummocks prior to impact. The natural moisture regime of Stand 15 is among the driest of the meadows sampled at CR. As such, it is the only stand in which the hummocks were not comprised of Sphagnum spp. and thus it is recognized by DCA as distinct from the apparent continuum formed by the other stands. On the other hand, the colonization of the newly-moist tracks through Stand 15 by Sphagnum squarrosum has brought them closer in composition to the more hygric tracked and untracked stands on the right.


1off
2off
1off
13off
15up
16up
2on
13on
15on
16on
1.75
1.25
0.75
0.25
-0.25
Axis 2
-0.25
0.25
0.75
1.25
1.75
2.25
Axis 1

APPENDIX 18

Sample DCA ordination biplot of drained peatlands and adjacent controls at CR

Ordination of the drained peatlands with their controls (**Appendix 18**) from upslope reveals only moderate species turnover between extreme ends of the gradients along axes I and II (2.007 and 1.863 s.d.) (**Appendix 19d**). Differences are most pronounced above and below the set of multi-pass tracks which are perpendicular to local slope across the center of a water channel (Stand 11). Change is evident but much less pronounced above and below a single-pass set of tracks which are diagonal to local slope (Stands 16up, 16dn). Previous analyses (TWINSPAN, DCA and CCA) had determined that there was no significant difference in vegetation or environment above and below tracks across the interfluve portion of the slope (Stand 15) and these samples were removed from subsequent analyses of drainage effects.



16 dn
12 dn
12 up
11 dn
16 up
11 up
1.75
1.25
0.75
0.25
-0.25
Axis 2
-0.25
0.25
0.75
1.25
1.75
2.25
Axis 1

APPENDIX 19

Summary tables for detrended correspondence analyses

A. Thule dwellings, housepads and trampled ground at CR, TL and RB

	Axes				
	1	2	3	4	
Eigenvalues	0.528	0.405	0.234	0.143	
Lengths of gradient	4.051	3.503	3.398	2.308	
Cumulative percentage variance of species data	11.6	20.5	25.7	28.8	
Sum of all unconstrained eigenvalues					4.547

B. Multi-pass vehicle tracks and controls at CR

	Axes				
	1	2	3	4	
Eigenvalues	0.556	0.294	0.157	0.098	
Lengths of gradient	3.646	2.371	2.309	1.874	
Cumulative percentage variance of species data	19.3	29.5	25.0	38.4	
Sum of all unconstrained eigenvalues					2.878

C. Single-pass vehicle tracks and controls at CR

	Axes				
	1	2	3	4	
Eigenvalues	0.312	0.150	0.086	0.052	
Lengths of gradient	2.154	1.898	1.474	1.244	
Cumulative percentage variance of species data	17.6	26.1	31.0	33.9	
Sum of all unconstrained eigenvalues					1.770

D. Drained peatlands and controls at CR

	Axes				
	1	2	3	4	
Eigenvalues	0.345	0.176	0.096	0.036	
Lengths of gradient	2.007	1.863	1.795	1.243	
Cumulative percentage variance of species data	26.1	39.4	46.6	49.3	
Sum of all unconstrained eigenvalues					1.324

APPENDIX 20

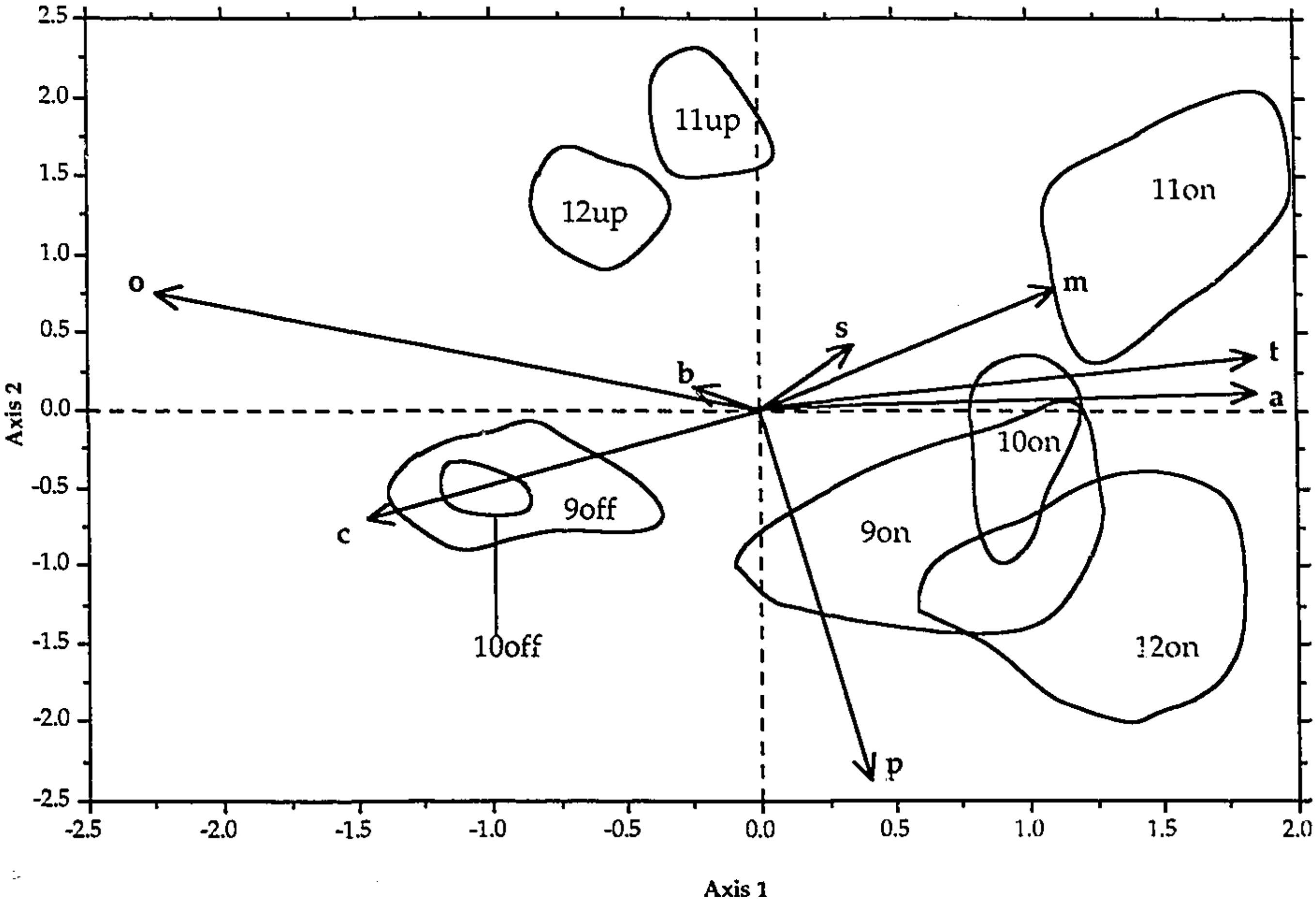
Sample CCA ordination triplot of multi-pass vehicle tracks and adjacent controls at CR

PLEASE NOTE !!

Environmental parameters in this and all other CCA ordination triplots are labelled as follows:
a=active layer depth; **b**=soil bulk density; **c**=soil compaction; m=soil moisture; **o**=organic mat depth; **p**=soil pH; s=slope; t=soil temperature

The triplot in **Appendix 20** is based on the same sample subset of the combined disturbed and adjacent control stands used in DCA with the addition of environmental variables. The eigenvalue of the first axis decreases somewhat from 0.556 to 0.469, while the other three axes change only slightly. The first axis and overall results were significant at p =0.01 in the Monte Carlo test, with the first axis most closely tied to organic mat depth (negative correlation, **Appendix 22a**), active layer depth and soil temperature (positive correlation, **Appendix 22a**). Compaction also had a strong negative correlation with the first axis and was highest in the the undisturbed portions of Stands 9 and 10. The second axis is clearly one of soil pH (correlation coefficient = -0.93). In Monte Carlo tests of the individual environmental factors, organic mat depth, pH and compaction were all significant at the ≤ 0.01 probability level. All other factors attained p -values of ≥ 0.05, with soil temperature being closest (p = 0.06). Species-environment correlations are high for the first two axes (0.926, 0.922).

As in the DCA analysis, the tracked stands exhibit greater intra-patch heterogeneity than their adjacent controls. Comparison of CCA analyses in both scaling 1 (**not shown**) and 2 show that stands are contracted in the scaling 1 ordination space and indicate that much of the heterogeneity is due to species composition rather than environment. Still, the increase after disturbance is noticeable and raises the question of whether the environmental heterogeneity has led to differential intra-patch colonization or vice-versa. Similarly, distances between stands in scaling 1 are contracted but they remain discrete and indicate the importance of their respective environmental conditions.



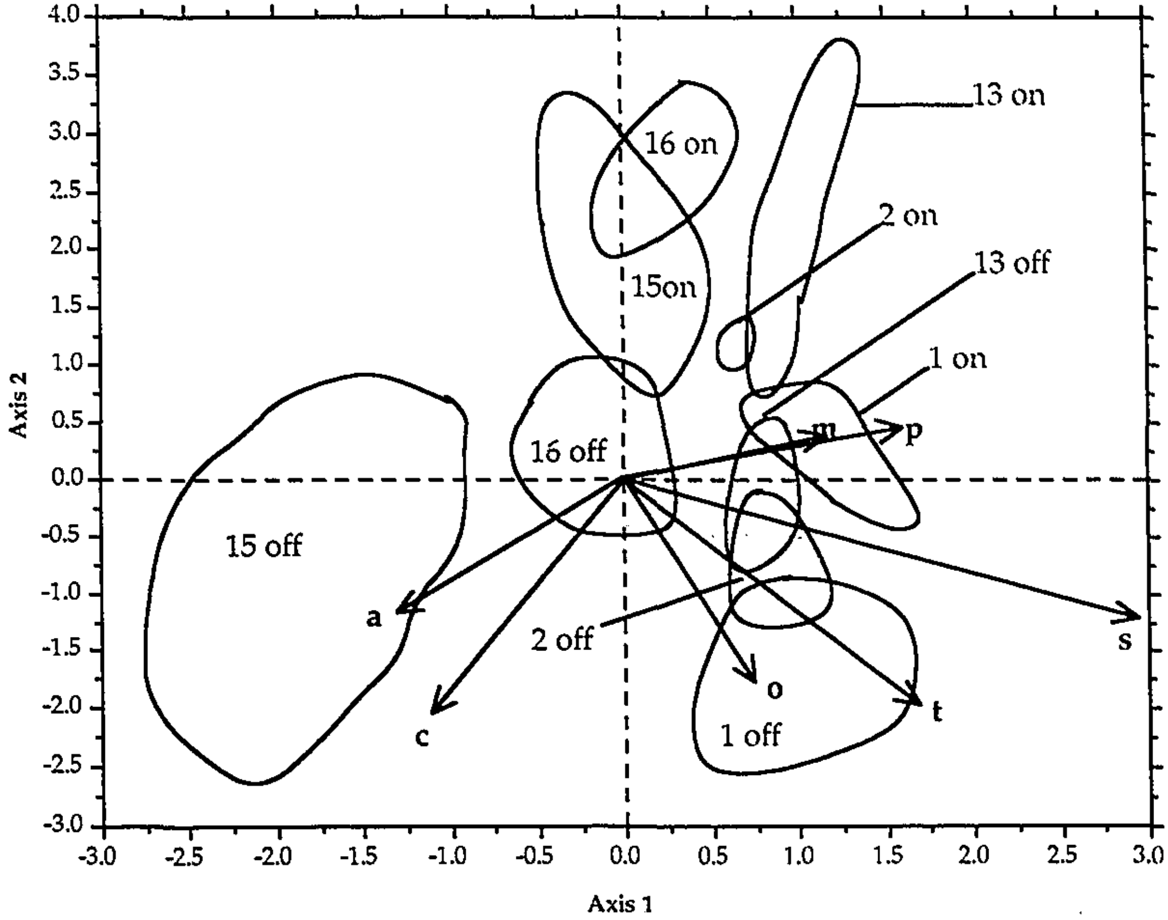
Axis 2
Axis 1
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
-2.5
-2.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
2.0
11up
12up
11on
o
m
s
t
b
a
10on
9off
9on
c
10off
12on
p

APPENDIX 21

Sample CCA ordination triplot of single-pass vehicle tracks and adjacent controls at CR

Compared to the DCA ordination of single-pass tracks at CR (**Appendix 19c**), eigenvalues in the CCA analysis decrease somewhat on all four axes, particularly the first (**Appendix 22b**). In the triplot (**Appendix 21**), the stands are more dispersed in the ordination space but retain much of the overlap evident in DCA. A second CCA triplot in scaling 1 (**not shown**) revealed greatly reduced chi-square distances between samples indicating that much of the dispersion is due to species variation among samples.

The first axis and overall results were significant at $p = 0.01$ in the Monte Carlo test, the first axis being correlated primarily with slope and exhibiting moderate correlation with soil temperature and pH, the latter of which is increased in tracked areas. The second axis is negatively correlated with compaction, organic mat depth and active layer depth. It is notable that active layer depth, compaction and bulk density are reduced in the tracked stands, contrary to what was expected. In Monte Carlo tests of the individual environmental factors, slope, active layer, organic mat depth, and compaction were significant at the ≤ 0.01 probability level. Soil temperature was significant at $p = 0.05$. All other factors attained p -values of >0.05. Species-environment correlations for the first two axes (0.872, 0.802) are not as high as in the multi-pass tracks.



4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
-2.5
-3.0
Axis 2
-3.0
-2.5
-2.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
2.0
2.5
3.0
Axis 1
13 on
16 on
2 on
13 off
15on
1 on
16 off
m
p
15 off
a
2 off
s
o
t
c
1 off

APPENDIX 22a. CCA summary for multi-pass tracks and controls at CR

Parameter	Canonical Coefficients Axis 1	Canonical Coefficients Axis 2	Inter-set Correlations Axis 1	Inter-set Correlations Axis 2
Organic Mat Depth	-0.873	0.295	-0.808	-0.273
Soil Moisture	0.429	0.303	0.398	0.280
Soil pH	0.157	-0.931	0.145	-0.859
Bulk Density	-0.096	0.051	-0.089	0.047
Soil Compaction	-0.694	-0.280	-0.643	-0.258
Soil Temperature	0.718	0.133	0.665	0.123
Active Layer	0.718	0.047	0.666	0.043
Slope	0.133	0.165	0.123	0.153

	Axes 1	2	3	4
Eigenvalues	.469	.296	.135	.105
Species-environment correlations	.926	.922	.693	.682
Cumulative percentage variance				
of species data	16.3	26.6	31.3	34.9
of species-environment relation	41.7	68.0	80.0	89.3

APPENDIX 22b. CCA summary for single-pass tracks and controls at CR

Parameter	Canonical Coefficients Axis 1	Canonical Coefficients Axis 2	Inter-set Correlations Axis 1	Inter-set Correlations Axis 2
Organic Mat Depth	0.216	-0.527	0.188	-0.423
Soil Moisture	0.340	0.099	0.296	0.079
Soil pH	0.468	0.133	0.408	0.106
Bulk Density	0.036	-0.122	0.032	-0.098
Soil Compaction	-0.329	-0.602	-0.287	-0.483
Soil Temperature	0.481	-0.488	0.419	-0.392
Active Layer	-0.382	-0.342	-0.333	-0.275
Slope	0.863	-0.359	0.752	-0.288

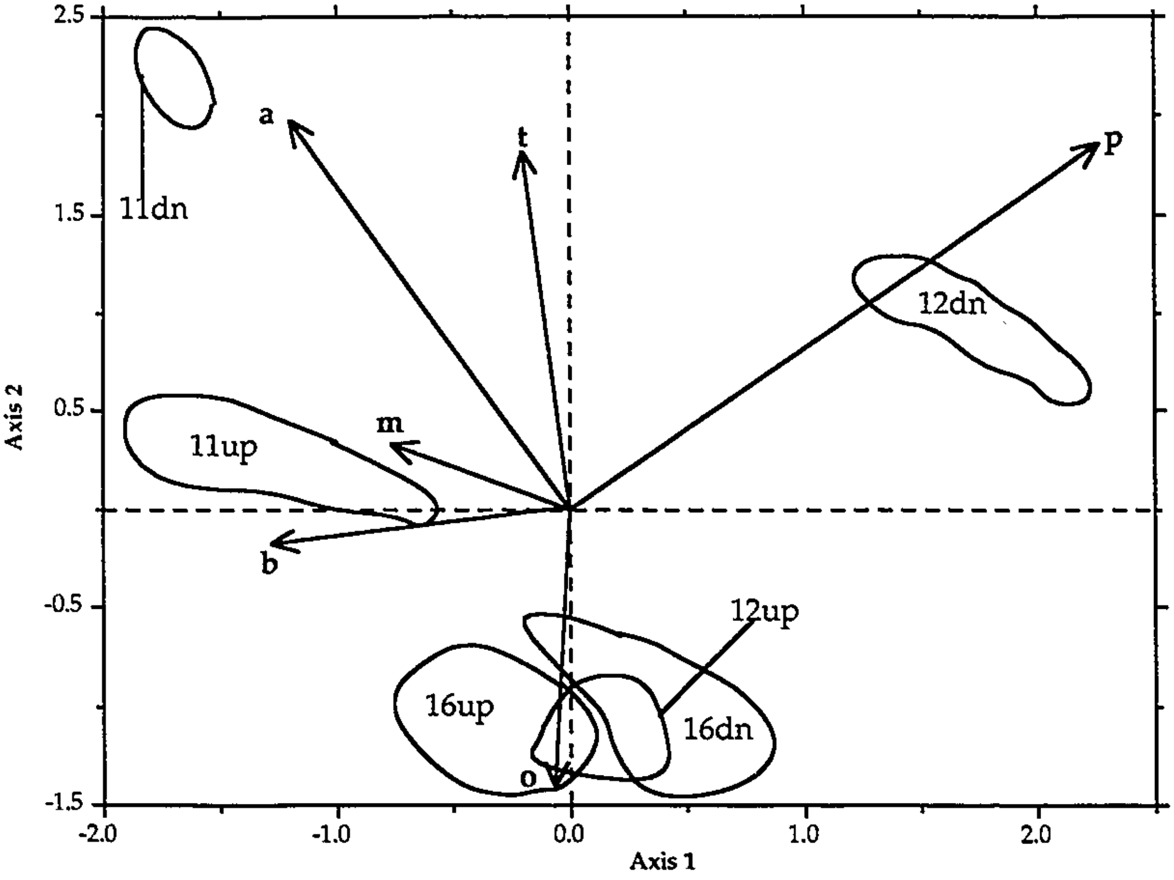
	Axes 1	2	3	4
Eigenvalues	.199	.108	.084	.024
Species-environment correlations	.872	.802	.731	.517
Cumulative percentage variance				
of species data	11.0	16.9	21.6	22.9
of species-environment relation	43.4	67.0	85.3	90.6

APPENDIX 23

Sample CCA ordination triplot of drained peatlands and adjacent controls at CR

In the triplot from CCA (**Appendix 23**) the positions of the stands differ somewhat from those in DCA and the eigenvalues drop for all four axes, particularly the first (**Appendix 25a**). Compaction and slope were found to have negligible variance and were omitted from the analysis. The stands are discrete and widely dispersed with the exception of Stand 16dn and its upslope control, which overlap only slightly. The first axis is most strongly correlated with pH, negatively correlated with active layer depth, and was significant at p =0.01 in the Monte Carlo test, as were the overall results. The second axis exhibits roughly equivalent correlation with three variables: soil temperature, pH and active layer depth. Organic mat depth has a moderate negative correlation with this axis.

Interestingly, soil pH is high in all drained peatlands relative to their controls and has a much stronger association with community variation than relative moisture. Changes in active layer depth are more variable, decreasing in Stand 12dn, but increasing in Stand 11dn. It should be noted that the use of pooled maximum active layer depths in CANOCO inevitably masks much of the intraseasonal variation in active layer development which is probably important, in stands such as drained peatlands, where thaw is delayed in desiccated vegetation with high surface reflectance (see **Appendices 32 and 37a**, see also **Section 3.10.i**). Distances between stands in the triplot are reduced in scaling 1 (**not shown**), but those that were discrete remain so, indicating that some of the dispersion was due solely to species variation. Monte Carlo tests of individual environmental variables found compaction and pH to be significant at p =0.01, and active layer depth at p =0.03. All others attained p -values of ≥0.05. Species-environmental correlations for the first two axes are fairly high at 0.896 and 0.798 respectively.


11dn
a
t
p
12dn
m
11up
b
12up
16up
16dn
o
2.5
1.5
0.5
-0.5
-1.5
Axis 2
-2.0
-1.0
0.0
1.0
2.0
Axis 1

APPENDIX 24

Sample CCA ordination triplot of abandoned 'contemporary' housepads and adjacent pedestrian trampled meadows at CR

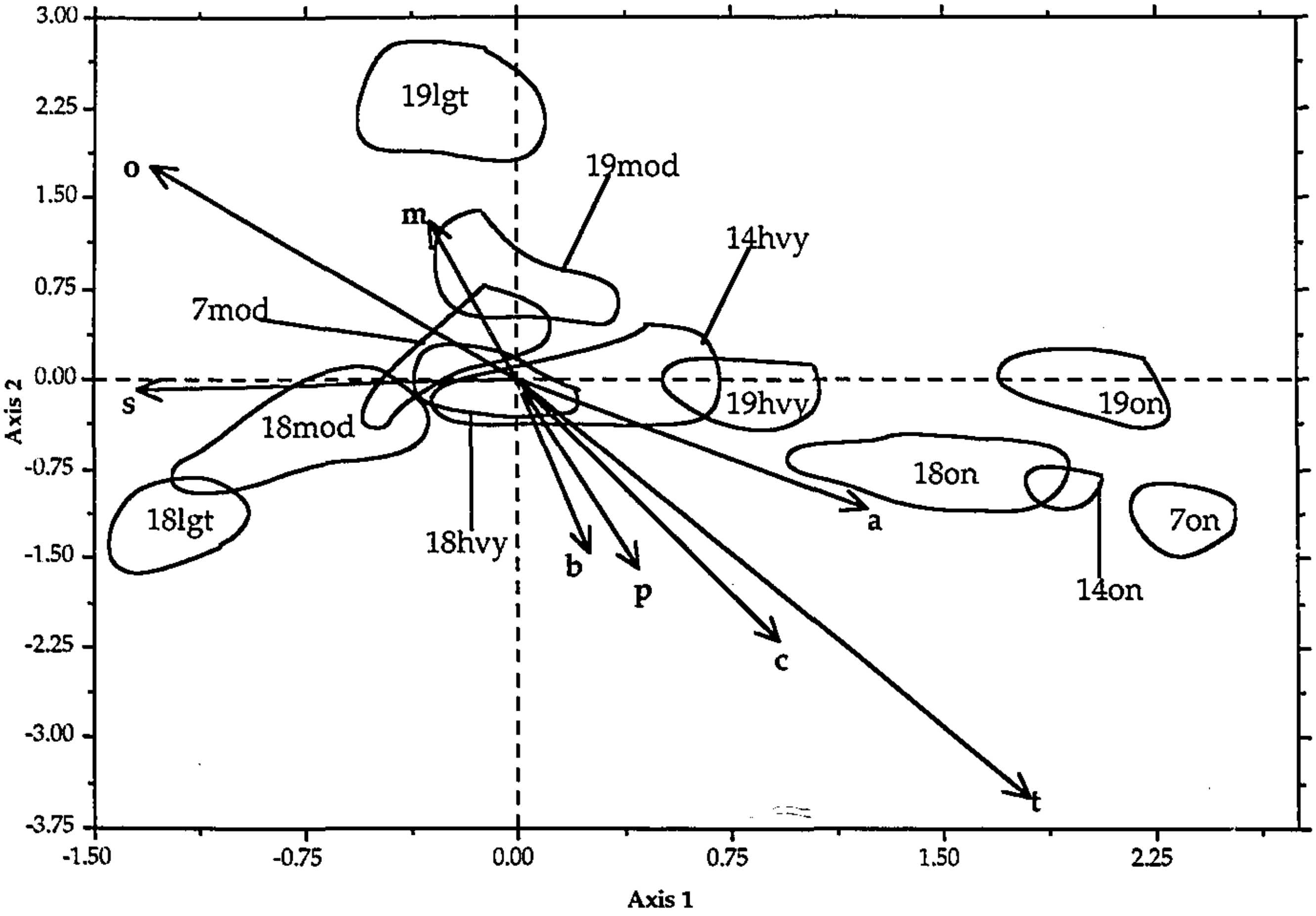
The overall structure of the triplot from the CCA ordination (**Appendix 24**) of the housepads and trampled stands is not unlike that from DCA (**Appendix 11**). The extracted gradients explain a significant amount of the variation in composition among stands. This is indicated by the moderate change in eigenvalues from DCA, and the fact that in a second CCA triplot using scaling 1 the distances between samples changes only minimally. The eigenvalues and species-environment correlations suggest that much of the variation in the data set is explained by the first two axes.

Compared to the other disturbance regimes there is a much greater range in composition among stands, particularly along the first two axes. This is true despite a reduction in number of active species in the analysis to 53 from 66, in vehicle tracks and drained meadows respectively, and 70 in the natural meadows. Once again, the first axis and overall significance achieved *p* -values of ≤0.01 in the Monte Carlo permutation. Of the individual environmental variables, only moisture and bulk density did not achieve *p* -values of ≤ 0.01, although bulk density had a *p* -value of 0.03.

The first axis is defined primarily by slope (**Appendix 25b**), which is lacking on the artificially-levelled housepads. This seems to be a surrogate variable for disturbance intensity as represented by the other factors combined, with intensity increasing from left to right. Several factors, such as active layer depth and compaction are clearly associated with the housepads in the lower right portion of the triplot. Removing slope from the analysis had the effect of switching soil temperature and active layer depth to the primary gradient, both of which remained negatively correlated with organic mat depth (triplot **not shown**). The arrangement of the stands changed somewhat in the ordination space to reflect this difference, but still retained their basic relationship to one another, indicating the importance of the disturbance intensity gradient.

The second axis represents a gradient of organic mat depth and pH. These tow variables are mutually uncorrelated, as are the respective variables moisture and bulk density (**Appendix 25b**). The analysis has resulted in a clearer separation of the moderately and lightly trampled portions of Stand 19, which were mostly lumped together in the floristic classification and DCA ordination. This separation is attributed to the greater moisture and deeper organic mat which characterize the lightly trampled terrain. The status of this stand is in apparent contrast to the lightly and moderately trampled components of the more mesic terrain in Stand 18. At increasing levels of disturbance, both vegetation and environment tend to converge toward the center of the triplot, as in the DCA analysis. However, while the plant communities of the differently constructed housepads tended to overlap with each other, and a bit with heavily trampled terrain in the DCA ordination, these stands are more discrete in the CCA triplot.

NOTE: To complete the gradient from severely disturbed housepads, through trampled terrain, to natural vegetation, adjacent mesic meadows were added to the data set previously used to create the biplot in **Appendix 15** and discussed above. Predictably, these natural meadows increased species turnover somewhat, were ordinated closest to the lightly trampled mesic meadow (Stand 18lgt) (**not shown**) in both DCA and CCA, and changed the structure of the triplot very little. However, the additional samples served to crowd the triplot, thus detracting from its among-stand interpretability, and were removed from subsequent analyses.



3.00
2.25
1.50
0.75
0.00
-0.75
-1.50
-2.25
-3.00
-3.75
Axis 2
-1.50
-0.75
0.00
0.75
1.50
2.25
Axis 1
19lgt
19mod
14hvy
7mod
18mod
18lgt
18hvy
19hvy
19on
18on
7on
14on
o
m
s
a
b
p
c
t

APPENDIX 25a. CCA summary for drained peatlands and controls at CR

Parameter	Canonical Coefficients Axis 1	Canonical Coefficients Axis 2	Inter-set Correlations Axis 1	Inter-set Correlations Axis 2
Organic Mat Depth	-0.023	-0.467	-0.020	-0.373
Soil Moisture	-0.253	0.113	-0.226	0.090
Soil pH	0.756	0.621	0.677	0.495
Bulk Density	-0.426	-0.059	-0.382	-0.047
Soil Temperature	-0.397	0.661	-0.356	0.527
Active Layer	-0.683	0.604	-0.612	0.482

	Axes 1	2	3	4
Eigenvalues	.181	.152	.043	.021
Species-environment correlations	.896	.798	.595	.395
Cumulative percentage variance				
of species data	13.7	25.2	28.5	30.0
of species-environment relation	42.9	78.8	89.1	94.0

APPENDIX 25b. CCA summary for housepads and trampled meadows at CR

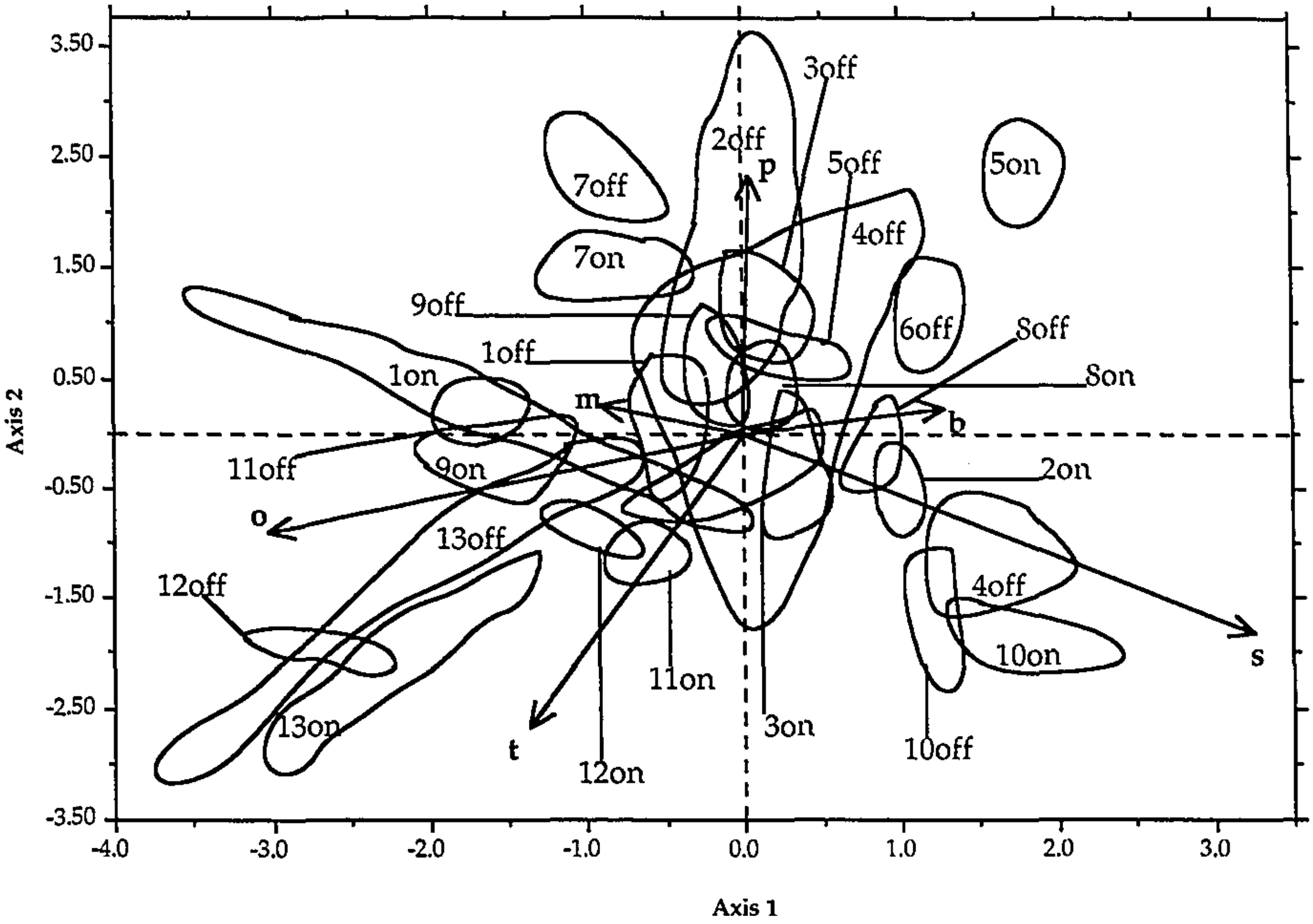
Parameter	Canonical Coefficients Axis 1	Canonical Coefficients Axis 2	Inter-set Correlations Axis 1	Inter-set Correlations Axis 2
Organic Mat Depth	-0.500	0.674	-0.464	0.593
Soil Moisture	-0.119	0.496	-0.111	0.437
Soil pH	0.161	-0.609	0.150	-0.536
Bulk Density	0.097	-0.556	0.090	-0.489
Soil Compaction	0.350	-0.281	0.325	-0.247
Soil Temperature	0.687	-0.515	0.638	-0.453
Active Layer	0.472	-0.411	0.438	-0.362
Slope	-0.990	-0.037	-0.918	-0.033

	Axes 1	2	3	4
Eigenvalues	.502	.373	.144	.113
Species-environment correlations	.928	.880	.688	.762
Cumulative percentage variance				
of species data	12.8	22.4	26.0	28.9
of species-environment relation	37.7	65.7	76.5	85.0

APPENDIX 26

Sample CCA ordination triplot of vehicle tracks and adjacent controls at TL

Eigenvalues in the CCA triplot are significantly reduced (**Appendix 28a**) compared to DCA on all four axes, indicating that the environmental variables measured do not account for a substantial proportion of the variation in species data. This conclusion is supported by the comparison of CCA triplots in scalings 2 (**Appendix 26**) and 1 (**not shown**). In the latter, overlap among stands is much greater than in the DCA biplot, which already has much overlap. Still, the first axis and overall results were significant at p =0.01 in the Monte Carlo test, with the first axis most closely tied to slope (correlation coefficient = 0.78), and negatively correlated with organic mat depth (coefficient = -0.73). The second axis is negatively correlated with soil temperature (coefficient = -0.63) and positively correlated with pH (coefficient = 0.56). Species-environment correlatations for the first two axes are 0.821 and 0.759 respectively. Individual environmental variables found to be significant at p =0.01 in the Monte Carlo test include slope, soil temperature, organic mat depth and pH. All others achieved p -values ≥ 0.05.

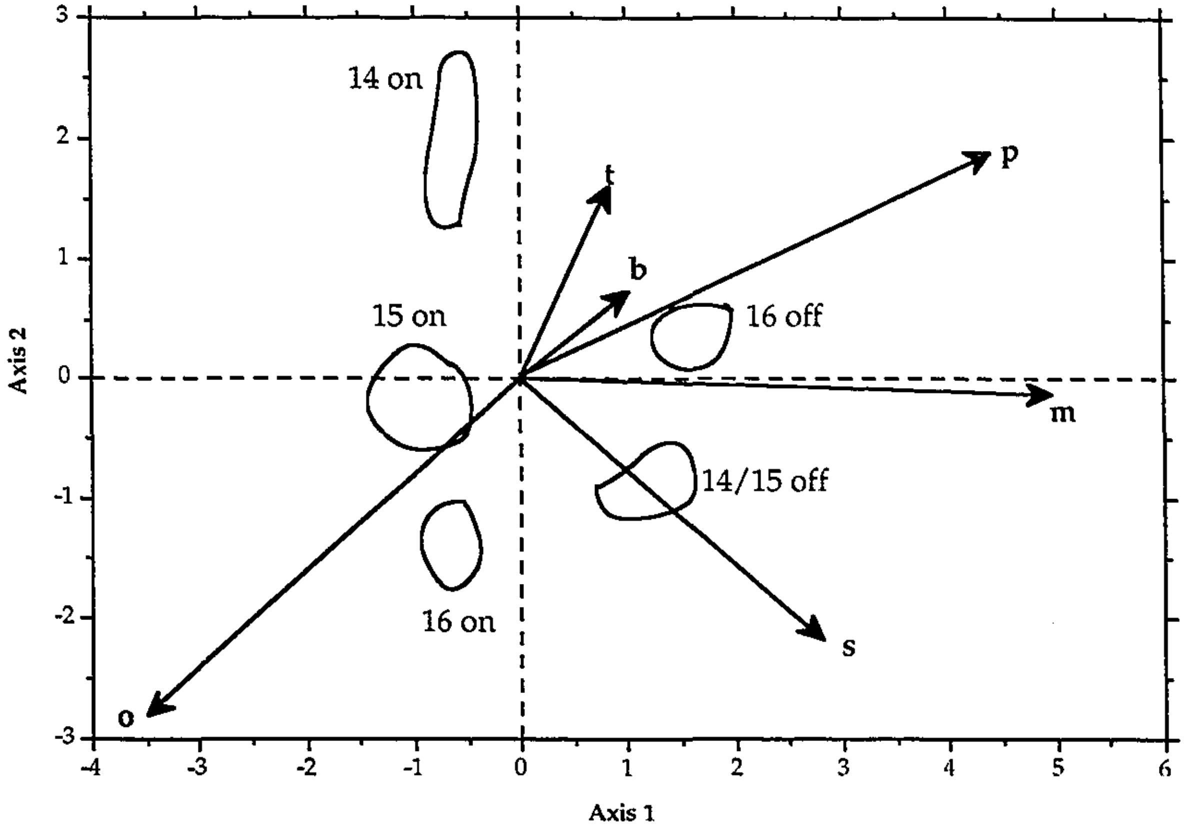

3.50
2.50
1.50
0.50
-0.50
-1.50
-2.50
-3.50
Axis 2
-4.0
-3.0
-2.0
-1.0
0.0
1.0
2.0
3.0
Axis 1
3off
2off
p
5off
5on
7off
4off
7on
9off
6off
8off
1off
1on
8on
m
b
11off
9on
2on
o
13off
12off
4off
10on
s
11on
13on
3on
10off
t
12on

APPENDIX 27

Sample CCA ordination triplot of Thule dwellings and adjacent beach ridges at TL

Prior to running CCA for this data subset, the Thule dwelling and adjacent beach ridge samples from Resolute Bay were removed due to the lack of environmental data for those stands. The eigenvalue for the first axis is decreased, from 0.640 to 0.550, while the value for second axis remains almost unchanged. The first axis is primarily one of moisture and pH, both of which are negatively correlated with organic mat depth (**Appendices 27 and 28a**). In observing that relative moisture is highest on the beach ridges, it should be noted that these values reflect the soil between the large cobbles which cover much of the surface. The substrate of the Thule dwellings, by comparison, was comprised almost solely of peat (and other organics), which was quite dry this late in the growing season, at least near the surface.

The second axis has a moderate negative correlation with organic mat depth (coefficient = -0.59) and the third axis (**not shown**) has a strong negative correlation with soil temperature (coefficient = -0.81). Both the first axis and overall results were significant at *p* =0.01 in the Monte Carlo test. All of the stands maintained significant distances from one another in both scaling 1 (**not shown**) and 2, indicating that both species and environment differ appreciably among stands. All individual environmental variables except organic mat depth and bulk density acheived *p* -values of 0.01 in the Monte Carlo test.


14 on
15 on
16 off
14/15 off
16 on
t
b
p
m
s
o
Axis 1
Axis 2
-4
-3
-2
-1
0
1
2
3
4
5
6
3
2
1
0
-1
-2
-3

APPENDIX 28a. CCA summary for vehicle tracks and controls at TL

Parameter	Canonical Coefficients		Inter-set Correlations	
	Axis 1	Axis 2	Axis 1	Axis 2
Organic Mat Depth	-0.728	-0.214	-0.598	-0.162
Soil Moisture	-0.216	0.054	-0.178	0.041
Soil pH	0.011	0.558	0.009	0.423
Bulk Density	0.306	0.100	0.251	0.076
Soil Temperature	-0.325	-0.631	-0.267	-0.478
Slope	0.776	-0.435	0.637	-0.330

	Axes			
	1	2	3	4
Eigenvalues	.108	.082	.052	.036
Species-environment correlations	.821	.759	.664	.705
Cumulative percentage variance				
of species data	5.0	8.8	11.2	12.8
of species-environment relation	33.4	58.6	74.6	85.7

APPENDIX 28b CCA summary for Thule dwellings & beach ridges at TL & RB

Parameter	Canonical Coefficients		Inter-set Correlations	
	Axis 1	Axis 2	Axis 1	Axis 2
Organic Mat Depth	-0.676	-0.590	-0.651	-0.496
Soil Moisture	0.955	-0.024	0.919	-0.021
Soil pH	0.849	0.345	0.817	0.306
Bulk Density	0.190	0.143	0.183	0.120
Soil Temperature	0.161	0.310	0.155	0.260
Slope	0.543	-0.421	0.522	-0.354

	Axes			
	1	2	3	4
Eigenvalues	.550	.234	.185	.119
Species-environment correlations	.962	.840	.807	.810
Cumulative percentage variance				
of species data	28.8	41.0	50.7	56.9
of species-environment relation	49.1	69.9	86.4	97.1

APPENDICES 29-39

Seasonal active layer development at CR

Appendices 29-34a and 35 illustrate mean seasonal active layer development during 1990 among stands representing various disturbance regimes surveyed at CR. These may be compared to means from many of the same stands during 1989 in **Appendices 34b and 36-39.** Responses were variable within disturbance regimes apparently depending on local drainage, bulk density of the soil, and the extent to which the organic mat remained compressed, all of which affect insolation. For example, Stands 2 and 13 are single-pass tracks on the same portion of a hummocky meadow with a 4-4.5° local slope. The tracks through Stand 2 are diagonal to the slope and the surface and soils are relatively moist compared to those of Stand 13. In the latter, tracks are perpendicular to local slope and only slightly wetter throughout the growing season. The differences are subtle but apparently control the rate of thaw in tracks, as can be seen from the 1990 profiles in **Appendix 29.** The more hydric tracks thaw more slowly than undisturbed soils in the early part of the season. This difference is reduced after the active layer reaches a depth of ca. 40 cm. Less than two weeks later, after thawing to > ca. 55 cm, thaw is once again accelerated in the control area. In contrast, the soils of more mesic tracks, with greater bulk densities, thaw at rates similar to controls during the early growing season. However, these rates diverge by the time thaw depth reaches 40 cm, at which point the rate of thaw is increased in the disturbed soils. These differences were fundamentally similar in 1989 (**Appendix 36**), although the timing of measurement varied, being determined by the time of snow melt.

The pattern of thaw was substantially different in the non-hummocky meadows with late-lying snow banks and poorly developed vegetation (**Plates 2.4 and 3.4**). Here, the organic mat was so thin that even a single-pass track was sufficient to either destroy or severely damage it. The spring runoff was thus able to easily erode the organic mat despite the near absence of slope (0-1.0°). Rutting allowed deeper snow to accumulate in the tracks (**Plate 2.4**), which melted slightly later and resulted in a lag in thaw rate. This lag was generally not overcome until a depth of ca. 70 cm (**Appendix 30**), a pattern which was repeated each year (**Appendix 37a**) despite the distinct differences between these two particular growing seasons, 1989 being the shorter and cooler of the two. Due to the lack of peat in this portion of the study area, most thaw occurred almost immediately after snow melt. By the second snow-free week in 1990, the undisturbed soils had thawed to a depth of almost 60 cm out of a seasonal total of 90 cm by the time of the thermal maximum in late August.

In hummocky meadows, comparisons between active layer development in water channels and adjacent interfluves revealed differences between single- and multi-pass tracks, drained areas downslope, and control areas upslope. Soils beneath single-pass tracks in the mesic interfluve

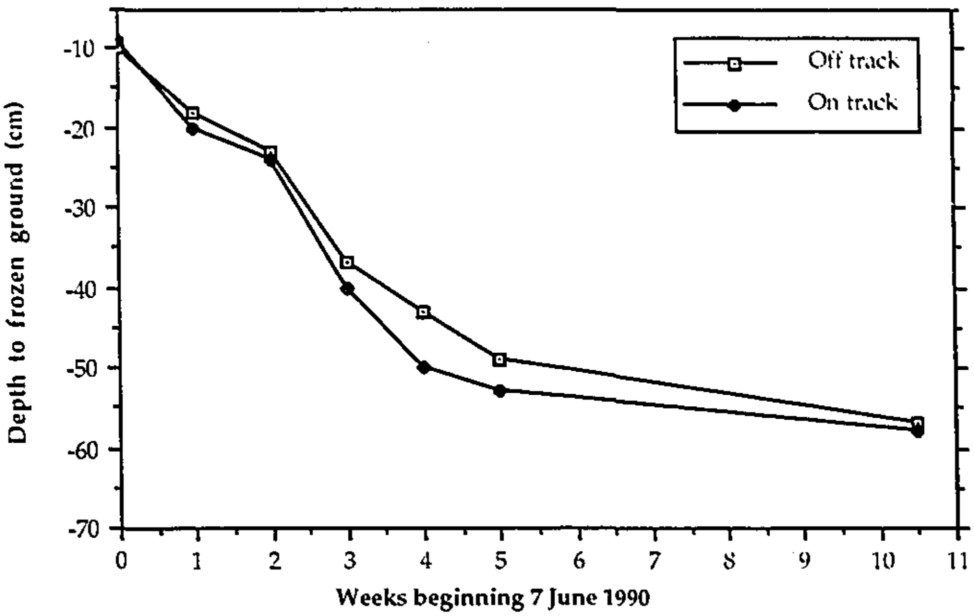
(**Appendix 31a**) thawed more quickly but to shallower depths overall than those in the adjacent controls. Soils in the drained peatland downslope thawed more rapidly than soils of either the tracks or the controls and to an overall depth equivalent to the latter. Where the same set of single-pass tracks dissects a water channel (**Appendix 31b**), the soils beneath were relatively loose (low bulk densities) and saturated and thawed more slowly than the controls, as was seen in other poorly drained stands elsewhere in the area, such as **Stand 13** (**Appendix 29b**). In contrast, drained soils downslope from these tracks thawed more slowly throughout most of the first half of the growing season.

Multi-pass tracks perpendicular to local slope across both interfluves and water channels elicited a similar response to single-pass tracks across water channels by delaying thaw in drained areas, at least in the early part of the growing season (**Appendix 32**). However, thaw in the tracks themselves was greatly accelerated relative to both drained peatlands and control areas. This response was expected, given the virtual lack of vegetation and peat and the moist, compact nature of the soils. This pattern was repeated in both years (**Appendix 37b**). After three or four weeks, thaw rate in drained areas increased and equaled (water channel) or surpassed (interfluve) that in control areas. The response in multi-pass tracks parallel to local slope was generally predictable. Thaw rate and overall depth were consistently greater in the tracks where the organic mat was destroyed but a dense cover of sedges and grasses had developed on the moist, slightly compacted soils (**Appendix 33, Plate 3.9**). Comparisons with profiles from 1989 (**Appendix 38**) reveal that the differences between the tracks and controls were significantly reduced in the cooler of the two years. However, the overall pattern of thaw remained the same.

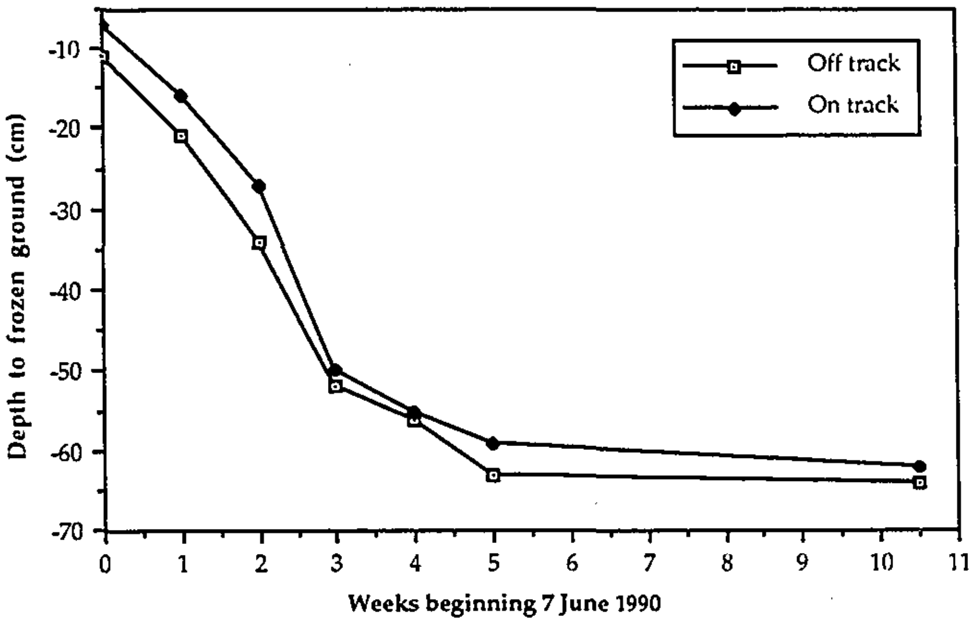
Profiles from an abandoned housepad with no added materials (e.g. sand, gravel) and from adjacent trampled terrain reveal a clear gradient in which thaw rate is positively correlated with intensity of disturbance at the beginning of the growing season. This gradient was apparent through both years (**Appendix 34**). These differences were either reduced or reversed after three to four weeks. Thus, soils beneath lightly trampled areas thawed slowly, about the same as undisturbed soils. The driest, most heavily compacted soils, those on the former housepad, thaw significantly faster and to greater depths than any of the trampled soils. The same pattern of thaw occurs on abandoned housepads where sand and gravel were used (**Appendices 35 and 39**).

APPENDICES 29a (top) and 29b (bottom)

Active layer - Clyde River - Stand 2
Single-pass tracks and adjacent controls

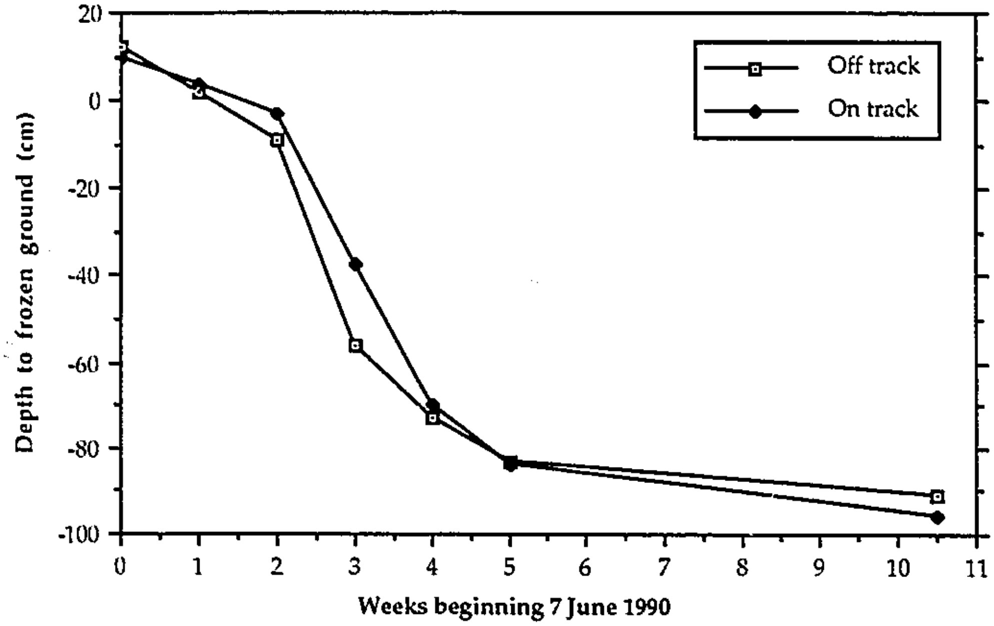


Active layer - Clyde River - Stand 13
Single-pass tracks and adjacent controls



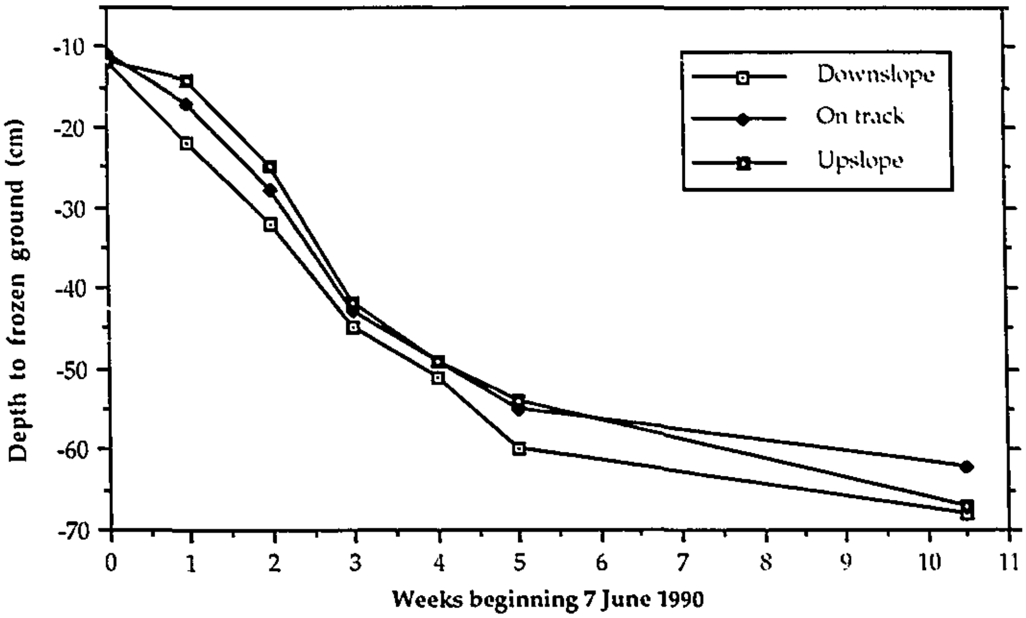
APPENDIX 30

Active layer - Clyde River - Stand 3
Single-pass tracks and adjacent controls

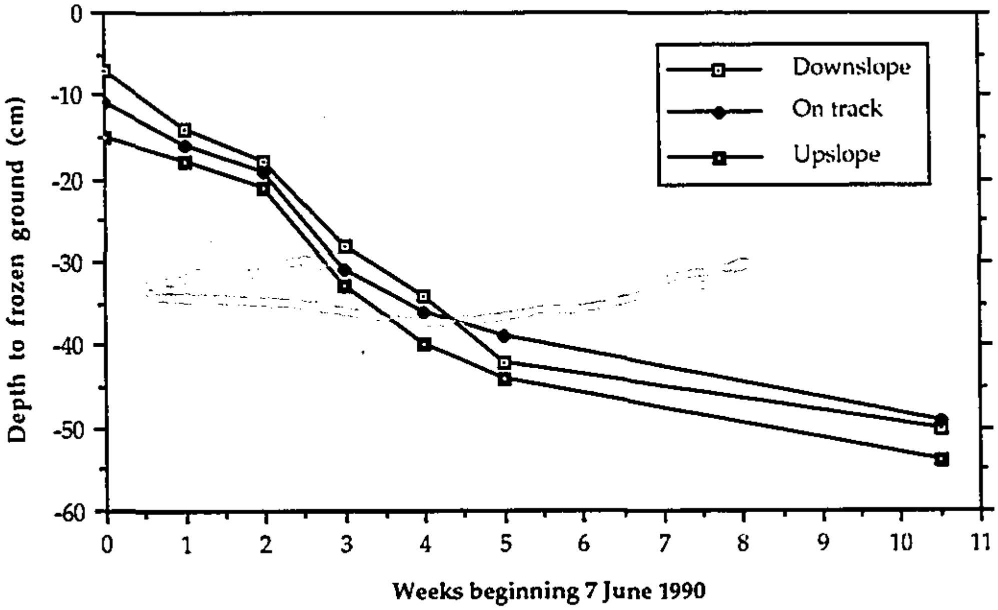


APPENDICES 31a (top) and 31b (bottom)

Active layer - Clyde River - Stand 15
Single-pass tracks, drained peatlands & adjacent controls

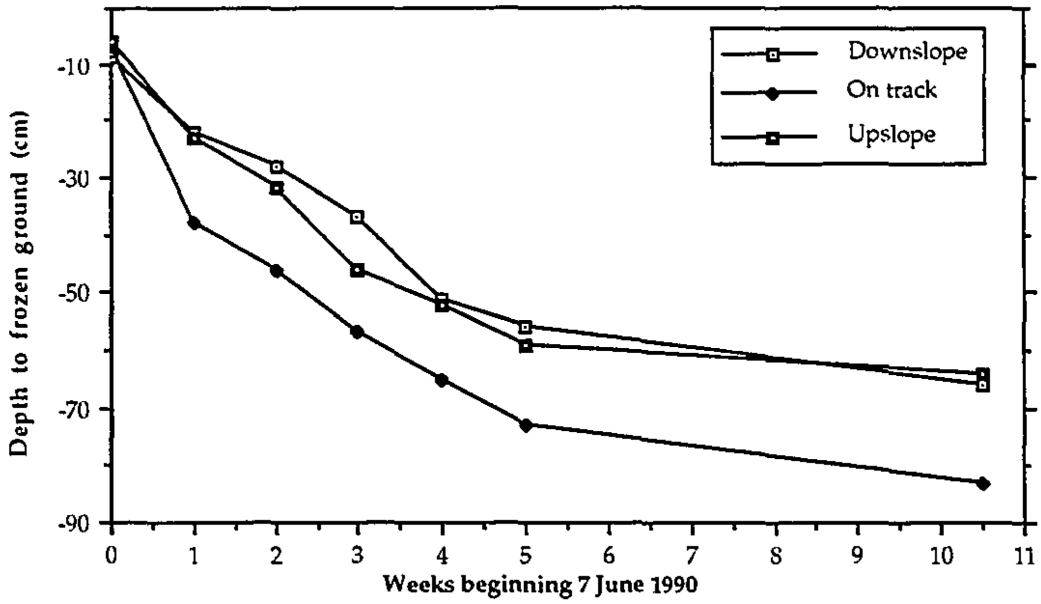


Active layer - Clyde River - Stand 16
Single-pass tracks, drained peatlands & adjacent controls

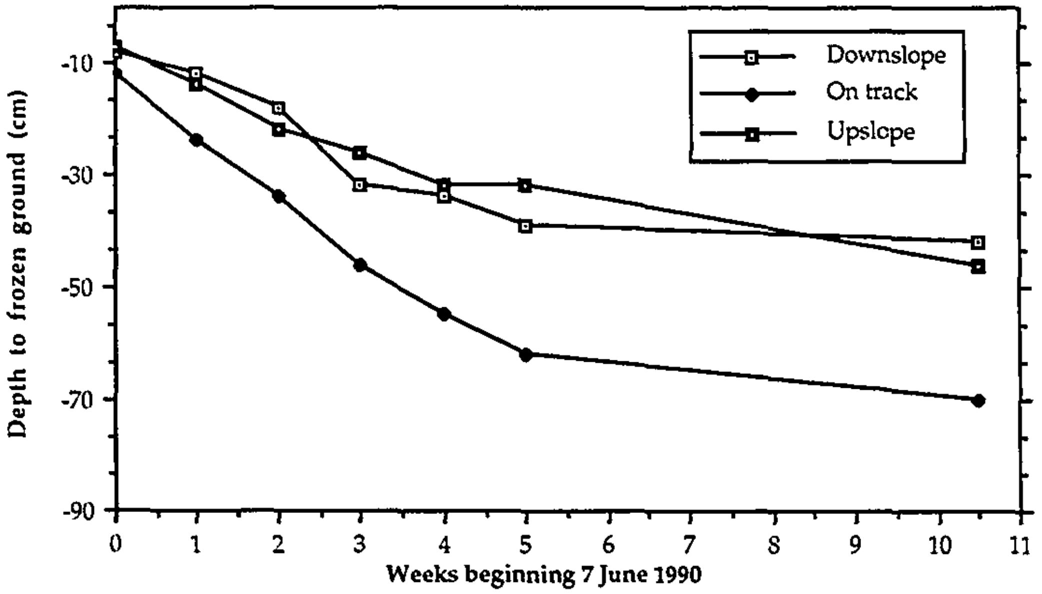


APPENDICES 32a (top) and 32b (bottom)

Active layer - Clyde River - Stand 11
Multi-pass tracks, drained peatlands & adjacent controls

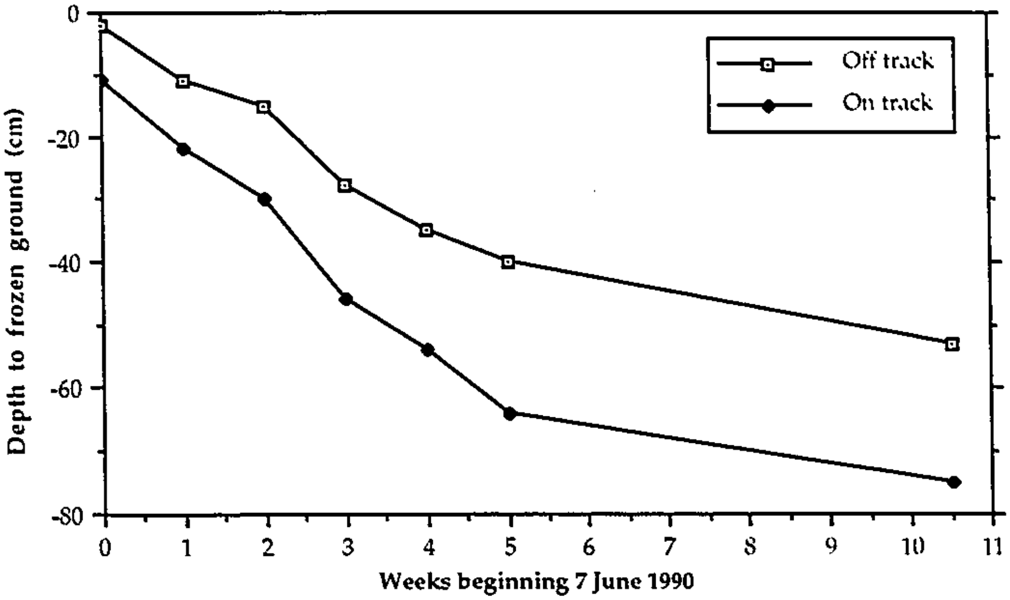


Active layer - Clyde River - Stand 12
Multi-pass tracks, drained peatlands & adjacent controls

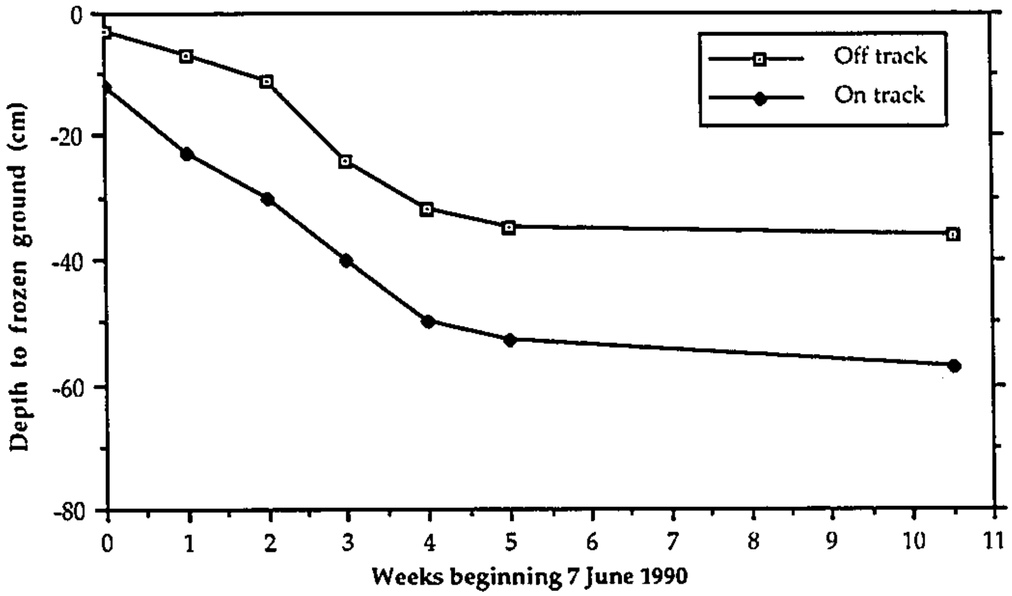


APPENDICES 33a (top) and 33b (bottom)

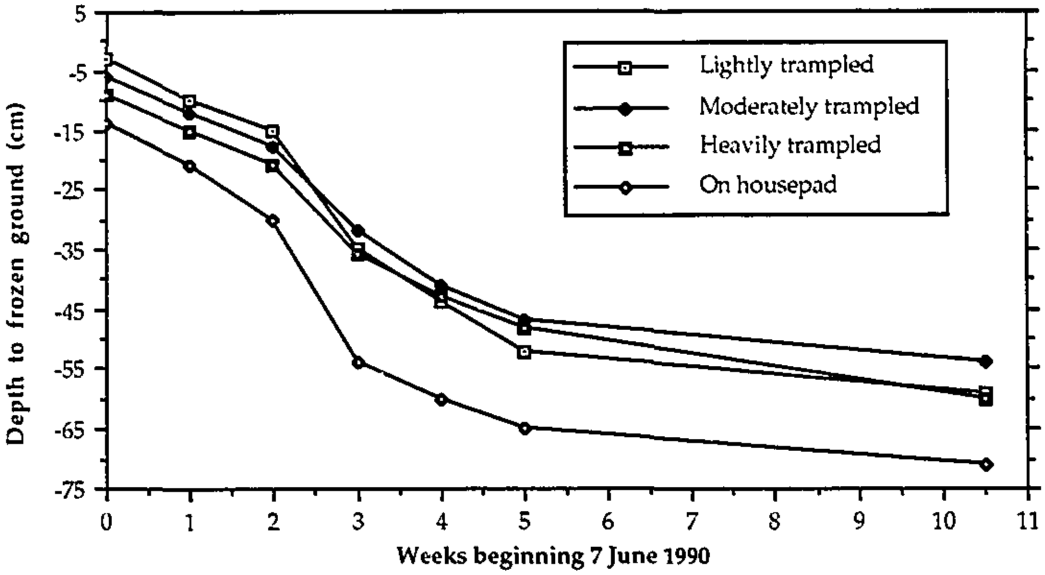
Active layer - Clyde River - Stand 9
Multi-pass tracks and adjacent controls



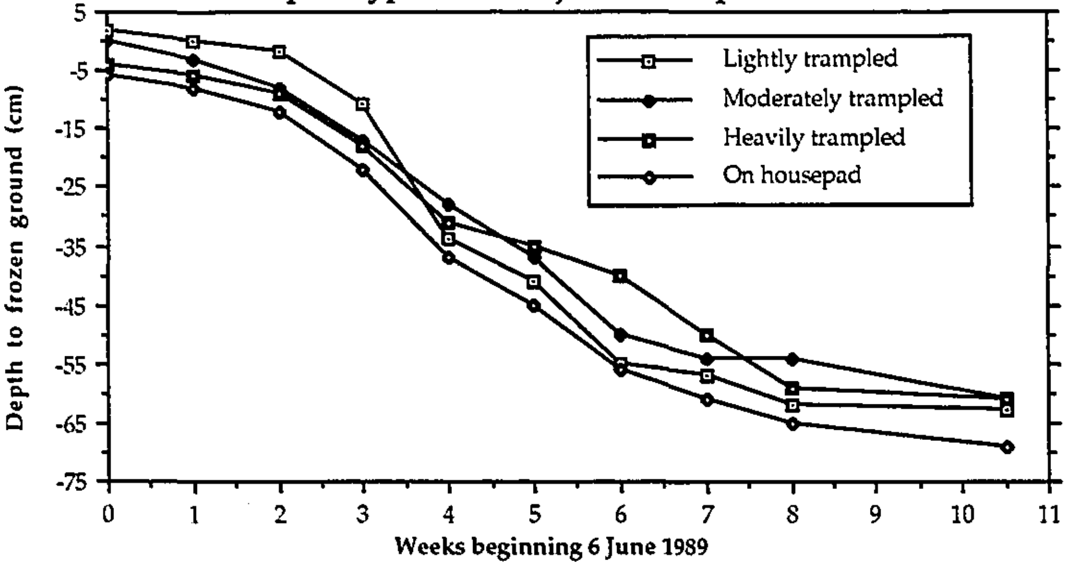
Active layer - Clyde River - Stand 10
Multi-pass tracks and adjacent controls



APPENDICES 34a (top) and 34b (bottom)

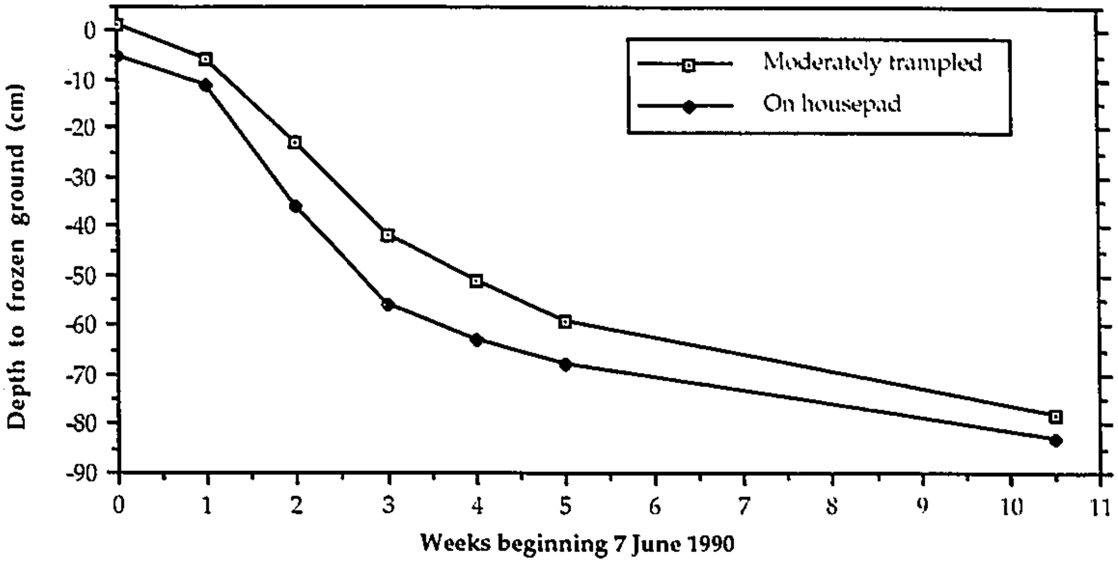


Active layer - Clyde River - Stand 18
Housepad Type A and adjacent trampled meadow

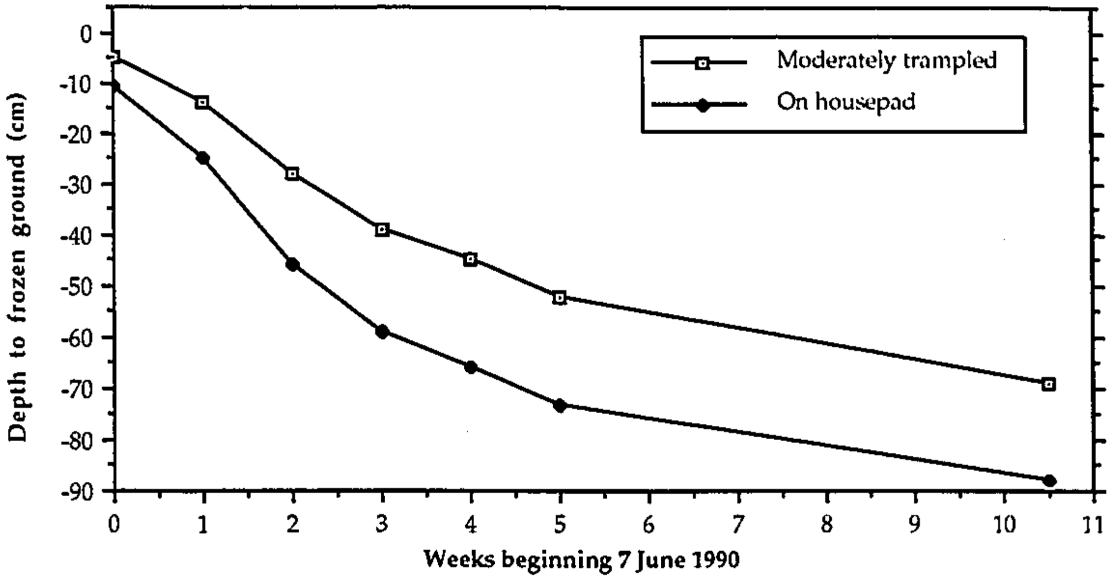


Active layer - Clyde River - Stand 18
Housepad Type A and adjacent trampled meadow

APPENDICES 35a (top) and 35 b (bottom)

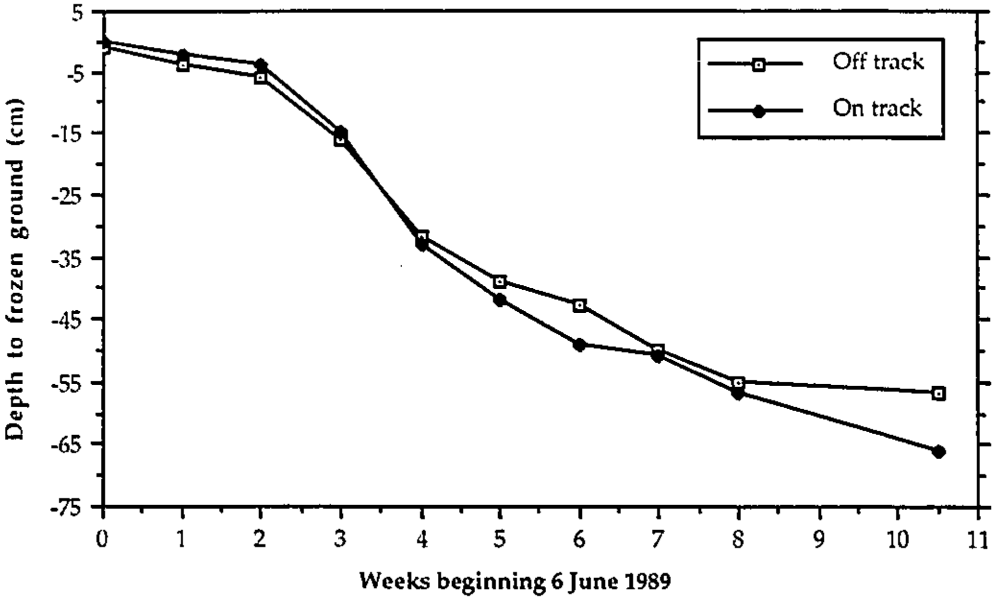


Active layer - Clyde River - Stand 7
Housepad Type B and adjacent trampled meadow

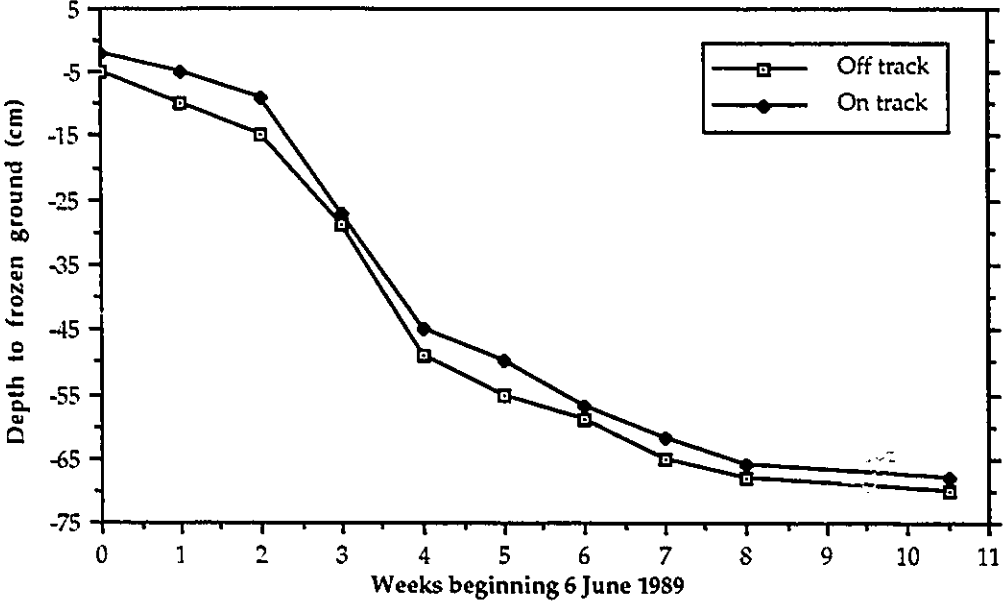


Active layer - Clyde River - Stand 14
Housepad Type B and adjacent trampled meadow

APPENDICES 36a (top) and 36b (bottom)



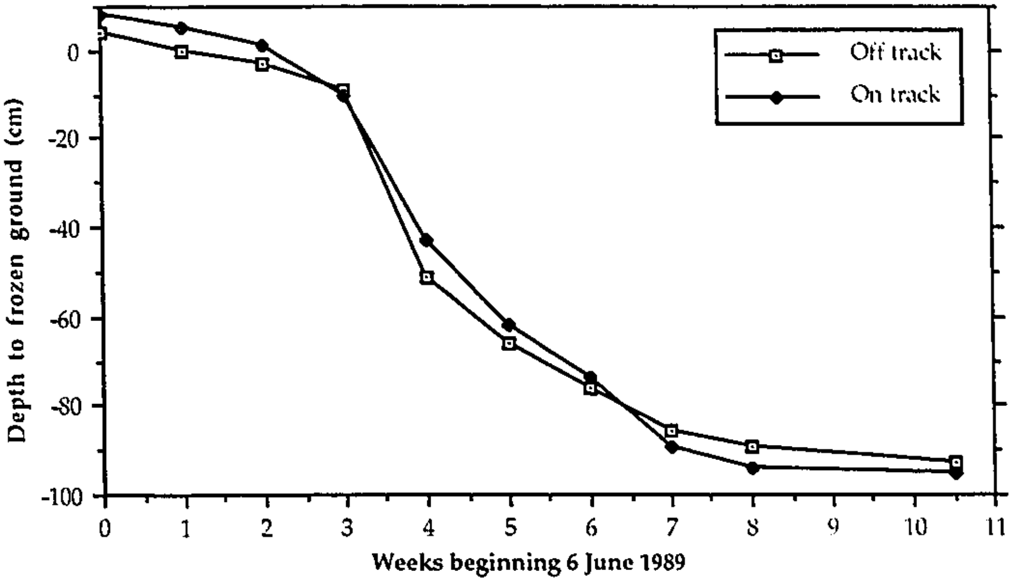
Active layer - Clyde River - Stand 2
Single-pass tracks and adjacent controls



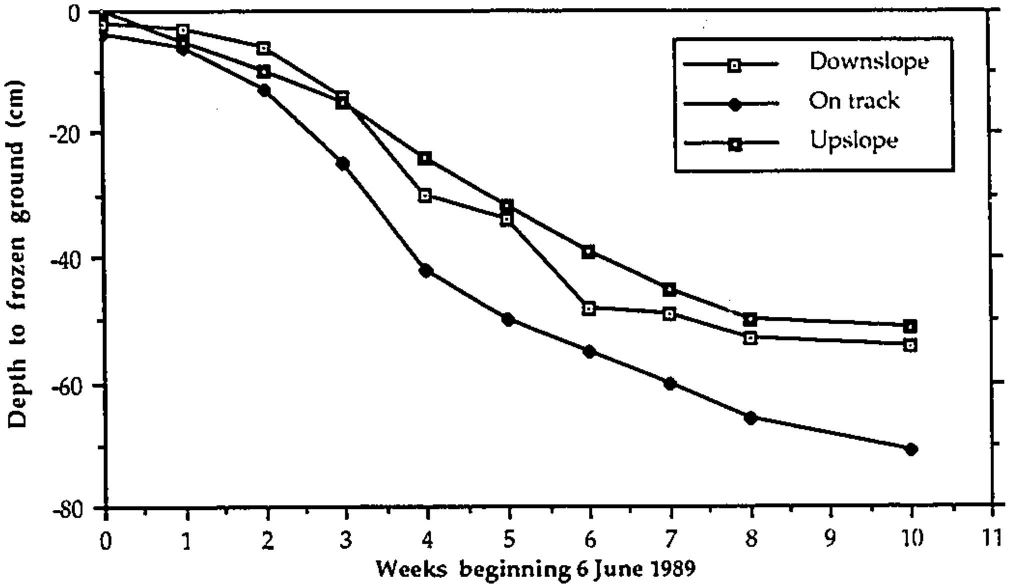
Active layer - Clyde River - Stand 13
Single-pass tracks and adjacent controls

APPENDICES 37a (top) and 37b (bottom)

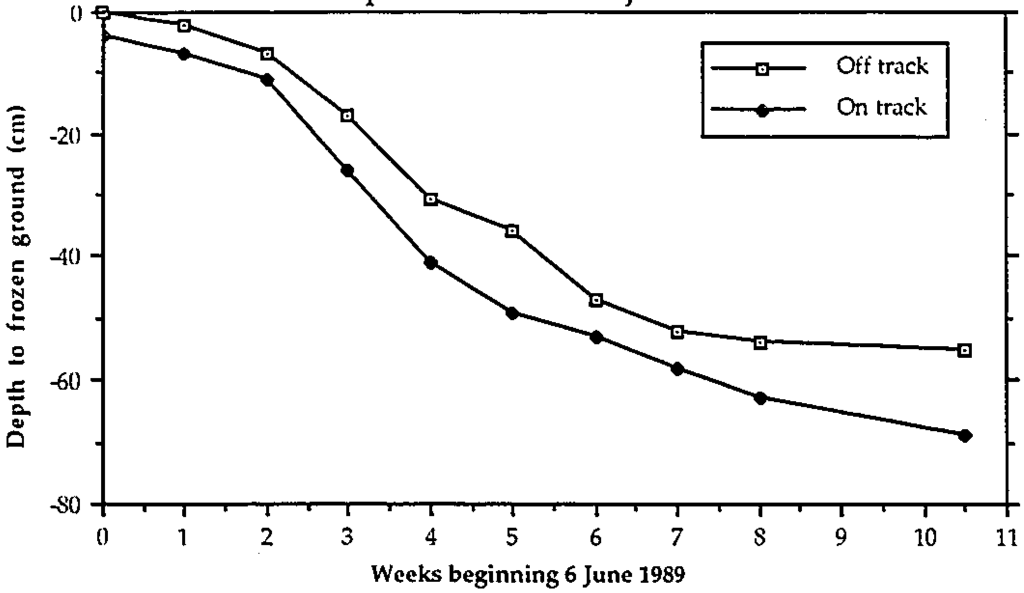
Active layer - Clyde River - Stand 3
Single-pass tracks and adjacent controls



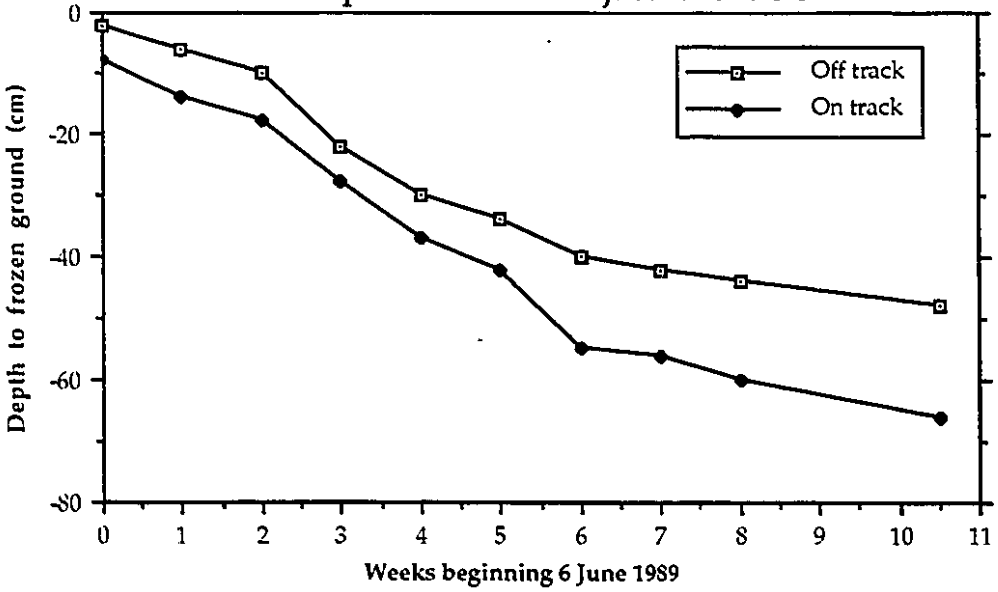
Active layer - Clyde River - Stand 12
Multi-pass tracks, drained peatlands and adjacent controls



APPENDICES 38a (top) and 38b (bottom)

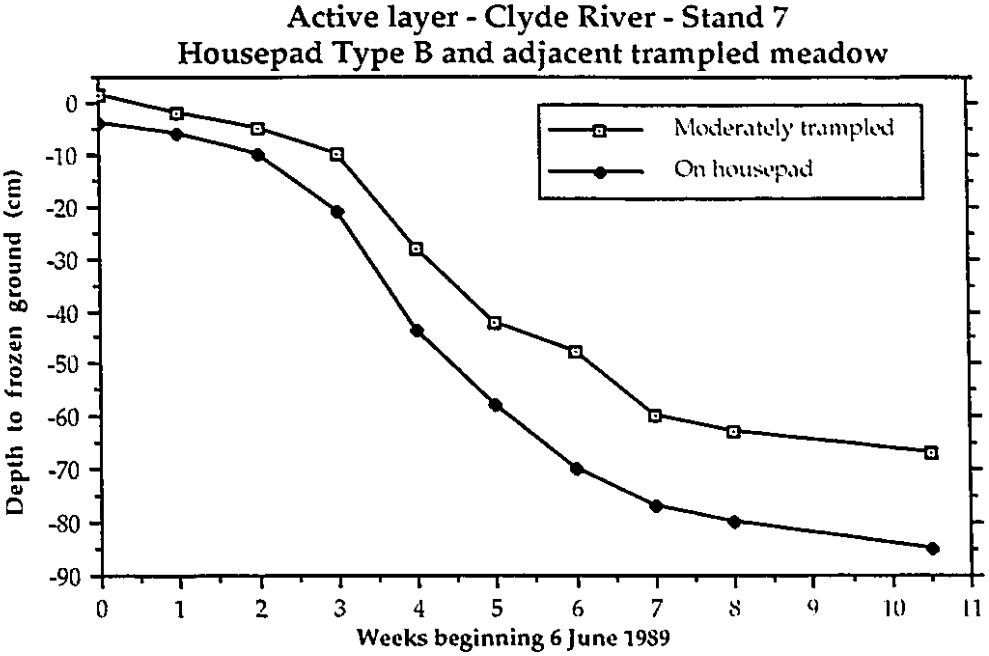


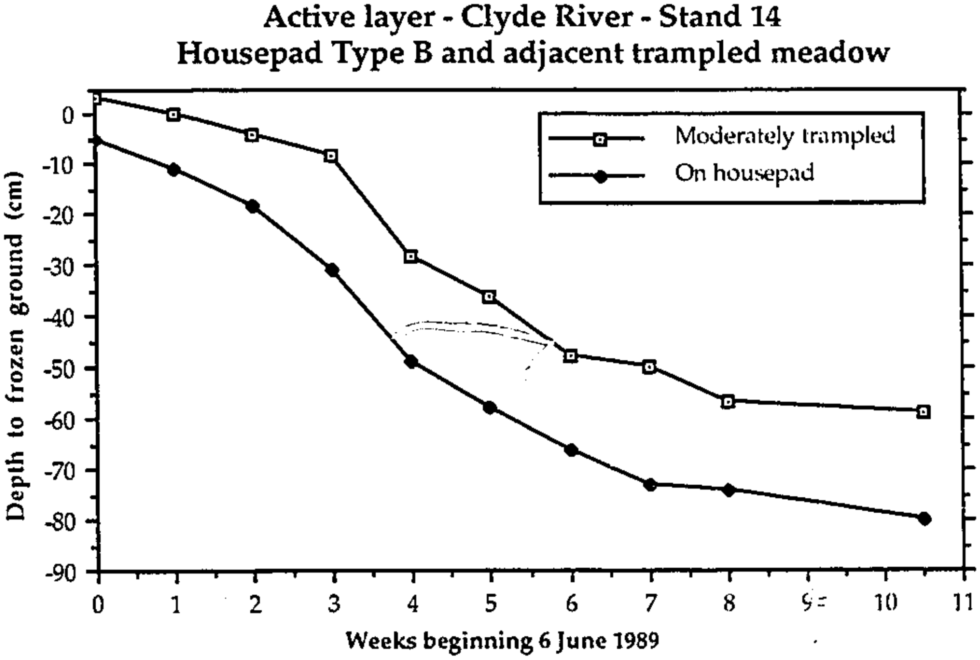
Active layer - Clyde River - Stand 9
Multi-pass tracks and adjacent controls



Active layer - Clyde River - Stand 10
Multi-pass tracks and adjacent controls

APPENDICES 39a (top) and 39b (bottom)



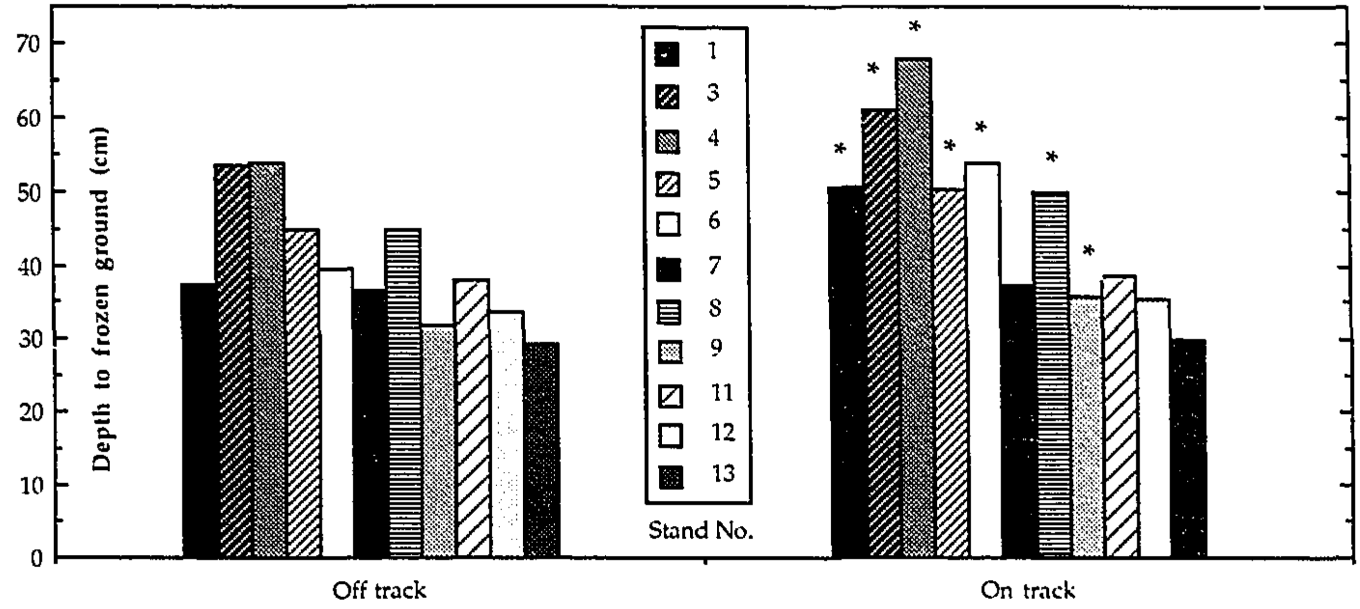


APPENDIX 40

Active layer development at TL

Mid-season thaw depths in vehicle tracks and adjacent controls at TL are illustrated in **Appendix 40** and reveal a variety of responses. The tracks which remain most severely disturbed, such as those in Stands 1 and 4, contained standing water throughout the growing season, supported only a thin cover of aquatic and emergent plants, and thawed to significantly greater depths than adjacent mesic and hygric sedge meadows. In the wettest meadows with standing or lightly flowing water throughout the summer, naturally recovering areas (Stands 7, 13) and sites of assisted restoration using sod plugs (Stands 11, 12) were no different from adjacent controls. In the recently (1986) disturbed areas (Stands 8, 9, **Plate 3.10**). As at CR, thaw depth was increased in more mesic tracks and controls (Stand 8) compared to an imperfectly drained area nearby (Stand 9). In mesic hummocky meadows where vegetation cover was lacking or remained sparse in the tracks (Stands 5, 6), thaw was significantly greater in tracks, as was the case at CR. Thaw depths in few-pass tracks through hummocky meadows (Stands 2, 10 - **not shown**) did not differ from their adjacent controls. Probing of thaw depths was not attempted on unexcavated Thule dwellings (Stands 15, 16) for fear of potential damage to artifacts beneath the surface. However, probing along the back wall of the recently excavated and reconstructed Thule dwelling (Stand 14) revealed a mean thaw depth of 37.2 cm, significantly greater ($p \leq 0.01$, Mann-Whitney test) than the mean depth of 26 cm beneath the adjacent beach ridge.

Active layer depth - Multi-pass tracks and adjacent controls - Truelove Lowland
28 July 1990



* = significant at p=0.05 (Mann-Whitney Test)

APPENDICES 41-45

Soil temperature regimes at CR

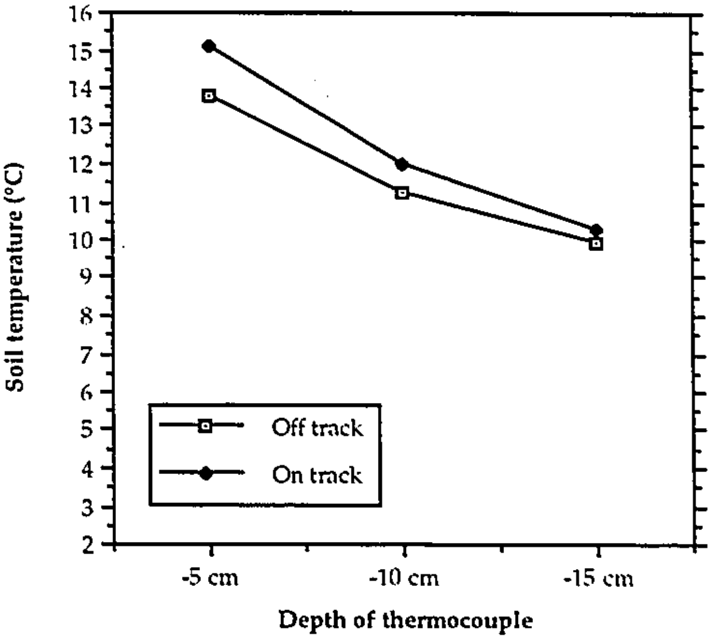
Single-pass tracks through **Stand 1** (**Appendix 41b**), a moist hummocky meadow displayed little difference in the upper layers of soil but at depths of 15 cm soils beneath tracks were up to 2°C warmer on a 'slightly-above-average' (7.5°C) day early in the growing season. In contrast, single-pass tracks through an area of late-lying snow which lacks hummocks (**Appendix 41a**) were only 0.5 to 1.5°C warmer than adajcent controls on a very warm (12.5°C) day. This is attributed to the lighter tone of the exposed mineral soils in the tracks compared to the darker and thin but more or less closed vegetation cover of the control area. In contrast, soils beneath single-pass tracks perpendicular to a water channel (**Appendix 42**) were significantly cooler at each depth on a similarly warm day. Referring back to the plot of active layer development for this stand in 1990 (**Appendix 31b**), this is consistent with observation that active layer development was retarded in tracks relative to controls upslope. This date immediately preceeded a time of transition when the rate of thaw in drained areas began to exceed that of tracked soils and approached that of control areas upslope. Thus, at a depth of 10-15 cm, drained soils downslope from the tracks remained cooler than both tracks and controls. At these same depths the soils beneath the 'berm' (see **Plate 3.2**) in between individual tracks were intermediate in terms of temperature.

In multi-pass tracks and drained peatlands, 5 July 1990 (**Appendix 43a**), temperatures were coolest in the control area, warmest in the tracks and intermediate in the drained area downslope. The active layer profile from this date (**Appendix 32b**) shows depths of thaw corresponding to this pattern; the control area being shallowest, the tracks deepest and the drained area intermediate. A similar pattern was apparent in Stand 11 on 19 July 1990 (**Appendix 43b**), except that the uppermost layers of soil in the drained area were slightly warmer than the control area. At a depth of 15 cm the temperatures were about the same and at a depth of 60 cm the active layers in these areas were roughly equivalent (**Appendix 32a**). Multi-pass tracks parallel to local slope exhibited the range of soil temperatures one might expect from the trajectory of active layer development (**Appendix 33**); tracked soils were substantially warmer than adjacent controls (**Appendix 45a**).

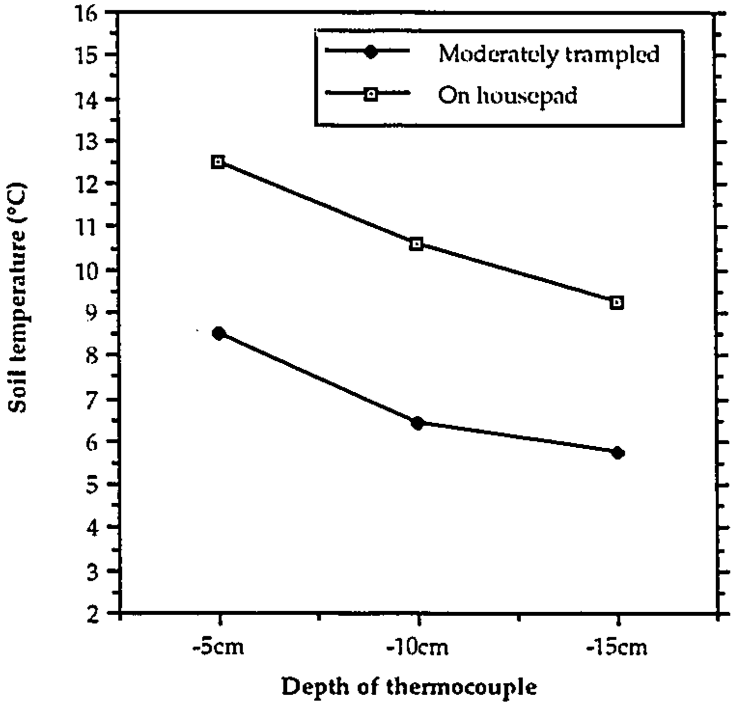
All types of housepads were significantly warmer than adjacent trampled meadows (**Appendices 44 and 45b**). In Stand 19 (**Appendix 45b**), where soils in different zones of trampling intensity were measured across a wet meadow, there is a clear temperature gradient at a depth of 15 cm, from coolest (lightly trampled areas) to warmest (heavily trampled areas). A different pattern is evident in the more mesic meadows of Stand 18 (**Appendix 44a**). There, lightly trampled portions of the meadows were warmest at a depth of 15 cm and heavily trampled areas were coolest. This would be consistent with the amount of cover and relative albedo of the vegetation in these respective zones. Neither pattern was consistent at shallower depths. The active layer profile from Stand 18 on this date (**Appendix 34a, week 4**) shows that the depth of thaw was similar in the lightly and heavily trampled zones, though slightly shallower in the moderately trampled zone. The readings from Stand 7 (**Appendix 44a**) are consistent with the substantial active layer differences in active layer depths between the two vegetation types.

APPENDICES 41a (top) and 41b (bottom)

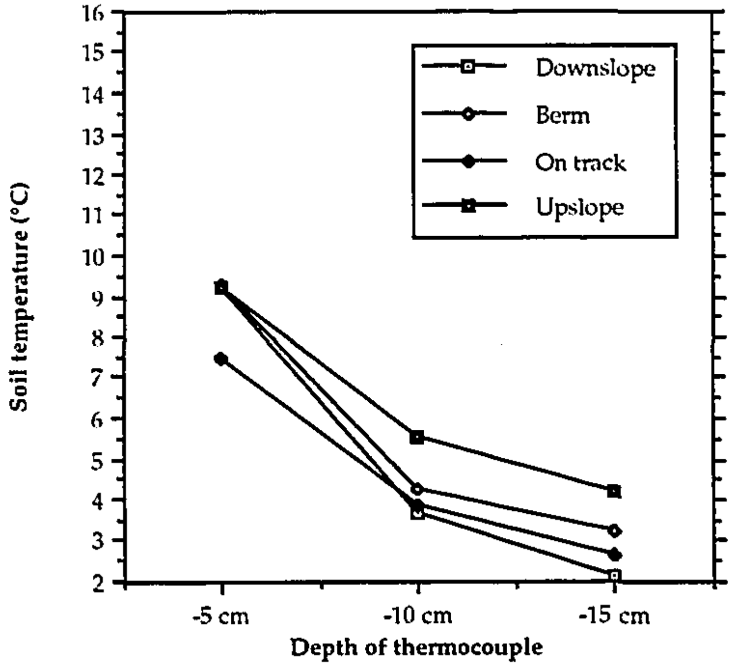
Stand 3 -Single pass tracks & adjacent controls
Clyde River - 19 July 1990 - Mean ambient temp. = 12.5°C



Stand 7 - Housepad Type B & adjacent trampled wet meadow
Clyde River - 5 July 1990 - Mean ambient temperature = 12.5°C



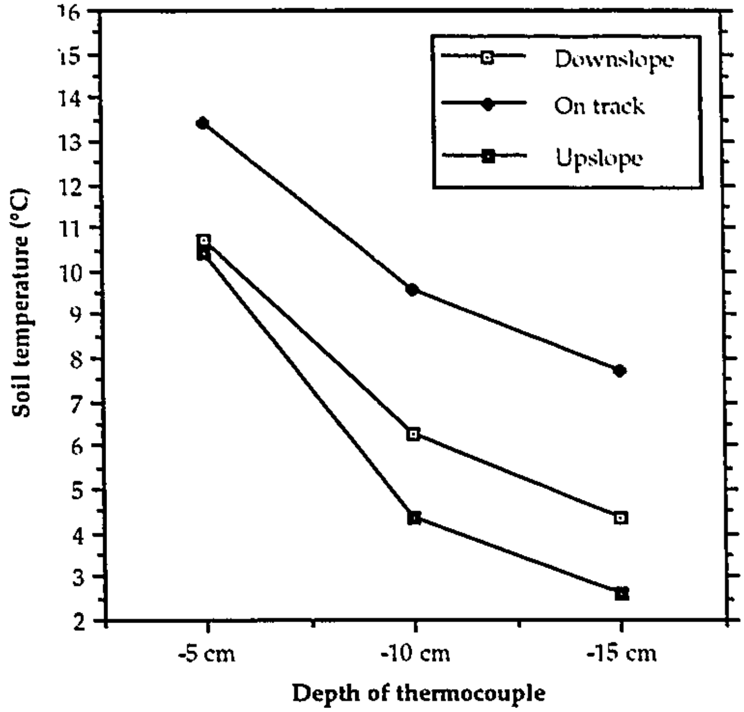
APPENDIX 42



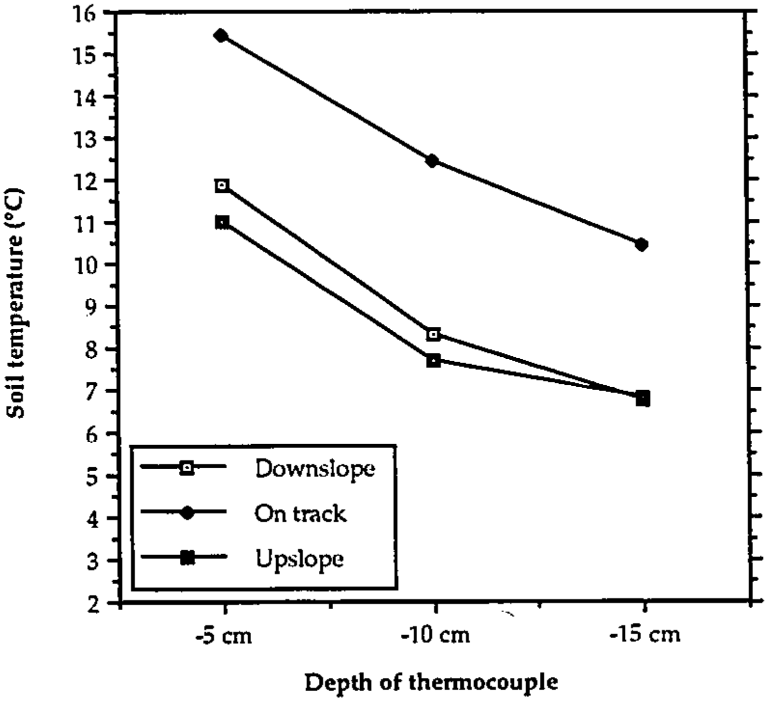
Stand 16 - Single-pass tracks & adjacent controls
Clyde River - 5 July 1990 - Mean ambient temp. = 12.5°C

APPENDICES 43a (top) and 43b (bottom)

Stand 12 - Multi-pass tracks, drained peatlands & adjacent controls
Clyde River - 5 July 1990 - Mean ambient temperature = 12.5°C

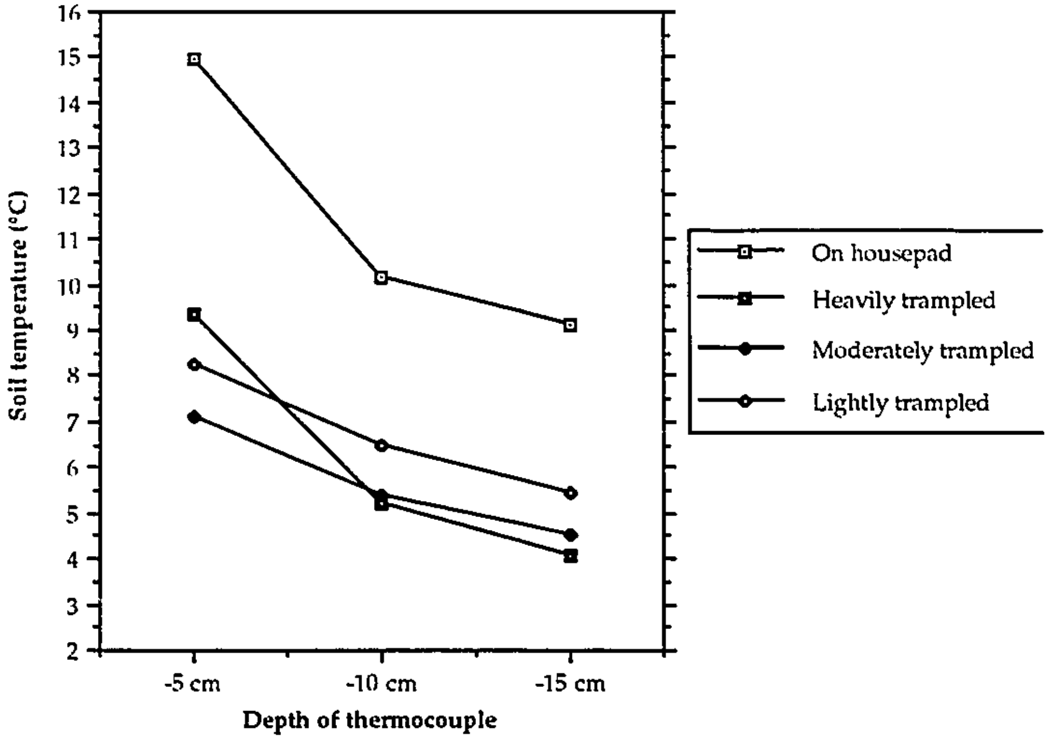


Stand 11 - Multi-pass tracks, drained peatlands and adjacent controls
Clyde River - 19 July 1990 - Mean ambient temperature = 12.5°C

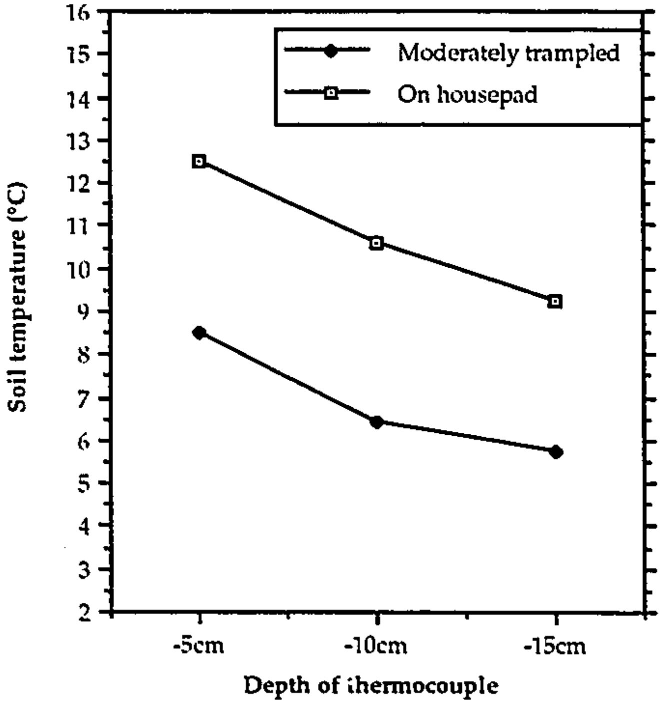


APPENDICES 44a (top) 44b (bottom)

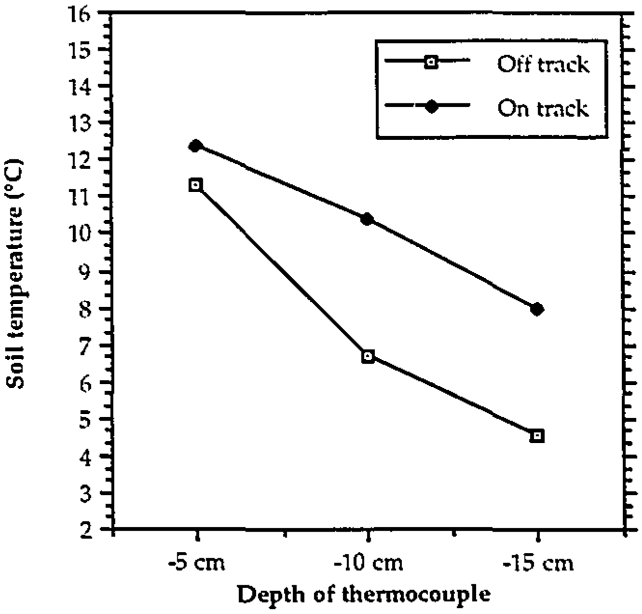
Stand 18 - Housepad Type A & adjacent trampled mesic meadow
Clyde River - 6 July 1990 - Mean ambient temperature = 9.5°C



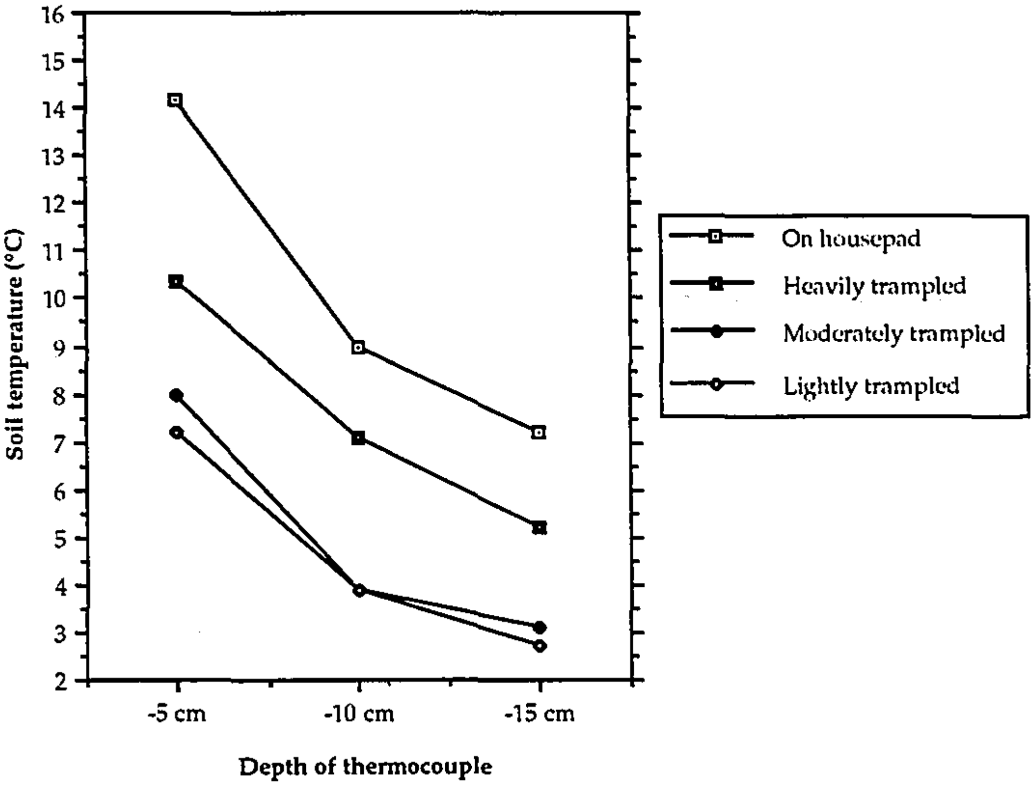
Stand 7 - Housepad Type B & adjacent trampled wet meadow
Clyde River - 5 July 1990 - Mean ambient temperature = 12.5°C



APPENDICES 45a (top) and 45b (bottom)



Stand 9 - Multi-pass tracks & adjacent controls
Clyde River - 7 July 1990 - Mean ambient temp. = 7.5°C



Stand 19 - Housepad Type C & adjacent trampled wet meadow
Clyde River - 6 July 1990 - Mean ambient temperature = 9.5°C

APPENDICES 46-49

Soil temperature regimes at TL

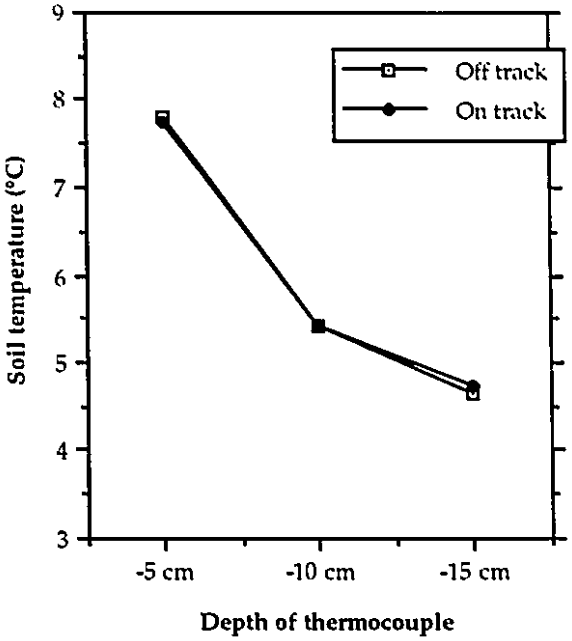
At TL, temperatures of soils beneath few-pass vehicle tracks were no different from those of adjacent controls in Stand 10 (**Appendix 46a**), but were substantially warmer than controls in Stand 2 (**Appendix 46b**). This was certainly related to the amount of surface moisture and vegetation cover (see subsection 3.10.iii). In fact, the soils in both stands were relatively moist when sampled, but the vegetation canopy in Stand 2 was open or lacking in the tracks. Meanwhile, the tracks in Stand 10 had a mostly closed vegetation canopy.

A pattern similar to that described for the older few-pass tracks is seen in the more recently tracked meadows in Stands 8 and 9 which were disturbed in 1986. In Stand 8 (**Appendix 47a**), which is slightly mesic, soil temperatures in tracks and controls were similar. The organic mat in the tracks, while mostly destroyed, did support tillers of Carex aquatilis var. stans (**Plate 3.10**). Stand 9, in contrast, was imperfectly drained and similarly disturbed but showed little or no recovery. Here, surface layers of soil were significantly warmer (**Appendix 47b**), though at 15 cm there was almost no difference.

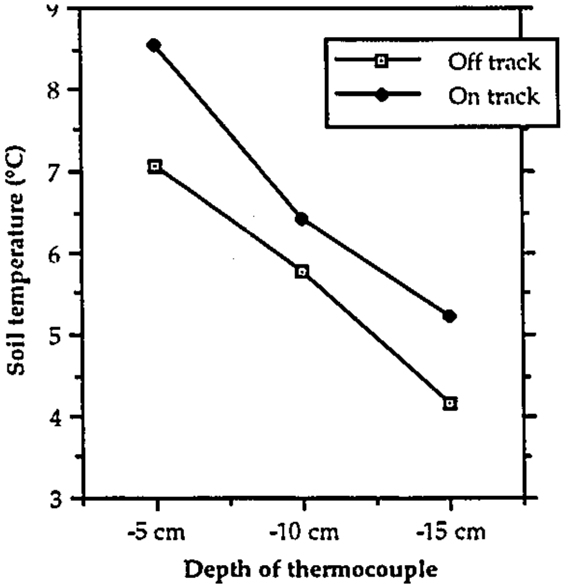
Across the Truelove Lowland, older tracks showed similar patterns. Where vegetation cover remained sparse, usually in more mesic meadows such as in Stand 5 (**Appendix 48**), soils were consistently warmer in the tracks, even after ≥48 hr of overcast skies. In wetter meadows, the vegetation canopy was generally closed and no significant differences were measured. At the archaeological sites, the peaty soils in the area of both excavated (**Appendix 49a**) and unexcavated (**Appendix 49b**) Thule winter dwellings were significantly warmer than immediately adjacent beach ridges.

APPENDICES 46a (top) and 46b (bottom)

Stand 10 - Few-pass tracks and adjacent controls - 28 July 1990
Truelove Lowland - Mean ambient temperature = 3°C

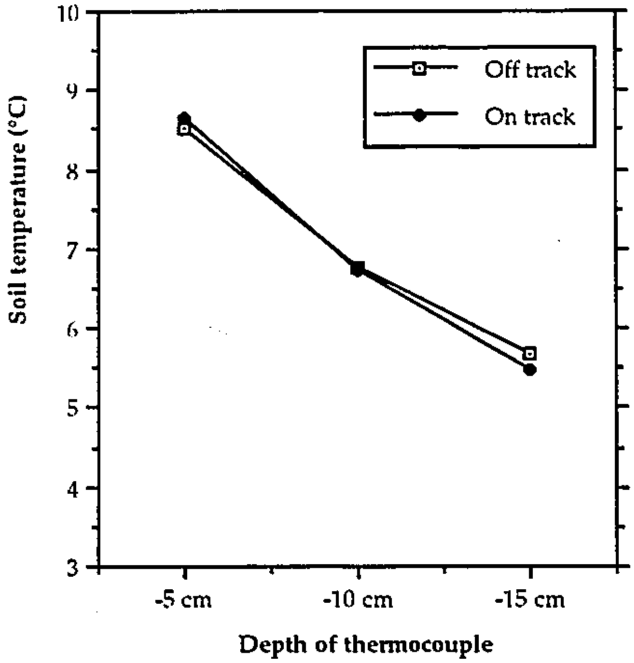


Stand 2 - Few-pass tracks and adjacent controls - 29 July 1990
Truelove Lowland - Mean ambient temperature = 3°C

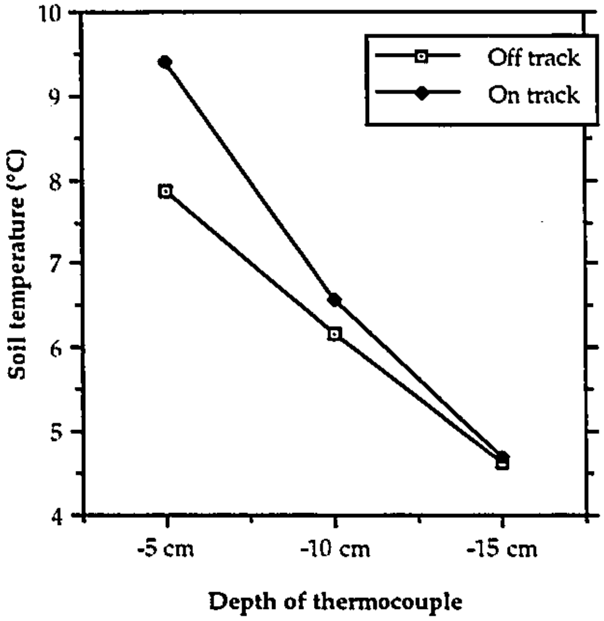


APPENDICES 47a (top) and 47b (bottom)

Stand 8 - Multi-pass tracks and adjacent controls - July 29 1990
Truelove Lowland - Mean ambient temperature = 3°C

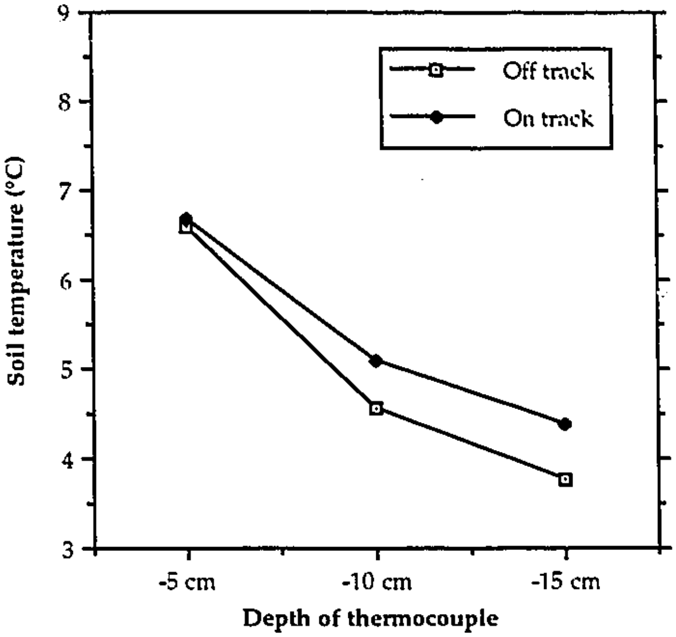


Stand 9 - Multi-pass tracks & adjacent controls - 29 July 1990
Truelove Lowland - Mean ambient temperature = 3°C



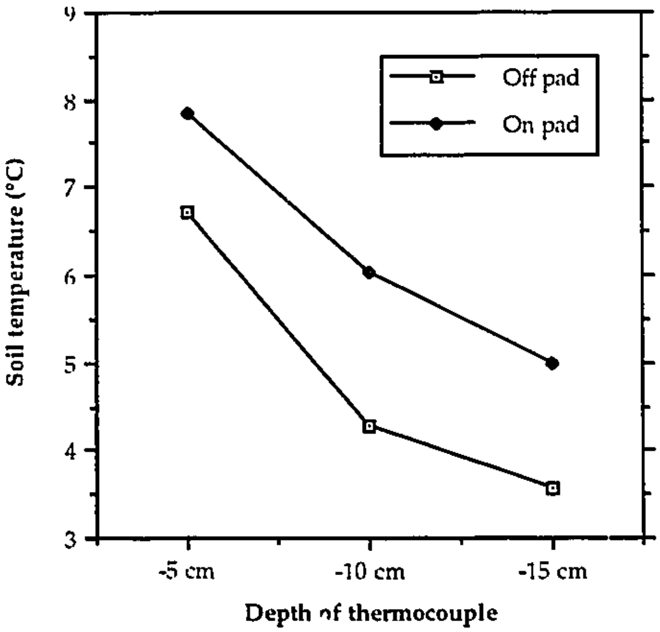
APPENDIX 48

Stand 5 - Multi-pass tracks and adjacent controls - 30 July 1990
Truelove Lowland - Mean ambient temperature (3°C)

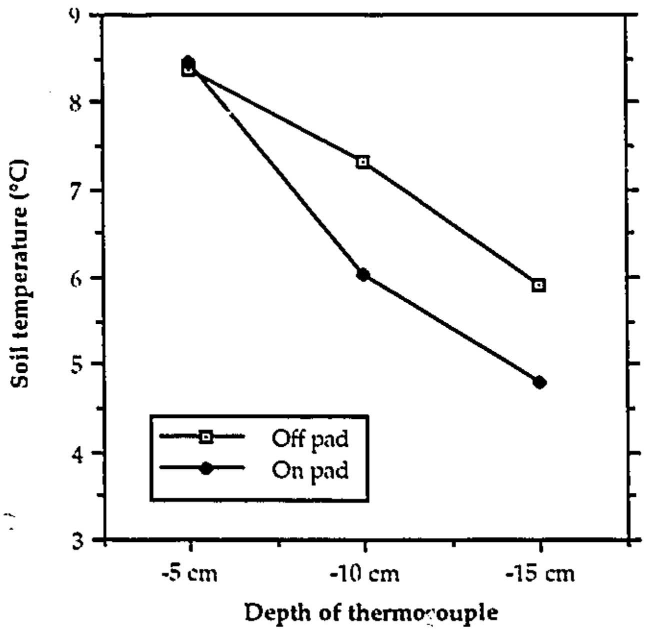


APPENDICES 49a (top) and 49b (bottom)

Stand 14 - Excavated Thule dwelling & adjacent beach ridge
31 July 1990 - Truelove Lowland - Mean ambient temp. = 3.75°C



Stand 16 - Unexcavated Thule dwelling & adjacent beach ridge
31 July 1990 - Truelove Lowland - Mean ambient temp. = 3.75°



APPENDIX 50a. Above-ground live vascular biomass in vehicle tracks and adjacent undisturbed tundra

Data are in grams dry weight per square meter and are means ± S.E. *, **, *** indicate significant difference from control at P≤ 0.05, 0.005, 0.0005, respectively; imp. indicates imperfectly drained.

Site		Carex aquatilis var. stans	Eriophorum angustifolium	Other graminoids	Salix arctica (leaf)	Salix arctica (stem)	Other dicotyledons (leaf only)	Total (including non leaf)
Clyde River								
SP no. 1 (mesic)¥								
On-track	*n=8*	7 ± 1	14 ± 2	7 ± 1	5 ± 1**	8 ± 2***	1 ± 1	42 ± 5***
Control	*n=8*	6 ± 2	6 ± 2	5 ± 1	28 ± 6	58 ± 8	3 ± 2	122 ± 8
SP no. 2 (mesic)								
On-track	*n=4*	8 ± 2*	11 ± 3	4 ± 1	1 ± 1*	1 ± 1*	0	26 ± 5***
Control	*n=4*	18 ± 3	6 ± 2	4 ± 1	15 ± 6	60 ± 18	14 ± 11	126 ± 8
SP no. 1(imp.)								
On-track	*n=4*	9 ± 2	20 ± 4	3 ± 1	0*	0*	1 ± 0	35 ± 5*
Control	*n=4*	13 ± 6	12 ± 5	1 ± 1	31 ± 8	97 ± 24	1 ± 0	142 ± 32
SP no. 2 (imp.)#								
On-track	*n=4*	3 ± 3	3 ± 1	6 ± 4*	0	0	0*	13 ± 6*
Control	*n=4*	0	9 ± 4	2 ± 1	6 ± 4	26 ± 16	2 ± 1	71 ± 15
SP no. 3 (imp.)#								
On-track	*n=4*	0	9 ± 3	11 ± 3	0*	0*	0	15 ± 1**
Control	*n=4*	4 ± 4	7 ± 2	9 ± 3	1 ± 1	2 ± 1	3 ± 3	35 ± 4
MP no. 1 (mesic)								
On-track	*n=8*	72 ± 18**	0	4 ± 3	1 ± 1***	1 ± 1**	1 ± 0	81 ± 17*
Control	*n=8*	11 ± 4	0	14 ± 6	35 ± 8	86 ± 25	12 ± 7	162 ± 29
MP no. 2 (mesic)								
On-track	*n=4*	44 ± 10**	33 ± 14*	4 ± 3	0***	0*	0***	83 ± 8
Control	*n=4*	1 ± 1	0	15 ± 4	21 ± 2	62 ± 21	5 ± 0	112 ± 21
MP WT no. 1 (mesic)#								
On-track	*n=4*	10 ± 4	29 ± 16	11 ± 3*	0***	0***	0	51 ± 13***
Control	*n=4*	10 ± 3	37 ± 7	2 ± 0	24 ± 4	77 ± 13	9 ± 5	158 ± 15
MP WT no. 2 (mesic)#								
On-track	*n=9*	9 ± 5	3 ± 1***	12 ± 2***	0***	0***	0*	26 ± 4***
Control	*n=9*	16 ± 3	41 ± 6	2 ± 1	29 ± 5	42 ± 6	2 ± 1	129 ± 13
SP (ridge)								
On-track	*n=5*	16 ± 2	44 ± 1	2 ± 0	4 ± 2	7 ± 3	2 ± 1*	81 ± 11**
Control	*n=5*	16 ± 5	31 ± 8	6 ± 3	26 ± 14	27 ± 12	27 ± 10	172 ± 27
SP (water track)								
On-track	*n=5*	9 ± 2	63 ± 8	6 ± 2	1 ± 0***	1 ± 1***	1 ± 1	80 ± 8**
Control	*n=5*	15 ± 3	37 ± 7	2 ± 1	29 ± 5	42 ± 8	2 ± 1	129 ± 13

¥ Abbreviations are the same as those in Table 2.I. # indicates tracks last used ca. 1971-72. All other tracks were last used ca. 1969.

APPENDIX 50b. Above-ground live vascular biomass in vehicle tracks and adjacent undisturbed tundra Data are in grams dry weight per square meter and are means ± S.E. *, **, *** indicate significant difference from control at P≤ 0.05, 0.005, 0.0005, respectively; imp. indicates imperfectly drained.

Truelove Lowland								
SP (imp.)								
On track	*n=4*	21 ± 3	3 ± 1	4 ± 1	0**	0***	0	28 ± 1*
Control	*n=4*	14 ± 2	4 ± 2	8 ± 2	14 ± 4	5 ± 1	1 ± 1	48 ± 8
FP (imp.)								
On track	*n=4*	21 ± 6	15 ± 4	9 ± 2	0**	0*	2 ± 1	50 ± 11
Control	*n=4*	26 ± 13	10 ± 2	4 ± 2	10 ± 2	13 ± 4	5 ± 4	74 ± 8
MP no. 1 (mesic)								
On track	*n=4*	24 ± 9	0*	0*	0***	0*	1 ± 1	29 ± 9**
Control	*n=4*	31 ± 10	9 ± 3	12 ± 5	6 ± 1	4 ± 1	6 ± 4	81 ± 12
MP no. 2 (mesic)								
On track	*n=4*	28 ± 17	5 ± 2	7 ± 4	0***	0*	0	36 ± 18
Control	*n=4*	34 ± 4	2 ± 1	8 ± 2	14 ± 2	9 ± 3	2 ± 1	71 ± 4
MP (wet)								
On track	*n=5*	63 ± 4	1 ± 0*	0	0	0	0	64 ± 4
Control	*n=5*	62 ± 5	4 ± 1	6 ± 4	0	0	0	73 ± 7
MP '86 (mesic) §								
On track	*n=4*	12 ± 6	0**	3 ± 2	0**	1 ± 1*	0*	13 ± 6**
Control	*n=4*	22 ± 9	3 ± 1	7 ± 2	10 ± 2	5 ± 1	1 ± 1	50 ± 8
MP '86 (imp.) §								
On track	*n=4*	29 ± 8	0	0**	0*	0*	0	29 ± 8*
Control	*n=4*	41 ± 9	2 ± 1	7 ± 1	13 ± 6	11 ± 5	1 ± 0	72 ± 13

§ indicates tracks last used 1986. All other tracks are assumed last used during or prior to 1971.

Appendix 51a. Importance of vascular growth form categories - Clyde River

Growth form	Total % cover in all stands (undisturbed)	% of taxa	Total % cover (heavily trampled)	% of taxa	Total % cover (moderately trampled)	% of taxa	Total % cover (lightly trampled)
1. Prostrate deciduous dwarf shrubs	19.6	11.4	0.0	0.0	0.8	7.7	19.2
2. Prostrate evergreen dwarf shrubs	0.5	2.8	0.0	0.0	0.0	0.0	0.0
3. Equisetoids	0.1	2.8	0.0	0.0	0.0	0.0	0.0
4. Stoloniferous graminoids	0.1	2.8	0.0	0.0	0.0	0.0	0.0
5. Rhizomatous graminoids	31.4	25.7	40.5	41.6	43.8	46.1	22.4
6. Caespitose graminoids	6.0	11.4	0.0	16.6	0.2	7.7	1.0
7. Prostrate matted forbs	0.3	8.6	7.2	8.3	1.7	7.7	0.6
8. Erect rhizomatous forbs	2.3	11.4	0.7	16.6	0.0	7.7	11.0
9. Erect caespitose forbs	0.1	5.7	0.0	0.0	0.0	0.0	0.4
10. Erect solitary forbs	0.6	17.1	9.3	16.6	3.3	23.1	2.0
Total	61.0	99.7	57.7	99.7	49.8	100	56.6

Appendix 51b. Importance of vascular growth form categories - Truelove Lowland and Resolute Bay

Growth form	Total % cover in all stands (undisturbed)	% of taxa	Total % cover (multi-pass vehicle tracks)	% of taxa	Total % cover on Thule house pads)	% of taxa
1. Prostrate deciduous dwarf shrubs	10.6	10.5	0.2	7.1	14.3	5.5
2. Prostrate evergreen dwarf shrubs	0.2	2.6	0.0	0.0	0.0	0.0
3. Equisetoids	0.5	5.3	0.2	7.1	0.0	0.0
4. Stoloniferous graminoids	0.1	2.6	1.0	7.1	0.0	0.0
5. Rhizomatous graminoids	52.5	23.7	39.6	35.7	28.8	27.7
6. Caespitose graminoids	0.3	5.3	0.0	0.0	0.4	5.5
7. Prostrate matted forbs	1.3	10.5	0.4	21.4	4.9	16.6
8. Erect rhizomatous forbs	1.7	10.5	0.2	7.1	0.8	11.1
9. Erect caespitose forbs	0.2	7.0	0.0	0.0	0.4	11.1
10. Erect solitary forbs	0.8	21.0	0.0	14.2	5.4	22.2
Total	68.2	99.0	41.6	99.7	55.0	99.7

Appendix 52. Cover/abundance of animal faeces on natural and anthropogenic disturbances sampled at each study site.

Site	Housepad Type A (18)	Housepad Type B (7,14)	Housepad Type C (19)	Heavily trampled (18)	Moderately trampled (18)	Lightly trampled (18)	Natural Meadows (all)
Clyde River	Dg/2	Dg/2	Dg/+	Dg/2	Dg/1	Dg/+	-/-

	Unexcavated Thule pad (15)	Unexcavated Thule pad 2 (16)	Excavated Thule pad (14)	Beach ridges (14, 16)	Multi-pass tracks (3)	Few-pass tracks (2)	Frost-boil meadow (4)
Truelove Lowland	Dg/1; Lm/+	Dg/1; La/+	Dg/2; Om/+ Lm/+; La/+	La/+	Dg/+	Dg/+	Dg/+

	Unexcavated Thule pad	Beach ridge
Resolute Bay	Dg/+	-/-

Legend: Dg = Dicrostonyx groenlandicus; La = Lepus arcticus; Lm = Lagopus mutus; Om = Ovibos moschatus; - = no feces observed; + = occasional and less than 5% of total ground cover; 1 = abundant with 5 to 10% of total ground cover; 2 = very abundant with >10% of total ground cover. Numbers in parentheses are stand designations.

APPENDICES 53-57

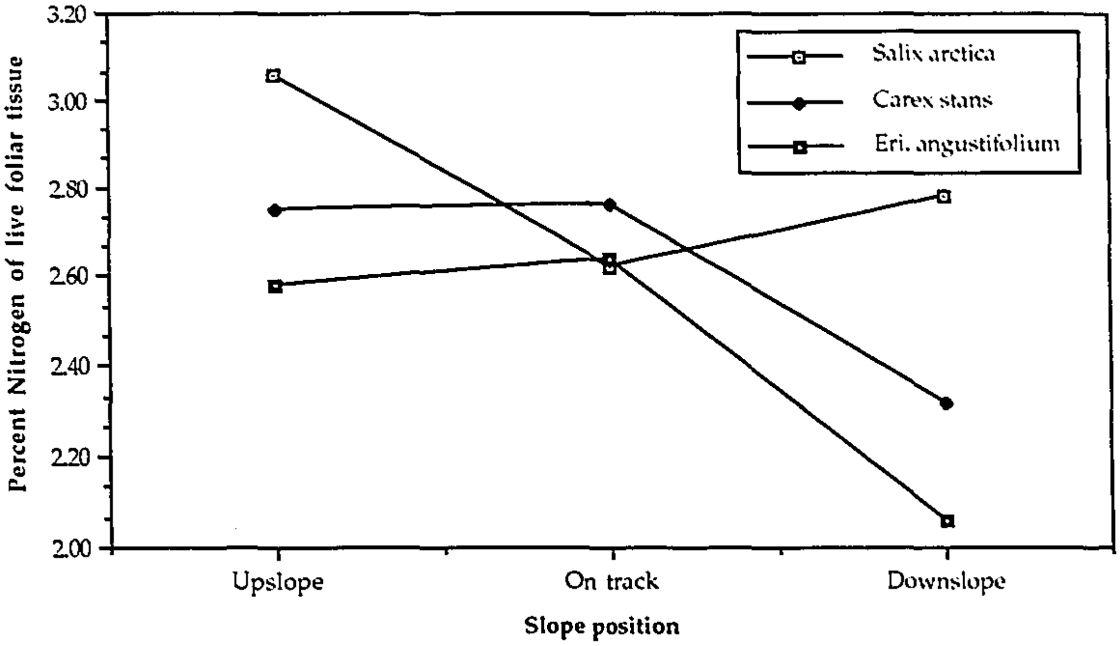
Peak season leaf tissue macronutrient status at CR and TL

Mid-season concentrations of macronutrients in vascular plant tissue are illustrated for dominant species and growth forms along disturbance gradients at CR and TL in **Appendices 53-57**. At CR, levels of phosphorus content among the sedges displayed a pattern similar to that observed for nitrogen (**Appendix 53**). Leaf tissue of Salix arctica registered a significant reduction in the same set of tracks, but phosphorus levels remained unchanged in drained areas, relative to controls upslope. Potassium levels increased in tracks in all species at both study sites, significantly in several cases (**Appendix 57**). Potassium was significantly lower in drained areas relative to controls in E. angustifolium and S. arctica (**Appendix 54a and 57a**). Differences in levels of magnesium were rare.

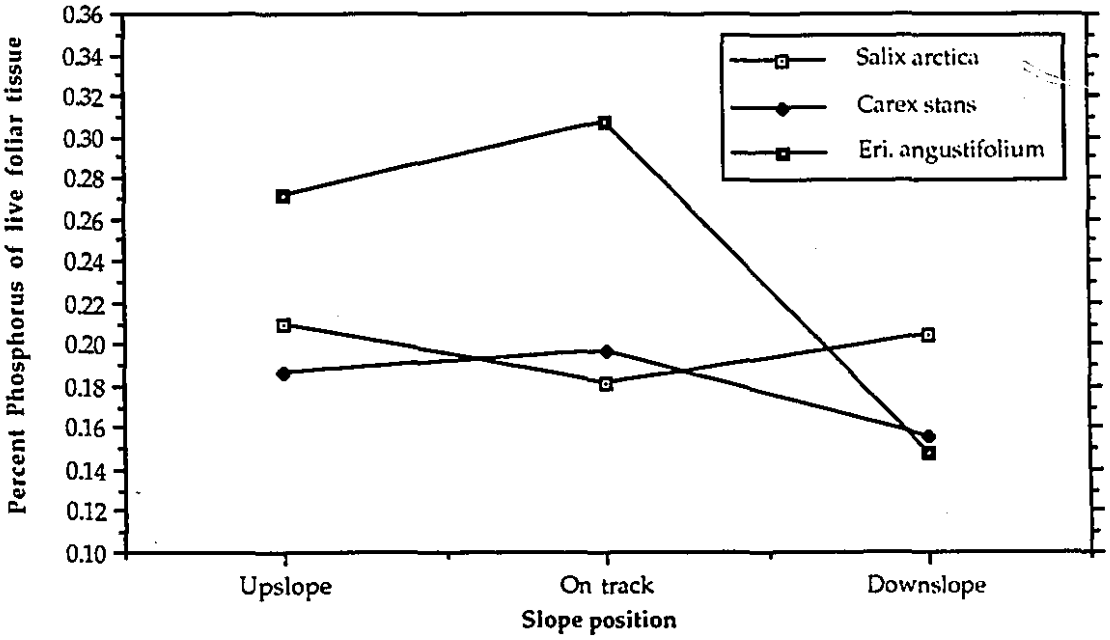
In vehicle tracks, magnesium levels changed significantly only in Carex at TL and in Salix at CR, both of which registered increases. In drained areas at CR, magnesium decreased significantly in both Carex and Salix (**Appendix 57**). Calcium levels decreased in all three species in tracks at CR, significantly so in Carex. At TL, calcium decreased significantly in Eriophorum in few-pass tracks. Decreases in drained areas were registered in all three species and were significant for the two sedges. **Appendix 55** details a gradient of drainage for nutrients in Carex aquatilis var. stans at CR. Although all nutrients tended to decrease substantially in areas drained by multi-pass tracks, both nitrogen and magnesium were significantly increased in areas drained by single-pass tracks. Tissues of Salix arctica registered pronounced differences in macronutrient concentrations among two different Thule winter dwellings and the adjacent beach ridge at TL. This gradient is illustrated in **Appendix 56b**.

APPENDICES 53a (top) and 53b (bottom)

Mid-season concentrations of Nitrogen in dominant species - Single-pass tracks, drained peatlands and adjacent controls - Stand 16 - Clyde River - 10 July 1990

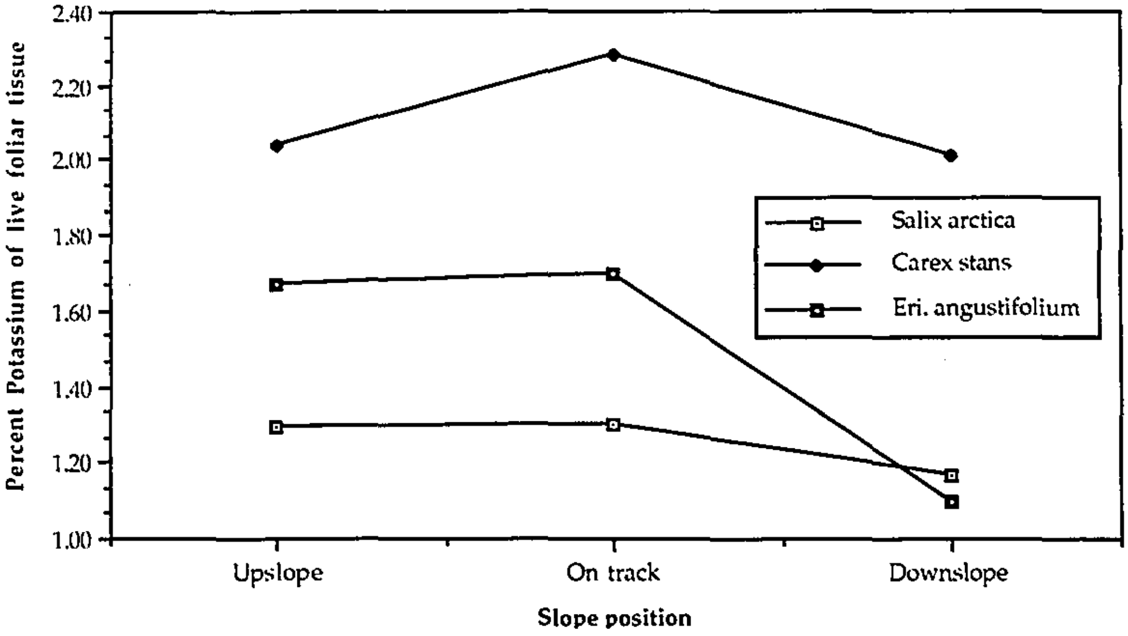


Mid-season concentrations of Phosphorus in dominant species - Single-pass tracks, drained peatlands and adjacent controls - Stand 16 - Clyde River - 10 July 1990

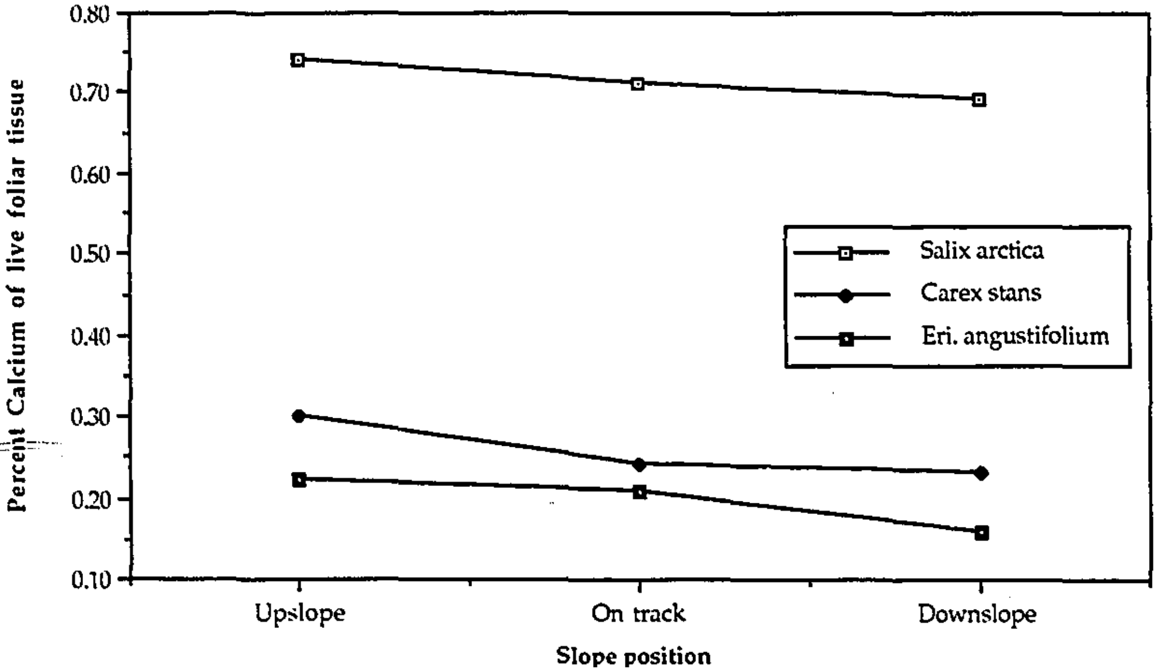


APPENDICES 54a (top) and 54b (bottom)

Mid-season concentrations of Potassium in dominant species - Single-pass tracks, drained peatlands and adjacent controls - Stand 16 - Clyde River - 10 July 1990

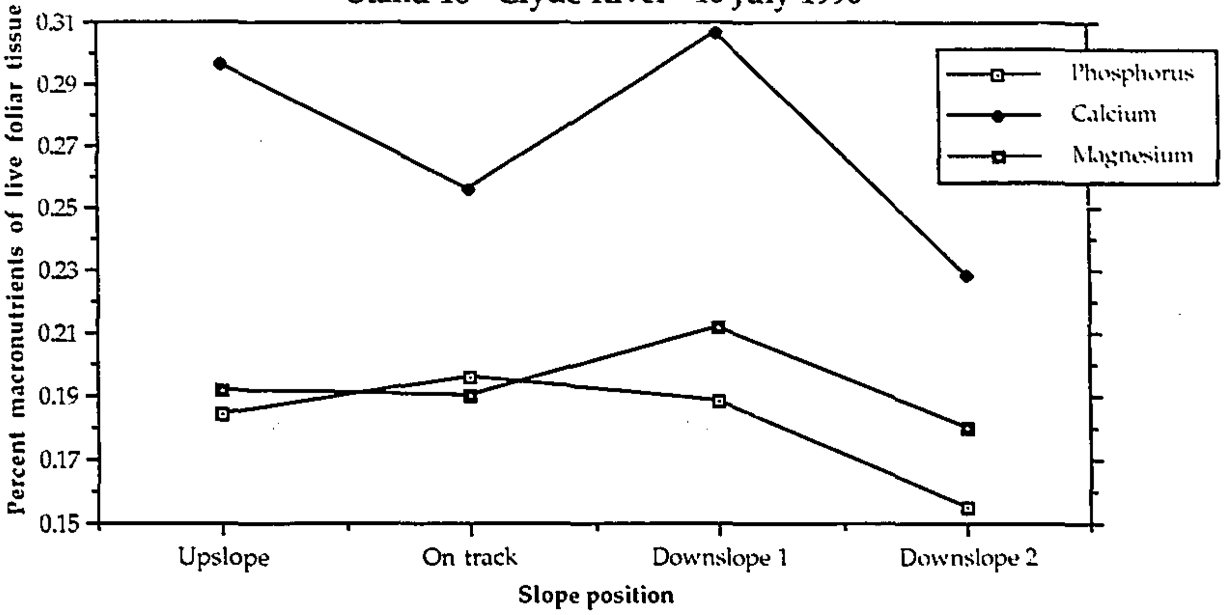


Mid-season concentrations of Calcium in dominant species - Single-pass tracks, drained peatlands and adjacent controls - Stand 16 - Clyde River - 10 July 1990

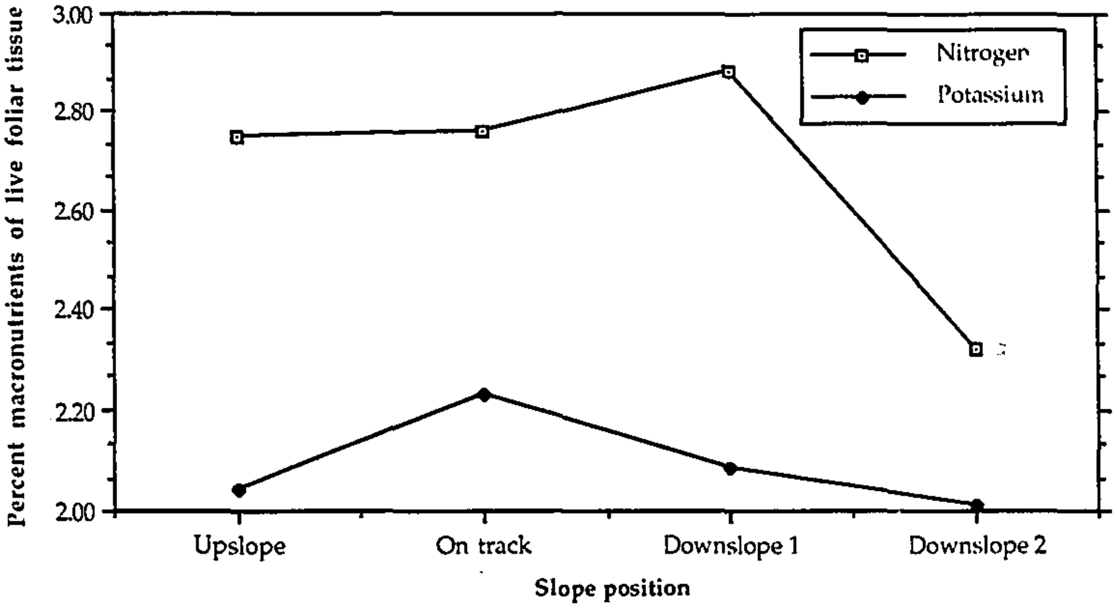


APPENDICES 55a (top) and 55b (bottom)

Mid-season concentrations of macronutrients in Carex aquatilis var. stans
Single-pass tracks, drained peatlands and adjacent controls
Stand 16 - Clyde River - 10 July 1990

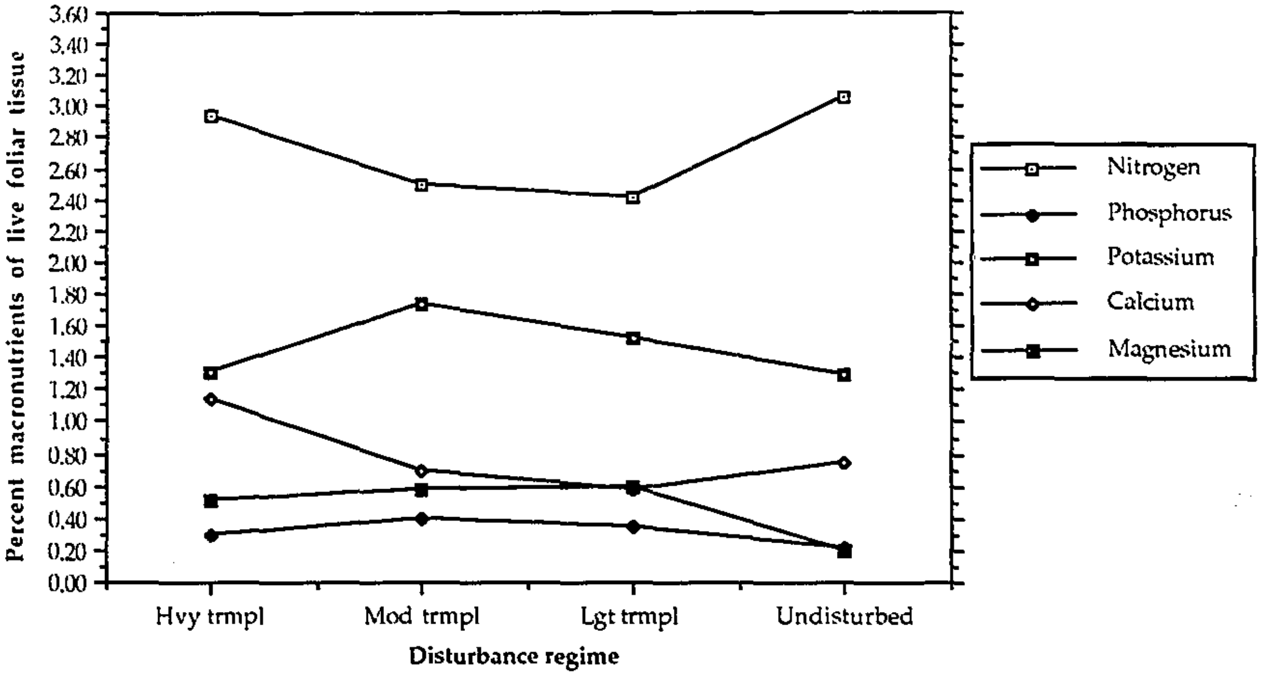


Mid-season concentrations of macronutrients in Carex aquatilis var. stans
Single-pass tracks, drained peatlands and adjacent controls
Stand 16 - Clyde River - 10 July 1990

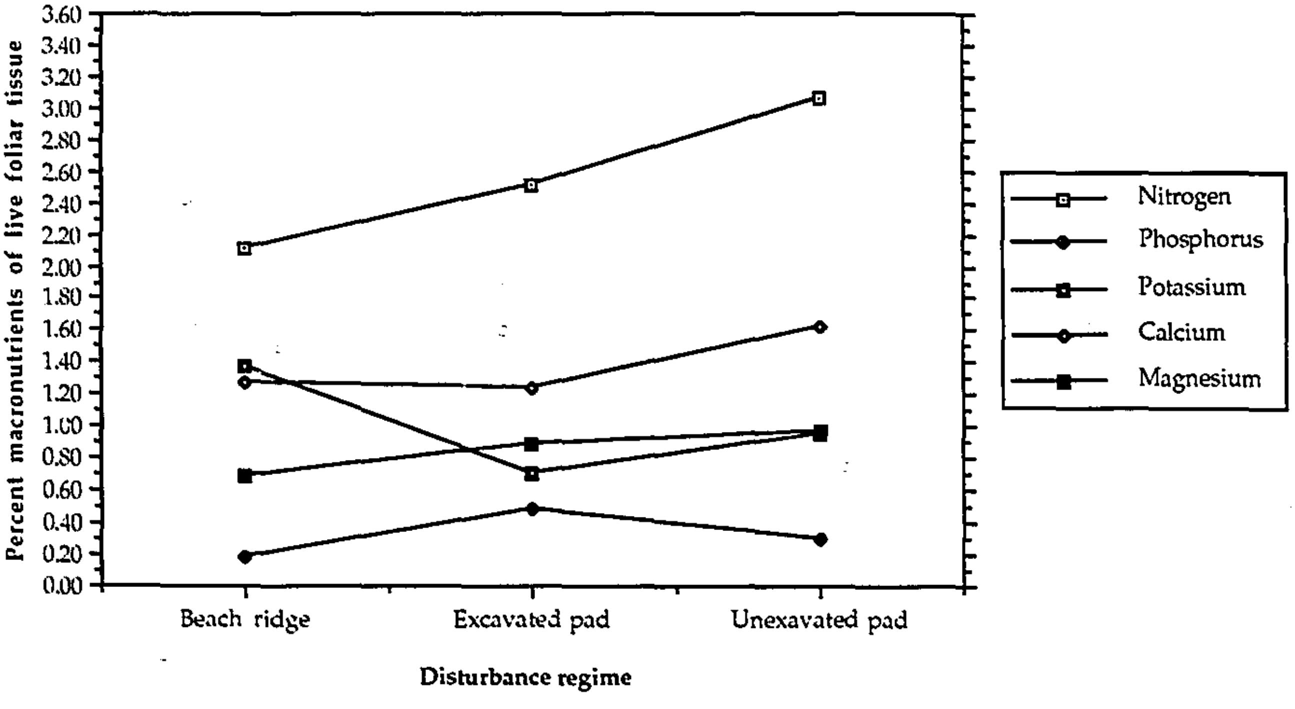


APPENDICES 56a (top) and 56b (bottom)

Mid-season concentrations of macronutrients in Salix arctica - Trampled meadows and adjacent controls - Stand 18 - Clyde River - 11 July 1990



Mid-season concentrations of macronutrients in Salix arctica - Thule winter dwellings and adjacent controls - Truelove Lowland - 28 July 1990



Appendix 57a - Leaf macronutrient status - **Clyde River, Baffin Island** (70°35"N, 68°40'W)

Taxon	Site status	Date	N %	P %	K %	Mg %	Ca %
Ea	Natural poor Sphagnum-peat meadow	10 July 1990	2.58±0.03	0.27±0.00	1.67±0.03	0.15±0.01	0.22±0.02
Ea	Single-pass vehicle track	10 July 1990	2.64±0.00*	0.30±0.00***	1.70±0.01	0.14±0.01	0.21±0.01
Ea	Drained peat meadow II	10 July 1990	2.06±0.01***	0.15±0.00***	1.10±0.00***	0.15±0.01	0.16±0.02*
Ea	Lightly trampled meadow	11 July 1990	2.29±0.01	0.24±0.00	1.38±0.01	0.16±0.01	0.17±0.02
Ea	Moderately trampled meadow	11 July 1990	2.47±0.08*	0.25±0.00	1.33±0.05	0.17±0.01	0.16±0.01
Sa	Natural poor Sphagnum-peat meadow	10 July 1990	3.06±0.07	0.21±0.00	1.29±0.01	0.47±0.02	0.74±0.02
Sa	Single-pass vehicle track	10 July 1990	2.62±0.02***	0.18±.000***	1.30±0.02	0.55±0.00**	0.71±0.01
Sa	Drained peat meadow II	10 July 1990	2.78±0.01***	0.20±0.00	1.17±0.00***	0.46±0.01*	0.69±0.04

Species abbreviations are as follows: Aa=Alopecurus alpinus; Ca=Carex aquatilis var. stans; Ea=Eriophorum angustifolium; Sa=Salix arctica

Appendix 57b - Leaf macronutrient status - Clyde River, Baffin Island (70°35"N, 68°40'W)

Taxon	Site status	Date	N %	P %	K %	Mg %	Ca %
Sa	Lightly trampled meadow	11 July 1990	2.41±0.01	0.35±0.00	1.52±0.01	0.59±0.01	0.57±0.01
Sa	Moderately trampled meadow	11 July 1990	2.49±0.07	0.39±0.01**	1.73±0.04**	0.58±0.02	0.69±0.03*
Sa	Lightly trampled meadow*	10 July 1990	2.64±0.04	0.23±0.00	1.44±0.01	0.61±0.01	0.92±0.04
Sa	Heavily trampled meadow*	10 July 1990	2.94±0.03***	0.29±0.00***	1.30±0.11***	0.52±0.01**	1.14±0.03**
Aa	Abandoned housepad (in use 1963-69)	11 July 1990	2.31±0.03	0.32±0.00	2.45±0.01	0.15±0.00	0.19±0.01
Aa	Moderately trampled adjacent meadow	11 July 1990	2.07±0.03**	0.35±0.00**	2.09±0.01***	0.15±0.00	0.24±0.01**
Ca	Natural poor Sphagnum-peat meadow	10 July 1990	2.75±0.08	0.19±0.00	2.04±0.01	0.20±0.00	0.30±0.02
Ca	Single-pass vehicle track	10 July 1990	2.76±0.04	0.20±0.00**	2.28±.12**	0.19±0.01	0.24±0.01**
Ca	Drained peat meadow I	10 July 1990	2.88±0.03*	0.19±0.00	2.09±0.07*	0.20±0.00	0.31±0.06
Ca	Drained peat meadow II	10 July 1990	2.32±0.04***	0.15±0.01**	2.01±0.12	0.18±0.00*	0.23±0.01**

*= Meadow is adjacent to former weather station where lime and 100% aluminum oxides have been dumped and appear to have been transferred via pedestrian traffic.

Appendix 57c - Leaf macronutrient status - **Truelove Lowland, Devon Island** (75°33'N, 84°40'W)

Taxon	Site status	Date	N %	P %	K %	Mg %	Ca %
Ea	Natural Ca-rich fen	28 July 1990	2.69±0.01	0.26±0.00	1.01±0.01	0.19±0.01	0.48±0.03
Ea	Few-pass vehicle track	28 July 1990	3.08±0.07**	0.30±0.00***	1.65±0.02***	0.20±0.00	0.39±0.01*
Sa	Natural Ca-rich cobble beach ridge	31 July 1990	2.11±0.01	0.18±0.00	1.37±0.02	0.68±0.00	1.27±0.35
Sa	Recently (5yr) excavated Thule house	31 July 1990	2.51±0.04***	0.49±0.00***	0.71±0.01***	0.89±0.01***	1.24±0.03
Sa	Unexcavated Thule house	31 July 1990	3.07±0.03***	0.30±0.00***	0.95±0.01***	0.97±0.01***	1.62±0.04***
Aa	Recently (5yr) excavated Thule house	31 July 1990	1.76±0.01	0.34±0.00	2.09±0.03	0.20±0.00	0.43±0.01
Aa	Unexcavated Thule house	31 July 1990	2.04±0.09*	0.26±0.02*	1.95±0.03*	0.19±0.01	0.38±0.01*
Ca	Natural Ca-rich fen	28 July 1990	3.51±0.02	0.27±0.00	1.31±0.01	0.14±0.01	0.34±0.02
Ca	Few-pass vehicle track	28 July 1990	3.28±0.02***	0.25±0.00***	1.54±0.01***	0.16±0.00*	0.38±0.00

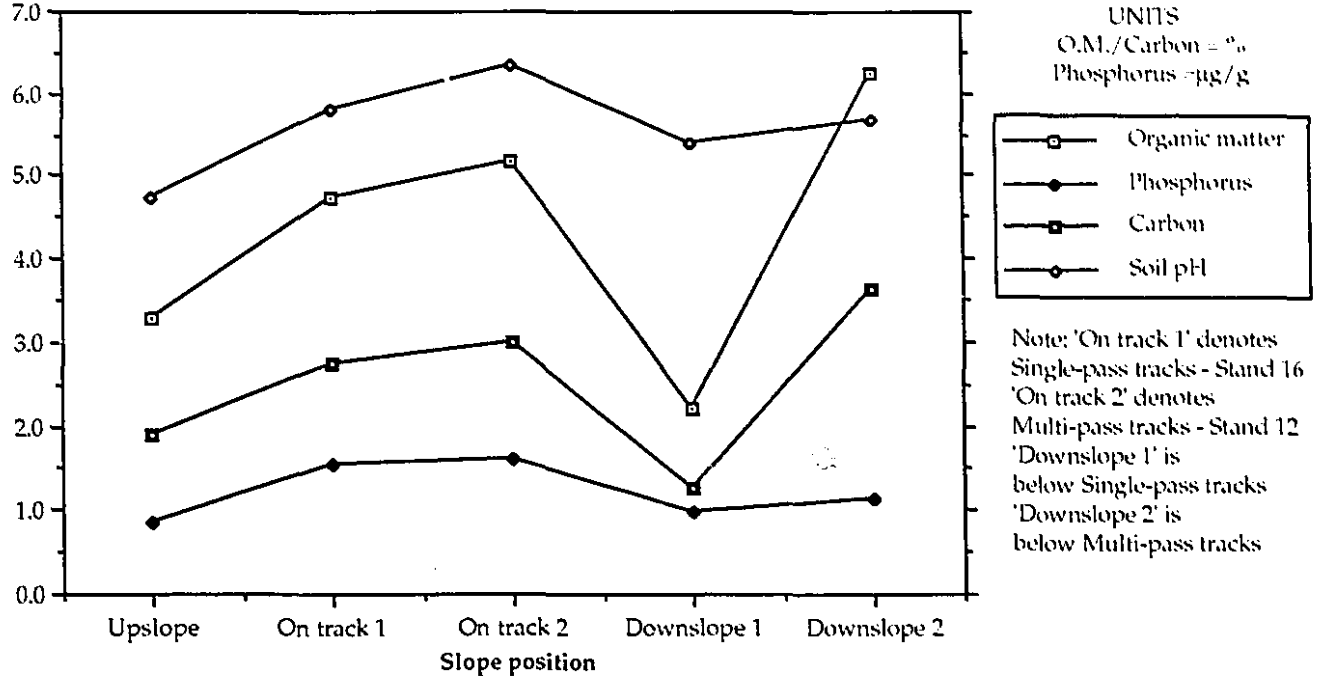
APPENDICES 58-61

Peak season mineral soils analyses for CR and TL

Most soil parameters measured (organic matter, pH, corrected conductivity, etc.) increased significantly in single-pass tracks, and also in multi-pass tracks. Many of these also increased in drained areas downslope from multi-pass tracks (**Appendix 58**). These same parameters differed little or not at all in areas drained by single-pass tracks compared to controls upslope. On the trampling gradient, most parameters increased relative to undisturbed ground (**Appendix 59**). An exception was phosphorus content, which was unchanged on moderately trampled ground. Corrected conductivity declined with light and moderate trampling, but increased significantly, along with phosphorus, potassium, organic matter, and carbon, on heavily trampled ground. On the Thule winter dwellings, soils were significantly enriched compared to the adjacent beach ridge, with the soils of the excavated dwelling having the highest organic matter, carbon and phosphorus contents (**Appendix 60a**). Potassium content was highest in the soils of the second housepad (**Appendix 60b**). It is clear that pH was decreased on each of the Thule dwellings at TL (**Appendix 61**).

APPENDICES 58a (top) and 58b (bottom)

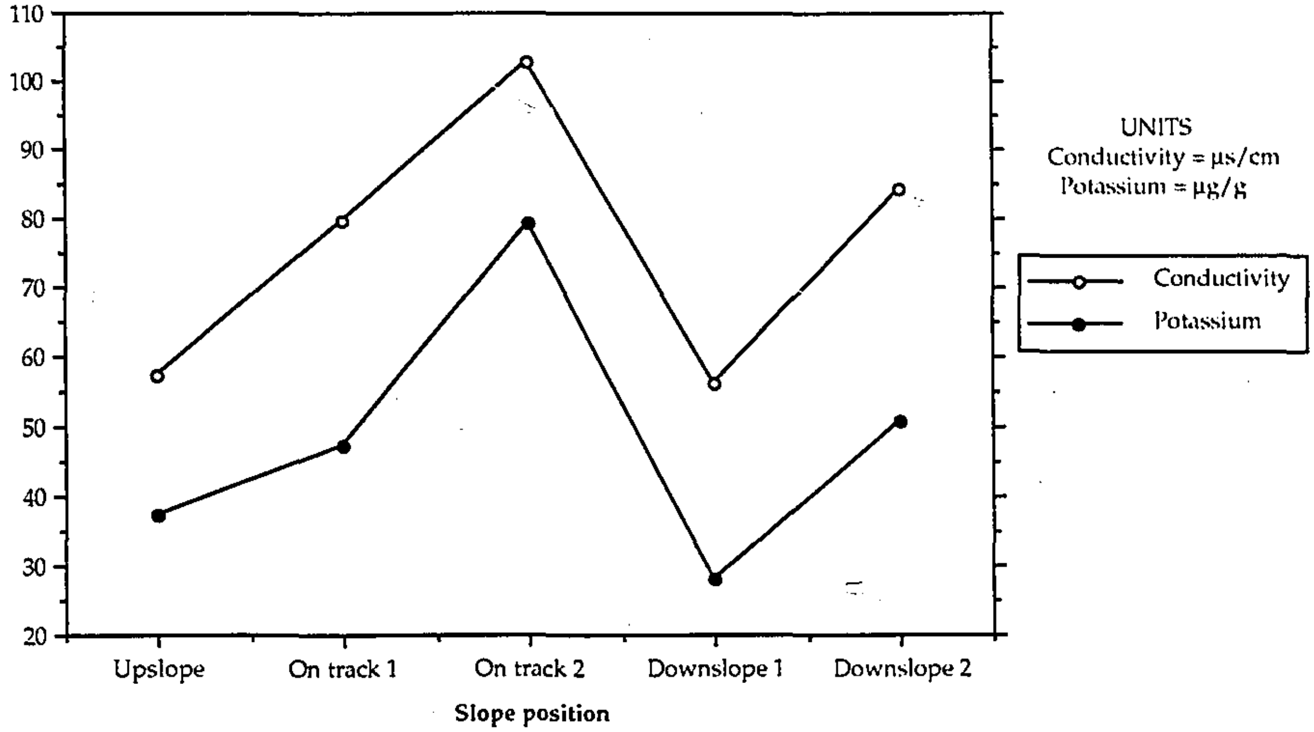
Mineral soils analysis from vehicle tracks, drained peatlands and adjacent controls - Stands 12 & 16 - Clyde River - 5 July 1990



UNITS
O.M./Carbon = %
Phosphorus = μg/g

Note: 'On track 1' denotes
Single-pass tracks - Stand 16
'On track 2' denotes
Multi-pass tracks - Stand 12
'Downslope 1' is
below Single-pass tracks
'Downslope 2' is
below Multi-pass tracks

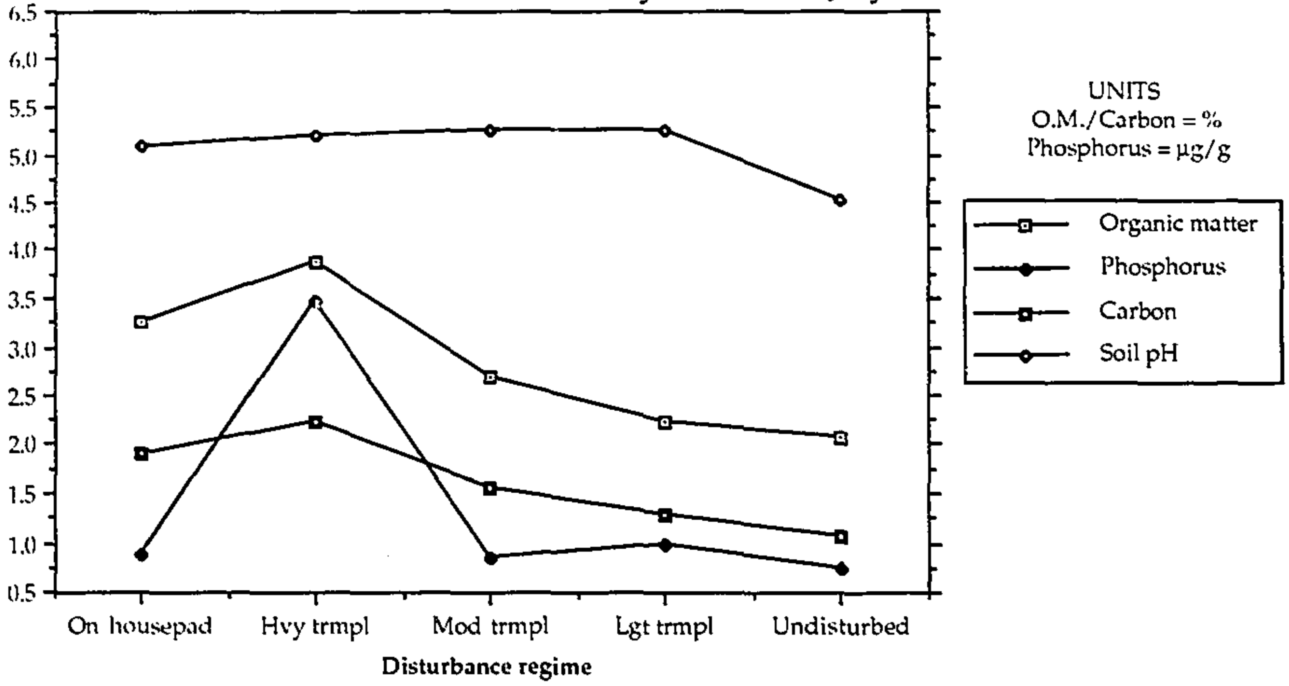
Mineral soils analysis from vehicle tracks, drained peatlands and adjacent controls - Stands 12 & 16 - Clyde River - 5 July 1990



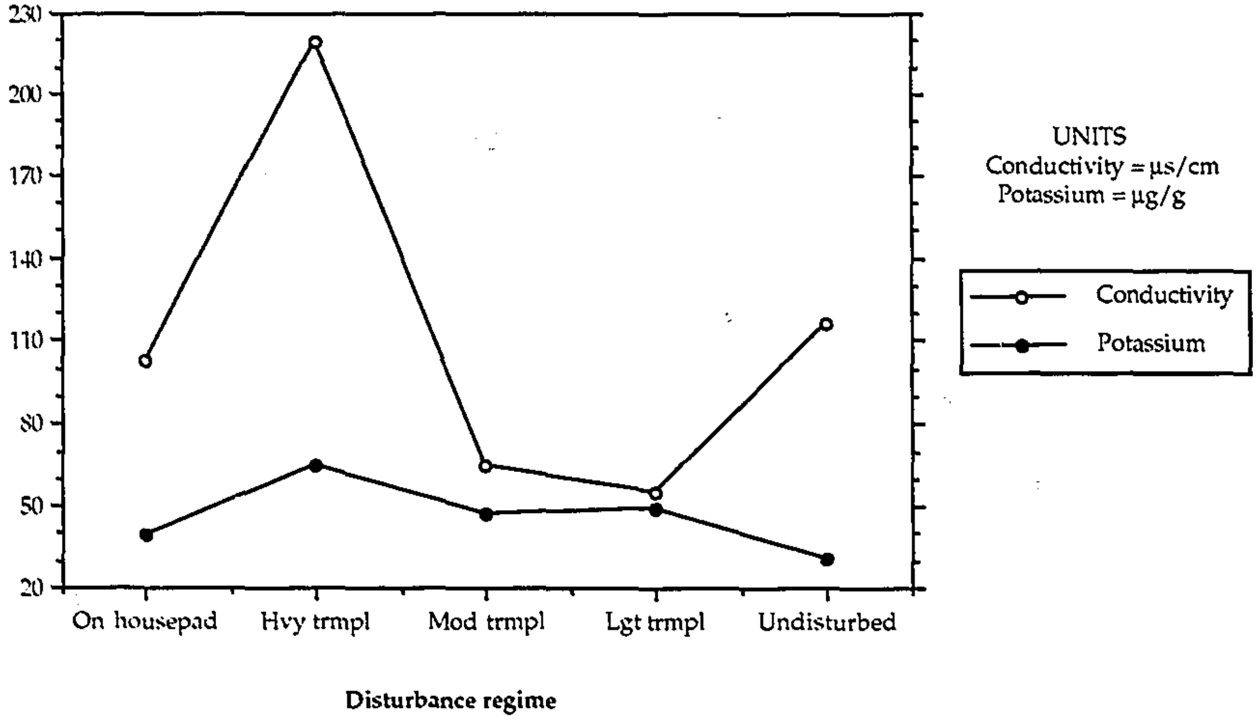
UNITS
Conductivity = μs/cm
Potassium = μg/g

APPENDICES 59a (top) and 59b (bottom)

Mineral soils analysis - Housepad Type A and adjadent trampled and natural meadows - Stand 18 - Clyde River - 6 July 1990

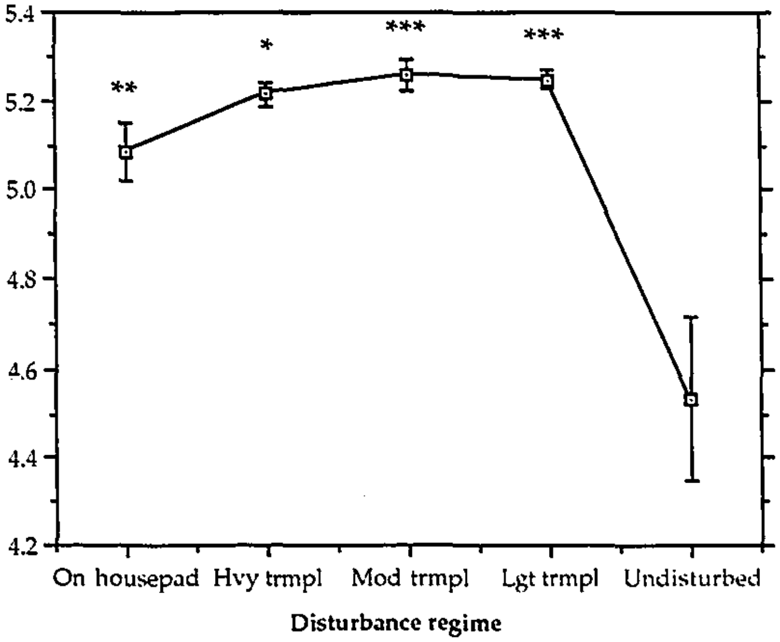


Mineral soils analysis - Housepad Type A and adjacent trampled and natural meadows - Stand 18 - Clyde River - 6 July 1990



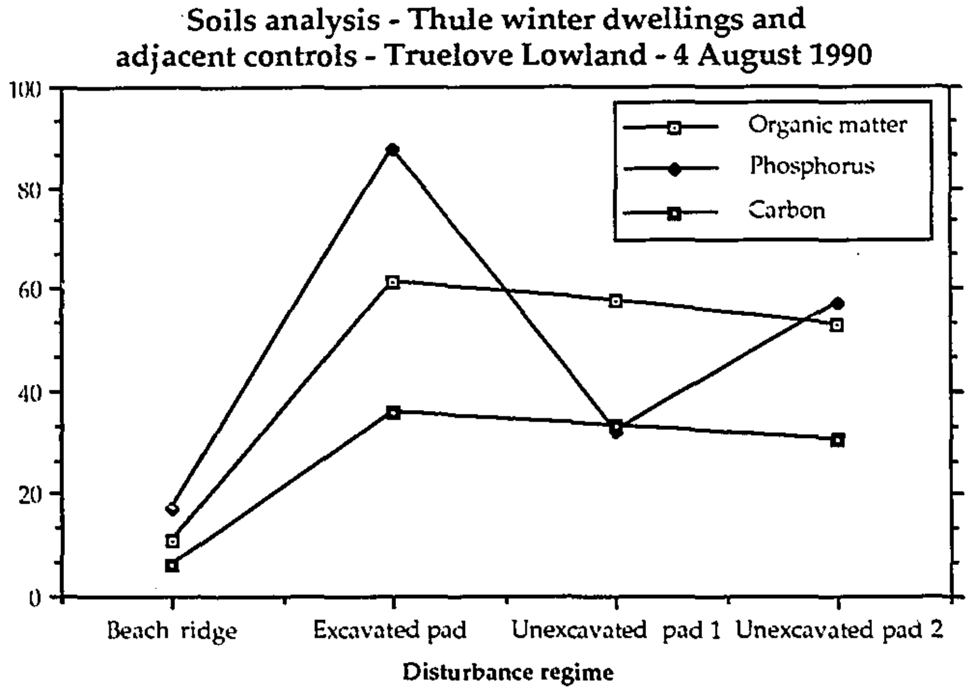
APPENDIX 59c

Mineral soil pH - Housepad Type A and adjacent trampled and natural meadows - Stand 18 - Clyde River - 6 July 1990



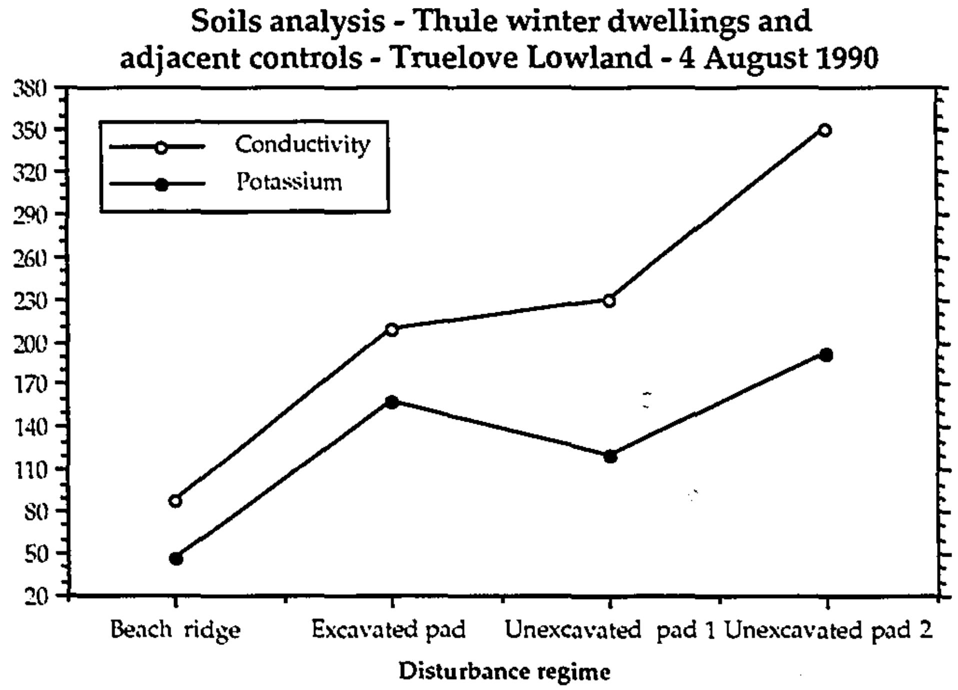
*,**,*** = significant at 0.05, 0.005, 0.0005 (t-test)

APPENDICES 60a (top) and 60b (bottom)



Soils analysis - Thule winter dwellings and adjacent controls - Truelove Lowland - 4 August 1990

UNITS
O.M./Carbon = %
Phosphorus = µg/g

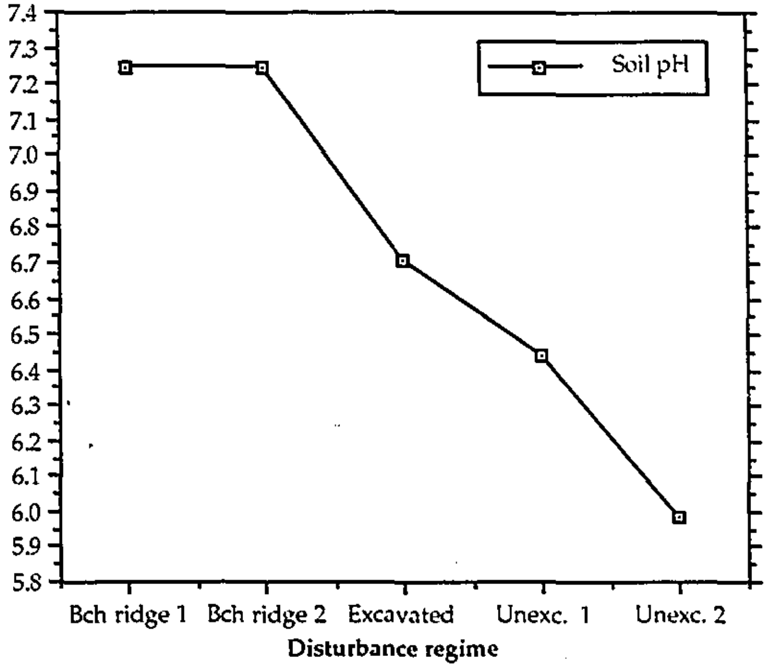


Soils analysis - Thule winter dwellings and adjacent controls - Truelove Lowland - 4 August 1990

UNITS
Conductivity = µs/cm
Potassium = µg/g

APPENDIX 61

Soil pH - Thule winter dwellings and adjacent controls
Truelove Lowland - 4 August 1990



Appendix 62. Floristics of natural and anthropogenic disturbances

Site	Natural disturbance	Species present
CR	Frost polygons	Hierochloë alpina, Luzula confusa, Dicranum elongatum, Pogonatum alpinum, Polytrichum piliferum, Racomitrium lanuginosum, Buellia sp., Lecanora sp., Parmelia spp., Rhizocarpon spp.
CR	Bird perch	Alopecurus alpinus, Draba nivalis, Hierochloë alpina, Poa arctica, Polygonum viviparum, Taraxacum lacerum, Pogonatum alpinum, Polytrichum spp., Xanthoria sp.
CR	Ice-push shore	Carex ursina, Cochlearia officinalis ssp. groenlandica, Puccinellia phryganodes, Stellaria humifusa
CR	Gravel river bar	Epilobium latifolium
TL	Gravel river bar	Epilobium latifolium
TL	Ice-wedge polygon margins	Alopecurus alpinus, Arctagrostis latifolia ssp. latifolia, Poa arctica, Ceratodon purpureus, Dicranella crispa, Leptobryum pyriforme, Psilopilum cavifolium, Stegonia latifolia
TL	Frost-boils	Carex membranacea, C. misandra, Eriophorum triste, Seligeria polaris (on calcareous pebbles), Nostoc commune
TL	Musk-ox dung	Aplodon wormskjoldii, Bryum spp., Tetraplodon mnioides, T. pallidus, Splachnum vasculosum var. heterophyllum, Voitia hyperborea
TL	Streams	Blindia acuta, Bryum cryophilum, Grimmia alpicola var. rivularis
TL	Lemming burrow	Alopecurus alpinus, Cerastium alpinum, Draba spp., Saxifraga cernua, Stellaria longipes, Desmatodon leucostoma, D. heimii var. arctica, Funaria microstoma, F. polaris

Anthropogenic habitats for which floras were sampled but no formal measurements were made.

EF	Abandoned sod/stone houses	Alopecurus alpinus, Papaver radicatum, Poa arctica, several others
PI	Abandoned sod/stone houses	Alopecurus alpinus, Matricaria ambigua, several others
RB	Abandoned sod/stone houses	Alopecurus alpinus, Cerastium alpinum, Chrysoplenium tetrandum, Draba alpina, Juncus biglumis Luzula nivalis, Minuartia rubella, Oxyria digyna, Poa spp., Polygonum viviparum, Puccinellia spp.
CR	Effluent spillway	Alopecurus alpinus, Arctagrostis latifolia ssp. latifolia, Oxyria digyna, Ranunculus pygmaeus
TL	Spoil heap from archaeological dig	Alopecurus alpinus, Cerastium alpinum, Festuca brachypyhlla, Papaver radicatum, Poa arctica, Polygonum viviparum, Saxifraga cernua, S. rivularis, Stellaria longipes, Silene uralensis, Brachythecium collinum var. subjulaceum, Bryum argenteum, Desmatodon heimii, Dicranum elongatum, Plagiomnium ellipticum, Racomitrium lanuginosum, Tortula ruralis

CR=Clyde River, Baffin Island, EF= Eglinton Fiord, Baffin Island, PI= Pond Inlet, Baffin Island, RB=Resolute Bay, Cornwallis Island, TL=Truelove Lowland, Devon Island. Sources include my own personal collections in addition to reports by Polunin (1948), Schofield & Cody (1955), Vitt (1975), Vitt & Pakarinen (1977) and Nosko (1984).