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Spatial Distribution of Vascular Plants in High Arctic Sedge Meadow Communities

BY

COLIN GRANT YOUNG ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfilment of the requirements for the degree of MASTER OF SCIENCE.

IN

PLANT ECOLOGY
DEPARTMENT OF BOTANY

EDMONTON, ALBERTA
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UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommended to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled SPATIAL DISTRIBUTION OF VASCULAR PLANTS IN HIGH ARCTIC SEDGE MEADOW COMMUNITIES submitted by Colin G. Young in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE in PLANT ECOLOGY.

Co-supervisor

Co-supervisor

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Date: August 4, 1994

ABSTRACT

High arctic plant communities occur in distinctive spatial patterns and can be delineated on the basis of their relationship to gradients of environmental variables, especially soil moisture. A study in one such community, wet sedge-dominated meadows, was conducted to determine the size and extent of patchiness in the vegetation. Analysis of the species-environment relation in the meadows was then related to the spatial arrangement of species.

Research was undertaken at two locations representing a grazed (Sverdrup Pass - 79°09' N; 79°40' W) and ungrazed (Alexandra Fiord - 78°53' N; 75°55' W) site on Ellesmere Island. Two sedge meadow (north and south sides of valley) were selected at Sverdrup Pass and one at Alexandra Fiord. Each meadow was sampled with a 100 metre transect running down the drainage slope, with an additional transect in the north meadow at Sverdrup Pass perpendicular to the first transect. The presence/absence of vascular plant species and several environmental parameters were recorded in a continuous sequence of 5 x 10 cm quadrats for the length of the transect. The measured environmental parameters were: percentage cover estimates of litter and moss; the relative elevation of the centre of the quadrat; and, the classification of each quadrat by a moisture (1-submerged; 2-wet; 3-dry) and a physiognomic (1-hollow; 2- side; 3-hummock) index. In addition, the water level and permafrost depth were measured every ten days and climatic conditions monitored during July 1991.

Investigation of the vascular plant distribution of the eight most common species on each transect indicated that each species had a scale of pattern between 1 and 14 quadrats (10-140 cm) in size which was constant the length of the entire gradient. A second scale of pattern was indicated between 15 and 70 quadrats in size (150-700 cm) and varied along each transect. Analysis examining the interspecific association between pairs of species at different scales indicated that there was greater organization of species in the Alexandra Fiord meadow at the smallest scale of pattern. When the analysis was expanded to examine the eight common species on each transect at once, no scale of pattern less than 15 quadrats in size was shown in the vegetation.

The examination of species-environment relationships using canonical correspondence analysis (CCA) found that litter and moss cover were inversely related and influenced the separation of the Alexandra Fiord and Sverdrup Pass sites along the first ordination axis. The second ordination axis was influenced by moisture and distinguished between the two Sverdrup Pass meadows. Multispecies association analysis showed that some species combinations occurred with a significantly high and low frequency. Analysis of each transect separately with correspondence analysis (CA) showed that there was no distinctive change in the vegetation along the transects related to the drainage gradient. The measured environmental variables were also found to be more important at explaining differences in species composition between transects than along transects.

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CHAPTER 1

GENERAL INTRODUCTION

An important characteristic of plant communities is the spatial arrangement of the vegetation. In almost all cases this arrangement is non-random and is typified by a certain pattern in the distribution (Pielou, 1974; Greig-Smith, 1983). Pattern is used here to mean a non-random periodicity in the density of the vegetation throughout the community (Dale and MacIsaac, 1989) and has been associated with many factors which contribute individually, and in complex interactions, to the spatial arrangement of plants.

Theses factors originate from two sources: biological and environmental influences (Pielou, 1974; Krebs, 1978; Greig-Smith, 1983; May 1984; Borcard *et al*, 1992). Biological influences are the result of life history characteristics of individual plants (e.g. reproductive strategy, growth form or dispersal ability) or the result of interactions between species (e.g. herbivory, predation, mutualism or competition). The environmental influences on species distribution are the result of differences in the physical characteristics of the landscape. These conditions have either a historical origin (e.g. fires, glaciation) or are related to present circumstances like topography, temperature, nutrients or soil moisture.

In the High Arctic, early descriptions of the spatial arrangement of species were based on subjective floristic-physiognomic and geomorphic criteria which described plant communities in terms of recognizable vegetation, key species, landforms and/or habitats (Muc and Bliss, 1977; Komarkova and Webber, 1980; Reznicek and Svoboda, 1982; Sheard and Geale, 1983a). More recent research has used statistical methods based on ordination or hierarchial classification in order to define communities of equal internal heterogeneity and relate them to different explanatory variables (Sheard and Geale, 1983a; Bergeron, 1988; Muc *et al*, 1989; Bliss *et al*, 1994).

Research on the spatial distribution of species within community types has focused on describing the position of species relative to apparent environmental influences (Beshel and Matveyeva, 1972; Muc 1976; Reznicek and Svoboda, 1982; Bliss and Svoboda, 1984; Henry, 1987; Muc *et al.* 1989; Daly *et al.*, 1989; Bliss *et al.*, 1994) or on the spatial coverage by individual species (Bliss, 1971; Shaver and Billings, 1985; Muc, 1976; Callaghan and Emanuelsson, 1985). However, there has been no research that has quantitatively measured the species pattern within arctic communities caused by the spatial coverage of individual species, or patches of one or more species. In addition, there have been no studies relating this spatial pattern to the spatial arrangement of biological and environmental factors influencing the distribution.

Vegetation Distribution - Environmental influences

A. *Arctic Ecosystems*

The distribution of vegetation in the arctic is influenced by environmental factors that have effects at different spatial scales from a regional to a very local level. At larger regional levels the length of the growing season, water availability and summer climate patterns have been used to differentiate between major regional classifications like the low and high arctic (Bliss, 1971; Saville, 1972; Babb and Bliss, 1974; Bliss and Svoboda, 1984; Crawford, 1989; Edlund and Alt, 1989). At a more local level, soil temperature, low nutrient availability, soil parent material, topography and soil moisture affect the distribution and survival of arctic plants within communities (Billings and Mooney, 1968; Haag, 1974; Shaver and Billlings, 1975; Sheard and Geale, 1983b; Bliss and Svoboda, 1984; Miller and Alpert, 1984; Henry, 1987; Muc *et al*, 1989).

Often these factors work together to limit the distribution of individual species (Chapin and Shaver, 1985) or to influence other environmental conditions (Crawford, 1989). Soil moisture gradients have been found to be correlated with topographic gradients in many studies resulting in distinct plant distributions associated with water drainage patterns (Miller and Alpert, 1984; Ostendorf and Reynolds, 1993) or snow accumulation patterns (Komarkova and Webber, 1980; Webber *et al*, 1980; Reznicek and Svoboda, 1982). These soil moisture gradients may also influence productivity by affecting water flow. Chapin *et al.* (1988) found that an increase in water flow increases the nutrient uptake by plants.

Soil temperature affects the species distribution in the Arctic either directly or indirectly through other environmental conditions. The rate of decomposition (Chapin *et al.*, 1979; Henry, 1987) and the rate of nutrient and water uptake by plants (Shaver and Billings, 1975; Muc, 1976) have both been shown to decrease with low soil temperatures. Low soil temperatures also effect the vegetation pattern by influencing the depth of the permafrost. A shallow active layer leads to high soil water (Komarkova and Webber, 1980; Sheard and Geale, 1983a), shallow roots (Shaver and Billings, 1975; Billings, 1987) and a decrease in the amount of nutrients released from the frozen substrate (Ryden, 1981).

B. *Sedge Meadows*

Sedge meadow communities are primarily associated with wet soil conditions (Muc, 1976; Muc and Bliss, 1977; Sheard and Geale, 1983b; Bergeron, 1988; Muc *et al.*, 1989) and therefore, environmental factors that affect the water regime within the meadows are usually the most important influences on the spatial pattern. Topographical changes on a meso- and a micro-scale have been shown to affect the distribution of water (Beschel and Matveyeva, 1972; Muc, 1976; Henry, 1987; Ostendorf and Reynolds, 1993). Areas that are submerged or are on the fringe of ponds have different species compositions than those areas in better drained meadows (Muc, 1976; Bliss and Svoboda, 1984). Microtopographical changes have also been shown to influence species distribution by establishing suitable microhabitats for species that are intolerant of flooding or "prefer" drier soil conditions (Beshel and Matvegeva, 1972; Muc, 1976; Henry *et al*, 1990).

In addition to topography, soil characteristics also influence species distributions in sedge meadows. Muc (1976) suggested that cryoturbation was important in determining species composition in meadows on Devon Island. Increased aeration in wet sandy soils was also found to effect the distribution and productivity of some sedge species (Henry, 1987).

Vegetation Distribution - Biological Influences

A. *Arctic Ecosystems*

Strategies adopted by both plants and animals influence the spatial distribution of vegetation in both positive and negative ways. The accumulation of dead biomass, the retention of most plant biomass below ground and tussock growth forms, establishes more hospitable microhabitats and allow species to be less susceptible to variations in climate (Billings and Mooney, 1968; Maesson *et al.*, 1983; Billings, 1987; Callaghan and Emanuelsson, 1985; Henry, 1987). These growth strategies, as well as, the predominance of slow-growing perennials in the Arctic (Billings and Mooney, 1968; Bliss, 1971), result in specific spatial patterns for arctic vascular plants.

Vascular plants have a better ability to survive in the extreme environmental conditions of the Arctic due to reliance on a vegetative reproductive strategy (Billings and Mooney, 1968; Bliss, 1971; Saville, 1972; Bell and Bliss, 1980; Billings, 1987). The low dispersal ability of the vegetative propagules results in a characteristically small spatial pattern (Shaver and Billings, 1975; Grulke and Bliss, 1985; Henry, 1987).

The distribution of vegetation is also influenced by interactions between plants (Callaghan and Emanuelsson, 1985). The occurence of evergreen dwarf shrubs have been thought to increase the productivity of adjacent plants by increasing the accumulation of snow, increasing the temperature of the microhabitat and providing protection from wind desiccation (Carlsson and Callaghan, 1991). Plant cover can further change the microhabitat and species composition by insulating the ground surface and affect the soil temperature and permafrost depth (Brown, 1977; Crawford, 1989). The accumulation of dead biomass has also been suggested as being important because it can increase the microtopography in meadows (Henry, 1987).

One of the most prominent biological influences on plant distribution in many communities is grazing by large herbivores (Pickett and White, 1985; McNaughton, 1979; Collins and Barber, 1985; Belsky, 1986). This is also important in the Arctic where it has both positive and negative effects on the biodiversity and spatial arrangement of vegetation (Archer and Tieszen, 1980; McKendrick *et al.*, 1980; Cargill and Jefferies, 1984; Bliss, 1985; Jefferies *et al.*, 1992; Henry and Svoboda, 1994).

B. *Sedge Meadows*

Arctic sedge meadows are dominated by the graminoid growth form (Muc, 1976; Bliss and Svoboda, 1984; Billings, 1987; Henry 1987; Muc *et al.*, 1989) and therefore, the observed spatial pattern is determined by the ecology of these plants. Due to the predominance of vegetative reproduction, these species have very short dispersal patterns (Shaver and Billings, 1975; Henry, 1987), which would probably result in patchiness in the vegetation. Daly *et al.* (1989) have also found that the distribution of the two most common graminoids, *Eriophorum triste* and *Carex aquatilis*, are influenced by the thickness of the peat layer.

Sedge meadows have been identified as the prime foraging habitat for muskox in the high arctic (Parker and Ross, 1976; Henry *et al.*, 1986; Jefferies *et al.*, 1992; Raillard *et al.*, 1992) and therefore, are influenced heavily by the presence or absence of grazing. Grazing increases the nutrient cycling, increases the productivity of some plants, decreases shading and affects soil temperature (Chapin, 1980; Mckendrick *et al.*, 1980; Henry, 1987; Raillard *et al.*, 1992; Henry and Svoboda, 1994). The absence of active herbivory encourages the establishment of species intolerant of grazers (Archer and Tieszen, 1980; Henry, 1987; Jefferies *et al.*, 1992) and the development of greater microtopographical relief due to the accumulation of litter and the decrease in trampling (Henry, 1987; Raillard *et al.*, 1992).

STUDY OBJECTIVES

The general objectives of the research were:

1. To determine whether the vegetation in selected sedge meadows exhibits any distinct spatial pattern and measure the distribution found.
2. To determine the effects of differences in soil moisture and grazing intensity on the distribution of vegetation between different meadows and on the vegetation pattern within the same meadows.

A list of more specific objectives are presented in the introduction of each subsequent chapter.

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CHAPTER 2

THE SPATIAL PATTERN OF VEGETATION IN HIGH ARCTIC SEDGE MEADOWS

INTRODUCTION

The analysis of species pattern in vegetation shows that plants are not arranged randomly. This arrangement can be attributed to the influence of several different factors that work both independently and in unison to structure the natural community (Greig-Smith, 1983; Quinn and Dunham, 1983). These factors can be broken into two categories. Those that arise from interactions (either positive or negative) between certain plants and their location (the local environment) and those that arise from interactions among organisms (e.g., competition, herbivory).

In the High Arctic, several distinct plant communities have been delineated and related to changes in environmental parameters along a gradient, such as soil texture or moisture (Bliss, 1977; Reznicek and Svoboda, 1982; Sheard and Geale, 1983a; Bergeron, 1988; Muc *et al*, 1989; Bliss *et al*, 1994). Studies of communities along gradients provide an understanding of the response of species to the physical environment (Webber *et al*, 1980), and the role of the environment in determining the composition and diversity of each community (Muc, 1976; Sheard and Geale, 1983b). However, these studies do not quantitatively describe the spatial pattern of species in these communities.

Efforts to explain the spatial mosaic of plant species in arctic sedge meadow communities have been mainly descriptive in nature. Species distributions have been associated with particular physical characteristics like hummocks (Beshel and Matieyeva, 1972; Muc, 1976; Henry, 1987; Muc et al., 1989), moss thickness (Daly *et al.*, 1989), soil types (Henry, 1987), and standing water (Muc, 1976; Bliss and Svoboda, 1984; Henry, 1987; Daly *et al*, 1989), or associated with processes like frequency of flooding (Henry, 1987) or cryoturbation activity (Muc, 1976). There is, however, several limitations with describing the distribution in this way.

Firstly, since most of the species found within sedge meadows have relatively broad ecological ranges (Muc, 1976; Bergeron, 1988; Muc et al., 1989), the spatial distribution of these species cannot be described by their association with only a few physical characteristics or processes. Secondly, these descriptions ignore the biological interactions that are occurring in the meadows that could be important in structuring the community. In high arctic communities where reproduction is primarily vegetative (Muc, 1975; Callaghan and Emmanuelsson, 1985; Henry, 1987; Henry *et al.*, 1990), the limited dispersal of vegetative propagules, could have important consequence on the spatial heterogeneity of the vegetation. In addition, in high arctic sedge meadows seedling establishment mainly occurs in areas of disturbance despite the presence of a large seed bank (Bliss, 1971; Freedman *et al.*, 1982). These areas of natural disturbances are often the result of grazers (Mckendrick *et al., 1980;* Bliss, 1985; Henry *et al.* 1986; Jefferies, 1988; Jefferies *et al.*, 1992; Raillard *et al.*, 1992).

The third limitation is that these descriptions of the vegetation distribution do not give a quantitative measurement of the extent and strength of the pattern. A quantitative measurement permits the comparison of the patchiness of species and relates the pattern, rather than the occurrence of individual plants, to the environmental variation present.

Objectives

The objectives of this study were: (1) to identify if individual species and groups of vascular plants are distributed in the sedge meadows in any distinguishable spatial pattern; (2) to measure the size and consistency of the pattern along a transect running down the drainage slope of three different meadows; and (3) to compare the spatial pattern of the species along each transect and between transects.

Study Site Description

The research was done at two sites on Ellesmere Island (Figure 2-1). The Sverdrup Pass site (79°09' N; 79°40' W) is found in an ice-free corridor running east-west through the central part of the island. Sparsely vegetated polar desert dominates the valley (Bergeron, 1988) with sedge meadows occurring on drainage fields and around the river running east down the valley (Figure 2-2). The drainage fields are fed by glaciers and melt water seepage from the northern and southern slopes of the valley. The Sverdrup Pass location has a large resident population of muskox that graze extensively on the sedge meadows (Henry *et al*, 1986; Raillard *et al.*, 1992).

The second site was at the Alexandra Fiord lowland (78°53' N; 75°55' W) on the east coast of central Ellesmere Island. The lowland has high cliff faces to the east and west, the tongues of two glaciers to the south and the Arctic Ocean to the north. Similar to Sverdrup Pass, the sedge meadows are restricted to areas that are wet throughout the growing season. This includes the lower slopes of the bordering cliff faces and the margins of the river and three streams in the lowland (Figure 2-3).

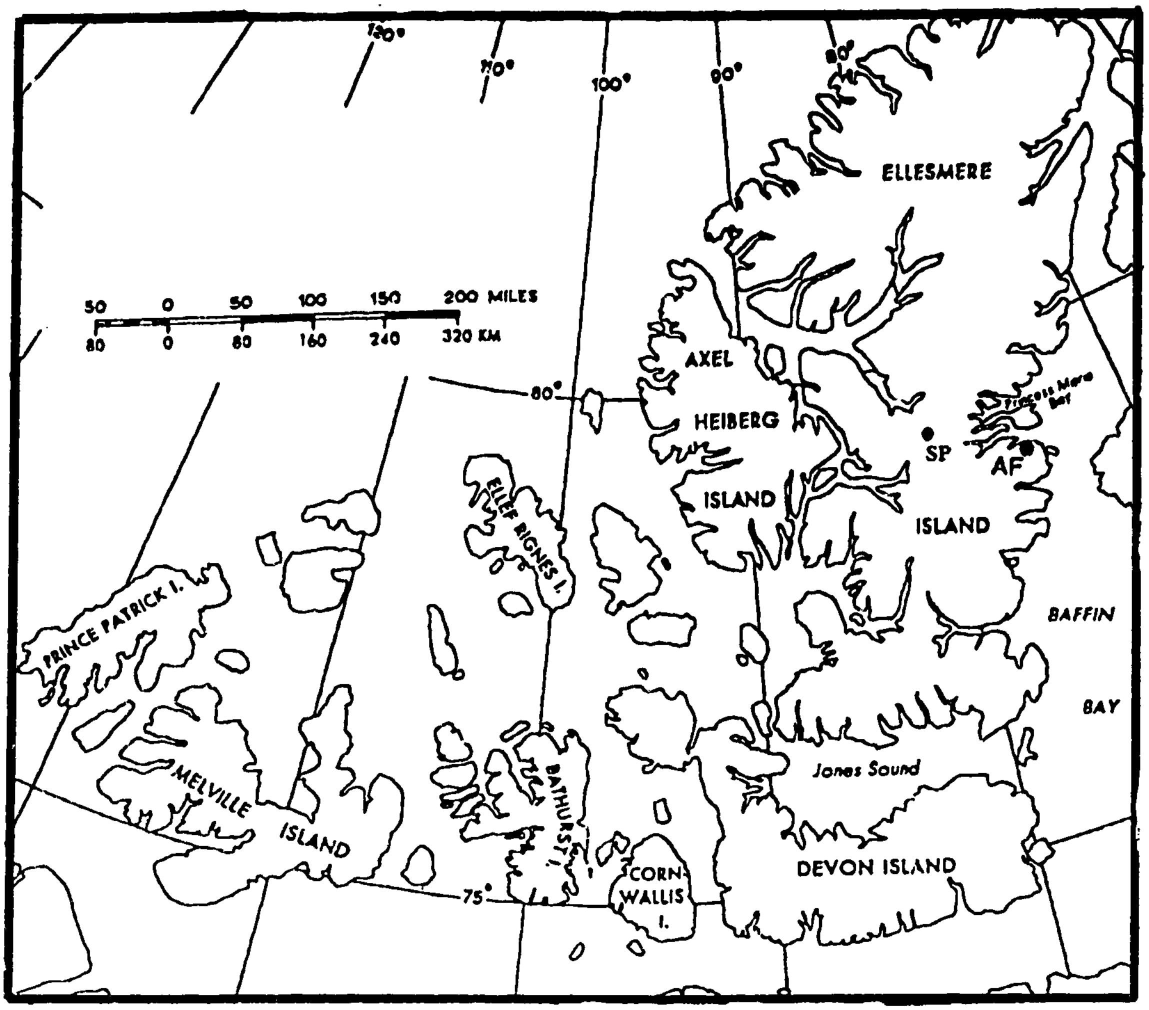


Figure 2-1. Map of the Queen Elizabeth Islands, Northwest Territories showing the location of Alexandra Fiord (AF) and Sverdrup Pass (SP).

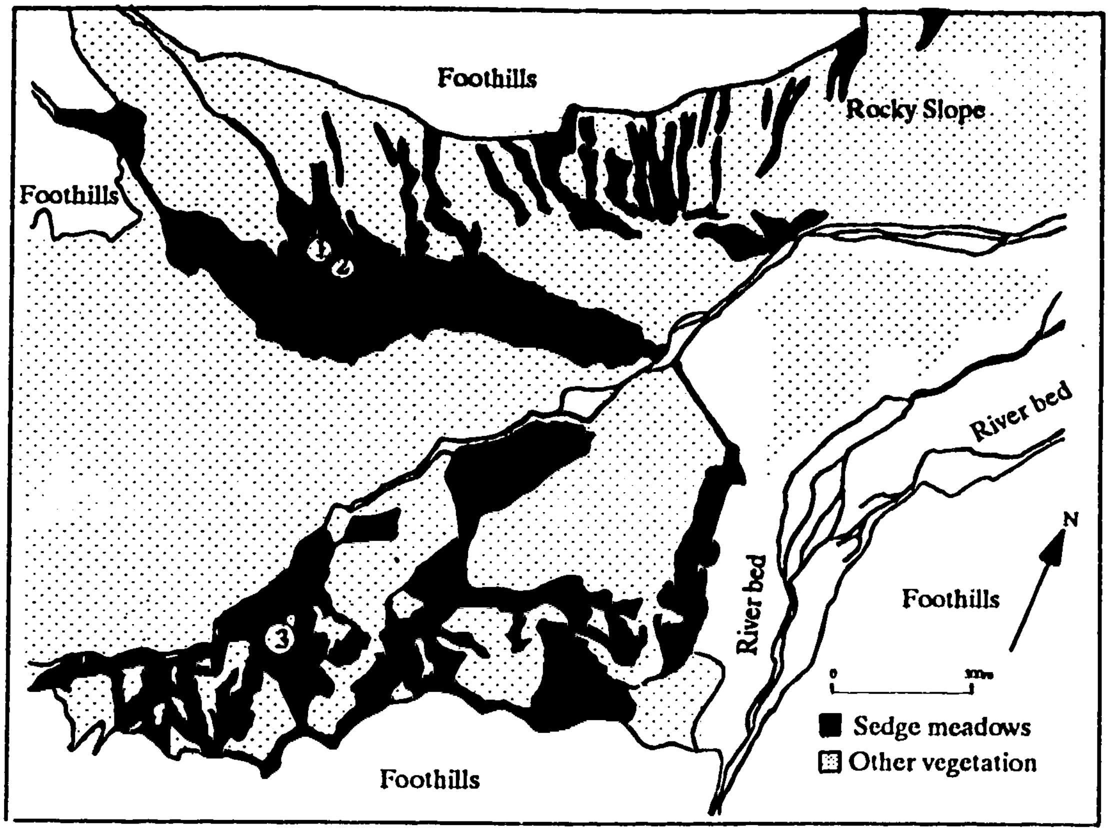


Figure 2-2. Map of the Sverdrup Pass site showing the distribution of sedge meadows (shaded area) in the lowlands and the location of the study transects: (1) transect BMS; (2) transect BRS; (3) transect CRT (adapted from Bergeron, 1988).

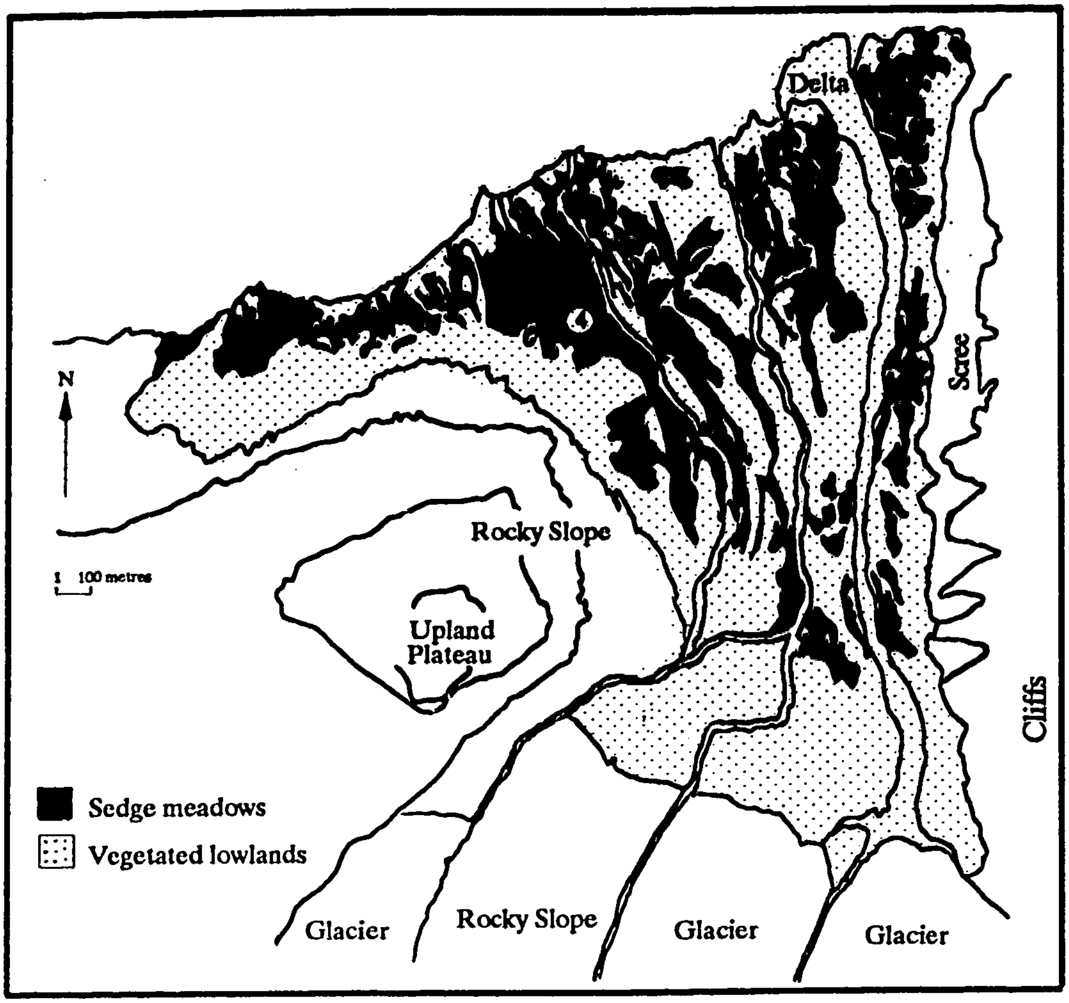


Figure 2-3. Map of the Alexandra Fiord lowland site showing the distribution of sedge meadows (shaded area) and the location of study transect OWT (4) (adapted from Muc *et al.*, 1988).

The Alexandra Fiord lowland, in contrast to Sverdrup Pass, has numerous well-vegetated plant communities covering a total of 47% of the lowland (Muc *et al*, 1989) and is visited only infrequently, if at all, by muskox from adjacent regions (Henry *et al*, 1986). The sedge meadows also differ at Alexandra Fiord due to the presence of large quantities of dead biomass and pronounced hummocks (Henry *et al*, 1986; Henry, 1987). Sverdrup Pass shows little dead biomass accumulation and little hummock formation.

METHODS AND MATERIALS

Sampling Method

The vegetation was sampled in two meadows at Sverdrup Pass and one at Alexandra Fiord using a continuous sequence of 10 cm x 5 cm quadrats along 100 m transects (1000 quadrats). The size of the quadrat was selected on the bases of two criteria. Firstly, the quadrat had to be large enough that there were a manageable number of quadrats sampled for a 100 m length and secondly, the quadrat had to be small enough so that no significant patterns in the vegetation were missed. The 10 cm x 5 cm quadrat was thought to satisfy both these criteria.

A single transect was placed in the centre of each meadow running down the drainage gradient (Sverdrup Pass - Figure 2-2, transects BMS and CRT; Alexandra Fiord - Figure 2-3, transect OWT) with an additional transect running perpendicular to the 50 m point on transect BMS (Figure 2-2 - transect BRS) from the edge of the meadow to the centre. The transects were placed running down the drainage slopes of the meadows in order to investigate the influence of position on the pattern found. It has been shown that the pattern of vegetation distribution can be related to the water regime along a drainage gradient (Reznicek and Svoboda, 1982; Ostendorf and Reynolds, 1993).

In each quadrat the presence or absence of all vascular plant species was noted. The use of presence/absence data has been found to not unduly influence the detection of spatial pattern in vegetation (Dale and Blundon, 1990), and it increased the number of sample quadrats that could be measured. Nomenclature for the vascular species followed Porsild and Cody (1980).

Microtopography Measurement

The microtopography and slope of each transect was measured using a survey level from a fixed point at the top of each slope. Measurements from the centre of each quadrat resulted in a profile of each transect. An indication of the microtopographical changes along each transect was found by calculating the average hummock to hummock and hummock to hollow distance using adjusted scores. Scores were found by first calculating a running average for each transect and then subtracting this value from the elevation value for each quadrat. By doing this, the elevation measurements used would not include the elevation change due to the slope of the transect. The running average value for each quadrat (q_ω) was calculated by taking the average elevation value of 9 quadrats ($q_{\omega-4}$ to $q_{\omega+4}$).

The average hummock to hummock distance was calculated using the distances between adjacent positive peaks found in the adjusted scores. Average hummock to hollow distance was calculated using the distance values found between adjacent positive and negative peaks in the same scores. The variation in the adjusted scores along each transect indicated the variation in height of the microtopography.

Data Analysis

The analysis of each transect was done using the data from the full transect and then separately using the data from the first 500 quadrats and then the last 500 quadrats. There were 27 vascular species in total in the meadows, but only the eight most common species were analyzed from each transect. The species pattern analysis was done on each transect using only those species that were present in greater than 50 quadrats (>5% of the quadrats), with the exception of *Juncus biglumis* on the Alexandra Fiord transect (OWT) (Table 2-1). The final list of species includes all the dominant vascular plants that have been found in the meadows (Henry, 1987; Bergeron,1988; Muc *et al.*, 1989; Henry, 1994) so the exclusion of the less common species was considered not to seriously bias the results.

Table 2-1. Vascular plant species found along transects at Sverdrup Pass (BMS, BRS, CRT) and Alexandra Fiord (OWT) and the number of quadrats out of 1000 in which each was present. A blank represents species found in less than 50 quadrats (< 5% of the quadrats along each transect). Species are arranged in order of abundance.

	TRANSECTS			
Species	**BMS**	**BRS**	**CRT**	**OWT**
Eriophorum triste (Th.Fr.) Hadac & Löve	899	900	264	867
Carex aquatilis Wahleb.	417	391	895	205
Salix arctica Pall.	319	310	56	93
Arctagrostis latifolia (R.Br.) Griseb	229	422	71	-
Juncus biglumis L.	396	166	-	57
Polygonum viviparum L.	97	76	-	195
Eriophorum scheurchzeri Hoppe	521	457	145	-
Dupontia fischeri R. Br.	-	-	881	-
Carex membranecea Hook.	-	-	-	485
Dryas integrifolia M. Vahl.	-	-	-	442
Saxifraga cernua L.	-	-	256	-
Pleuropogon sabinei R. Br.	150	81	-	-
Carex misandra R. Br.	-	-	-	150
Saxifraga oppositifolia L.	-	-	-	147
Cardamine pratensis L.	-	-	61	-

Although *J. biglumis* was present in more than 50 quadrats, it was not included in the analysis in order that the same number of species (eight) were analyzed along each transect. *J. biglumis* was present in only 57 quadrats and therefore was not expected to have a strong pattern along the transect. The exclusion of *J. biglumis* can also be justified because it has a distinctly lower frequency than the other species.

In order to determine if differences occurred in hummock to hummock distance, hummock to hollow distance and mean number of species per quadrat between transects ANOVAs were performed on the various data sets. The statistical package used was SYSTAT.

A. *One and Two Species Pattern Analysis*

Pattern refers to the nonrandom spatial distribution of vegetation and is the result of periodic changes in the density of plant species over an area (Dale and MacIsaac, 1989). The periodicity of vegetation pattern is described in terms of two characteristics; scale and intensity. Scale is the average distance between the centre of a region of high density ("patch") and the centre of a region of low density ("gap"). Intensity as described by Dale and Blundon (1990) is the difference between the average density of a patch and that of a gap.

Many methods used to analyse the patchiness of single species have relied on techniques that use a series of contiguous quadrats to describe quantitatively the dispersion (e.g., Hill, 1973; Grieg-Smith, 1983). Quadrats are grouped into successively larger blocks and a variance estimate is calculated for each block size. A graph of the variance estimate against the block size indicates a scale of pattern where a "peak" occurs in the plot. The amplitude of the peak roughly indicates the intensity of the scale of pattern.

In this study the pattern analysis used for the study of individual species was Three Term Local Quadrat Variance (3TLQV). Three Term Local Quadrat Variance has been recommended as the best basic method for analyzing the pattern of single species because of several factors (Hill, 1973; Ludwig, 1979; Greig-Smith, 1983; Leps, 1991): it eliminates the influence of the starting position of the blocking; it allows variance estimates to be calculated at all block sizes up to one third the total number of quadrats; and it is influenced less by trends in the data.

Three Term Local Quadrat Covariance was used to determine the spatial pattern of species pairs. Three Term Local Quadrat Covariance (3TLQC) is analogous to 3TLQV but instead calculates a covariance value for a particular species pair at each block size.

Both variance and covariance values were calculated using the procedures outlined in Dale and Blundon (1991). The scale of spatial pattern was determined by identifying the location of peaks in the variance-blocksize plots and covariance-blocksize plots and then adjusting the noted blocksize value (Dale and Blundon 1990). The adjustment was done because peaks occur at a block size smaller than the true scale of the pattern. The intensity of each scale of pattern was found by eliminating the additive effect of each peak using the method suggested by Dale and MacIsaac (1989).

From previous work on the pattern of species pairs, the peaks detected in multispecies plots were often found not to match those found in the variance plots. Dale and Blundon (1991) have suggested that this is due to irregularities in the spacing of patches. Since differences were found in the spacing of patches of most of the species, only peaks less than 15 quadrats in size were considered because of the difficulty in interpreting what the larger scales of pattern represented. In addition, the purpose of the TTLQC analysis was to investigate interactions between species. These types of interactions occur mainly at short distances and therefore, they should occur to the greatest extent at the first scale of pattern. Within the range only the presence of a peak and the value of the peak (negative or positive) was noted.

B. *Multiscale Ordination Analysis*

Multiscale ordination analysis was used to investigate the relationship between the spatial patterns of all eight species. In this analysis an ordination technique is combined with a contiguous quadrat blocking method. Initially a covariance-variance matrix for each blocksize is derived using the results from the 3TLQV and 3TLQC analysis. The values in each matrix are then converted to intensity values (Dale and Blundon, 1991) and all the matrices are added together. After Principle Component Analysis (PCA) is done on the adjusted matrix, the derived eigenvalues are partitioned among the different blocksizes based on the amount that each contributed to that eigenvalue. Since the original matrix for each blocksize consisted of intensity values, the derived eigenvalues are finally adjusted using the relationship between intensity and variance values outlined by Dale and MacIsaac (1989). The location of peaks in a eigenvalue-blocksize plot are used to indicate the scale at which a pattern exists. Similar to the TTLQC analysis only peaks that were less than 15 quadrats in size were noted.

In the multiscale ordination analysis, the proportion of the total variation in the sample data accounted for by the first axis of the ordination was found for all four transects. This value was calculated by using the results of the ordination of the total covariance-variance matrix to obtain the first eigenvalue and the sum of the variances of all eight species. The proportion of variation accounted for by the first ordination axis is found by dividing the first eigenvalue by the sum of variances (Pielou, 1984).

RESULTS

Microtopography

Figure 2-4 shows the elevation change along the four transects found at Alexandra Fiord (OWT) and Sverdrup Pass (BMS, BRS and CRT). Transect OWT had the greatest change in elevation (650 cm), while transects BMS, BRS and CRT all ranged between 150 and 200 cm.

Table 2-2 contains the results of the microtopographical analysis of each transect. No significant difference was found between the average hummock to hummock distance of each transect or the average hummock to hollow distance of each transect. The largest hummock to hummock and hummock to hollow distances were found along the Alexandra Fiord transect (67 and 34 cm, respectively), while the shortest distances were found along the CRT transect at Sverdrup Pass (46 and 23 cm, respectively).

By eliminating the effect of the slope of the transect (running average minus the elevation of each transect) a comparison of the height of the hummocks and hollows could be made (Table 2-2). Transect OWT showed the greatest variation (SD = 3.21) and greatest range (-9 cm to 8 cm) in values. The three other transects (BMS, BRS and CRT) had less variation and similar standard deviations (1.1, 1.13 and .94, respectively) and ranges (-4 cm to 4 cm; -4 cm to 3 cm; -4 cm to 3 cm, respectively) in their hummock and hollow heights.

Species Distribution

The eight most abundant species (displayed in order of abundance) along each transect are presented in Figures 2-5 to 2-8 in patch/gap size graphs. The graphs represent the size of the patches or gaps (number of adjacent quadrats with the species present or absent) sequentially displayed from the top to the bottom of the transect.

The patch/gap size graphs show the number of patches present and the relationship between the size of patches and the size of the gaps. On all four transects the most frequent and the least frequent species were found to have the fewest number of patches along their respective transects. This was due to combinations of either large patches with small gaps or small patches with large gaps (Figures 2-5 to 2-8): large meaning greater than thirty quadrats long (300 cm), and small meaning less than three quadrats long (30 cm).

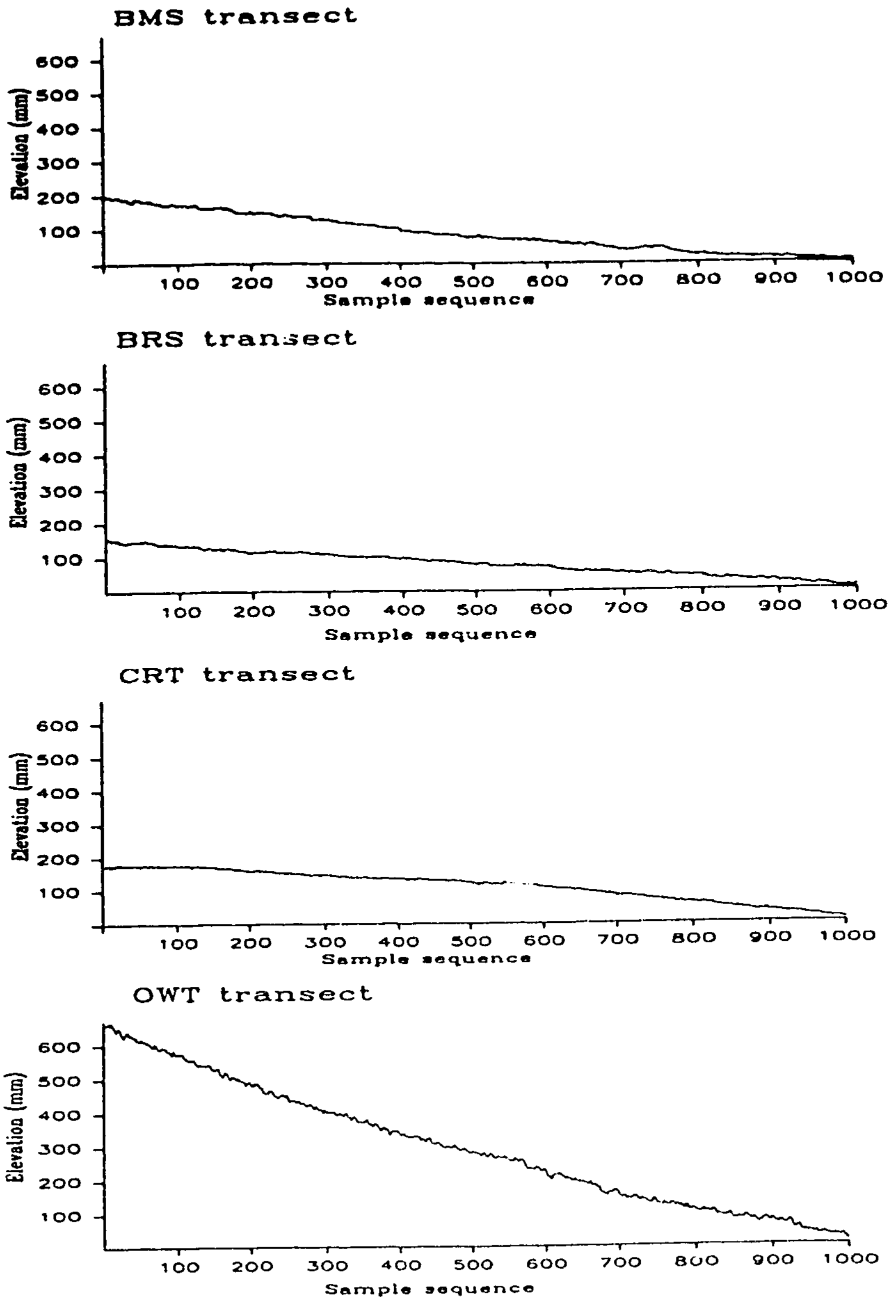


Figure 2-4. Profiles of the study transects at Sverdrup Pass (BMS, BRS and CRT transects) and Alexandra Fiord (OWT transect) showing the change in elevation (mm) along the transects (quadrat sequence).

Table 2-2. Microtopographical measurements along the Sverdrup Pass (BMS, BRS and CRT) and Alexandra Fiord (OWT) transects. Data are means (± SD). The running average was found by calculating the average value of 9 quadrats centred around each quadrat.

	BMS	BRS	CRT	OWT
Average distance from hummock top to hummock top (cm, n = # samples)	56 ± 27 (n =177)	57 ± 26 (n = 174)	46 ± 20 (n = 213)	67 ± 26 (n = 148)
Average distance from the top of a hummock to lowest point in the next hollow (cm, n = # samples)	28 ± 17 (n = 354)	29 ± 16 (n = 348)	23 ± 14 (n = 426)	34 ± 18 (n = 296)
Average difference between the slope of the transect (running average) and the elevation of each quadrat along the transect (cm, n = 1000)	.00 ± 1.10	.00 ± 1.22	.00 ± .94	.00 ± 3.21
Range of height values along adjusted transect (cm, n = 1000)	-4 to 4	-4 to 3	-4 to 3	-9 to 8

Figure 2-5 Graphs showing the size of patch and gap blocks (number of quadrats) that occur sequencially for 8 species along the BMS transect at Sverdrup Pass. Each bar corresponds to one patch or gap. The thickness of the bars varies depending on the number of patches and gaps along the transect. Those bars above the shaded part of the strip that is under each graph are found in the top half of the transect. Plant species are shown in descending order of frequency.

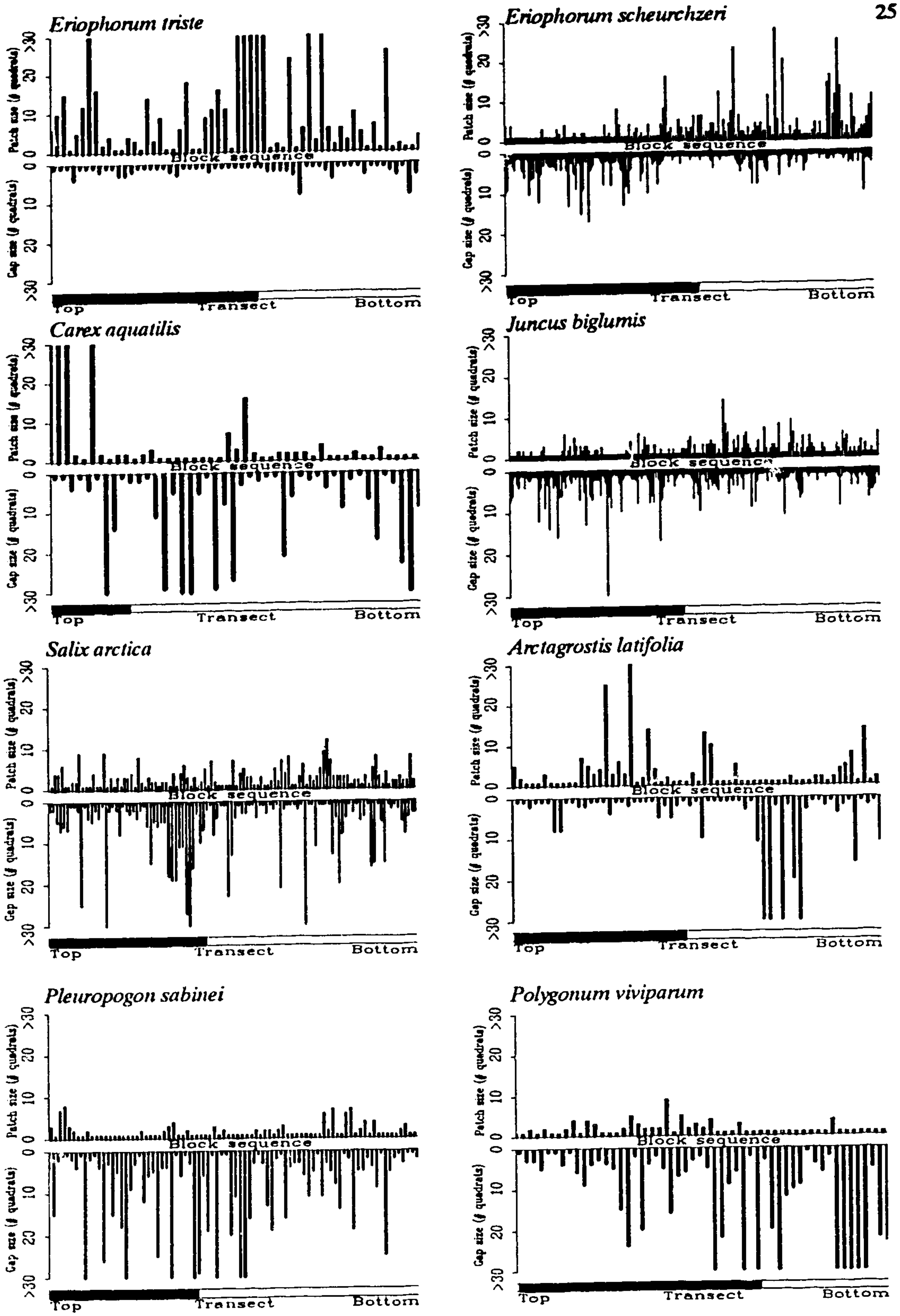
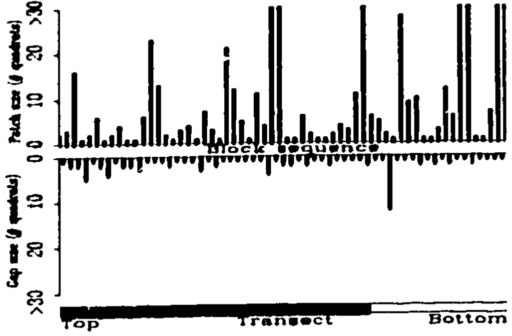
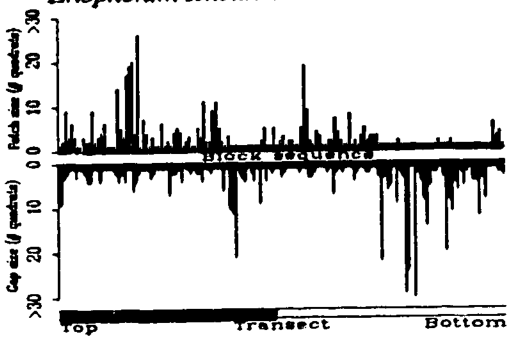

Eriophorum triste
Eriophorum scheurchzeri
Carex aquatilis
Juncus biglumis
Salix arctica
Arctagrostis latifolia
Pleuropogon sabinei
Polygonum viviparum
Patch size (# quadrats)
Gap size (# quadrats)
0
10
20
>30
Block sequence
Top
Transect
Bottom

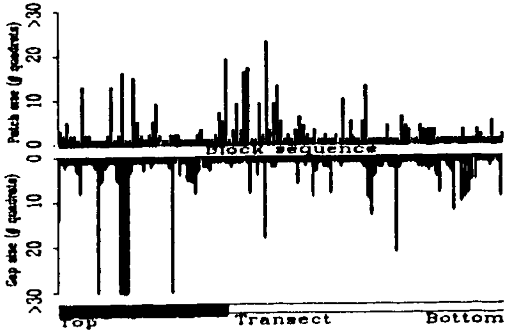
Figure 2-6 Graphs showing the size of patch and gap blocks (number of quadrats) that occur sequencially for 8 species along the BRS transectat Sverdrup Pass. Each bar corresponds to one patch or gap. The thickness of the bars varies depending on the number of patches and gaps along the transect. Those bars above the shaded part of the strip that is under each graph are found in the top half of the transect. Plant species are shown in descending order of frequency.



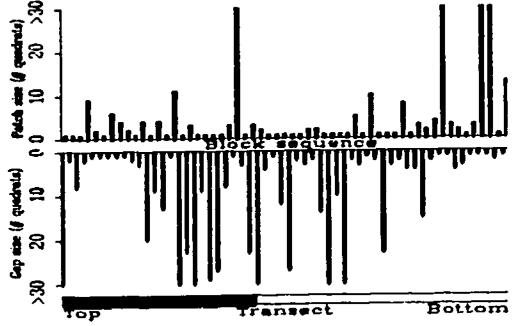
Eriophorum triste



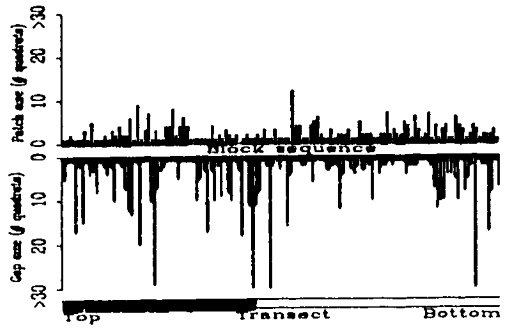
Eriophorum scheurchzeri



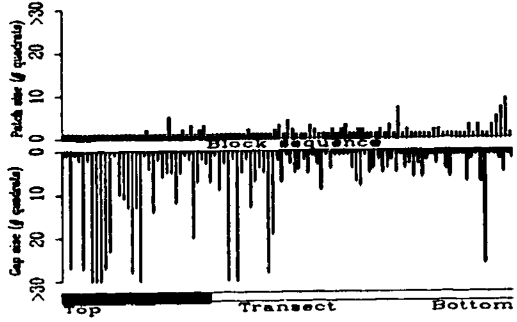
Arctagrostis latifolia



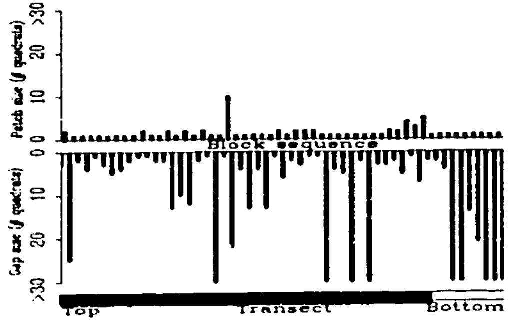
Carex aquatilis



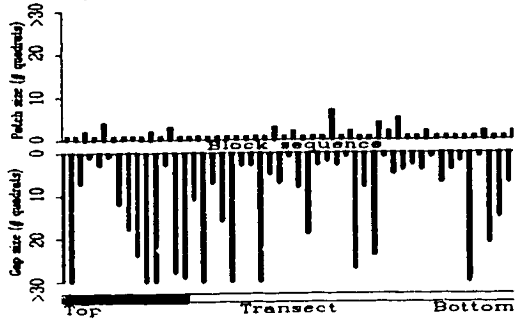
Salix arctica



Juncus biglumis



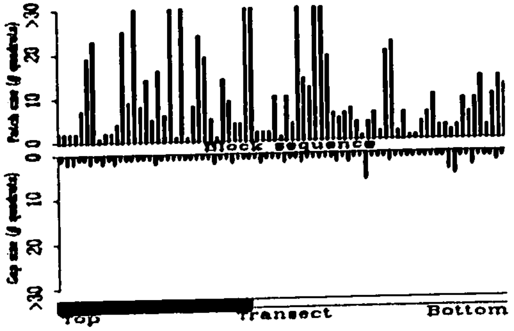
Pleuropogon sabinei



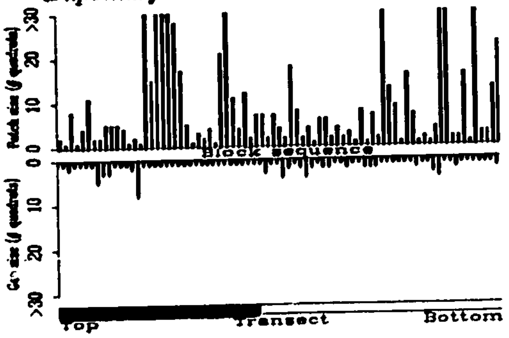
Polygonum viviparum

Figure 2-7. Graphs showing the size of patch and gap blocks (number of quadrats) that occur sequencially for 8 species along the CRT transect at Sverdrup Pass. Each bar corresponds to one patch or gap. The thickness of the bars varies depending on the number of patches and gaps along the transect. Those bars above the shaded part of the strip that is under each graph are found in the top half of the transect. Plant species are shown in descending order of frequency.

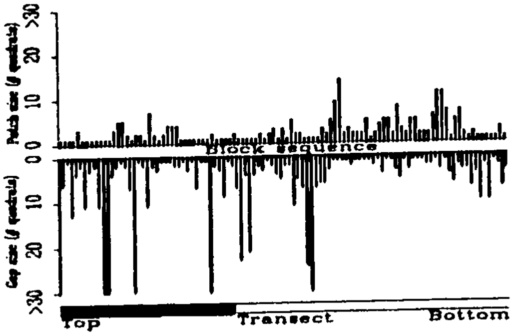
Carex aquatilis



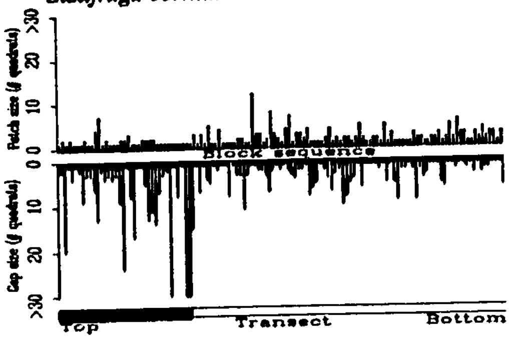
Dupontia fisheri



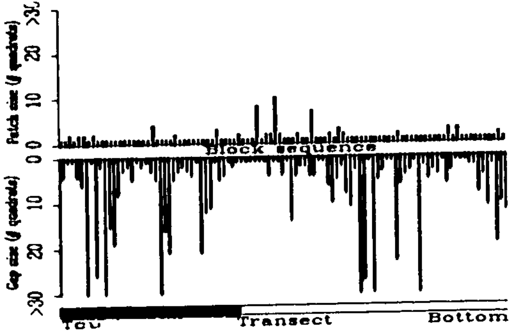
Eriophorum triste



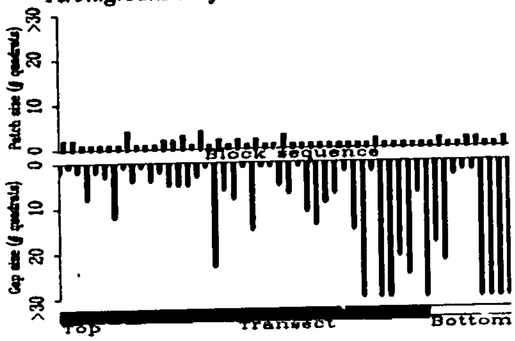
Saxifraga cernua



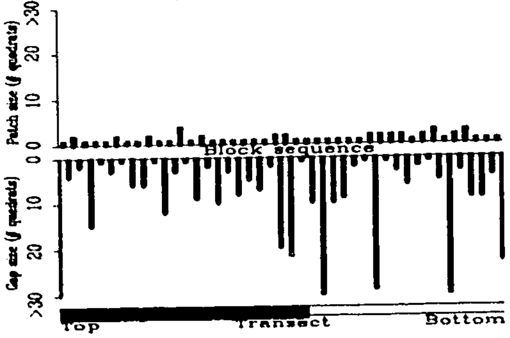
Eriophorum scheurchzeri



Arctagrostis latifolia



Cardamine pratensis



Salix arctica

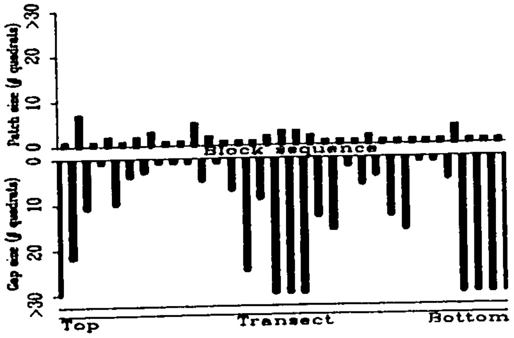
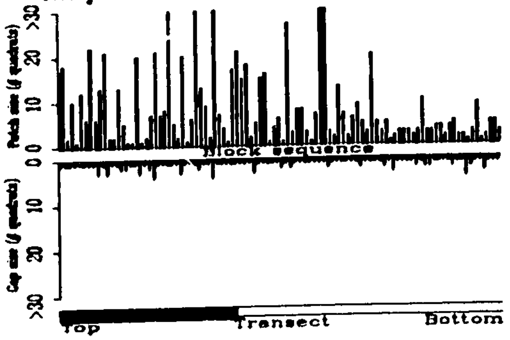
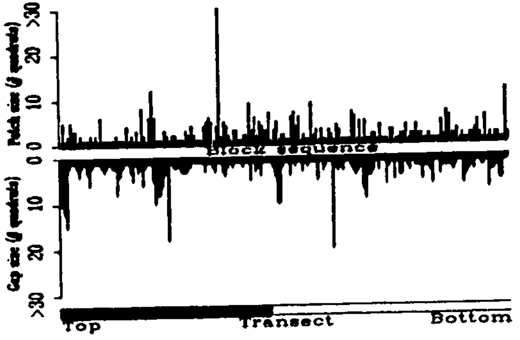


Figure 2-8 Graphs showing the size of patch and gap blocks (number of quadrats) that occur sequencially for 8 species along the OWT transect at Alexandra Fiord. Each bar corresponds to one patch or gap. The thickness of the bars varies depending on the number of patches and gaps along the transect. Those bars above the shaded part of the strip that is under each graph are found in the top half of the transect. Plant species are shown in descending order of frequency.

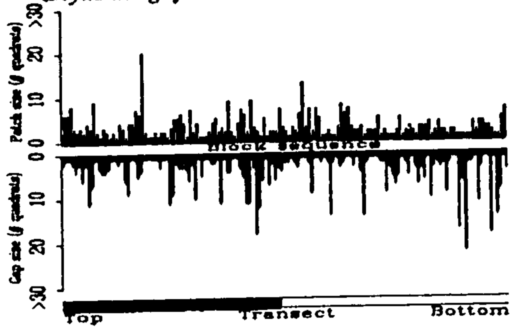
Eriophorum triste



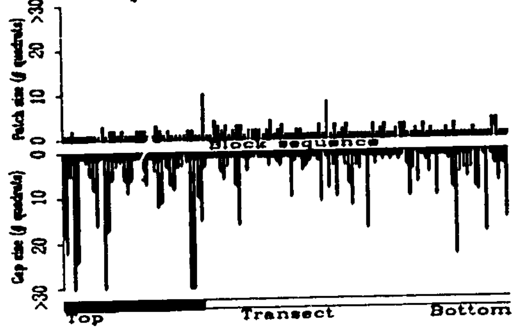
Carex membranacea



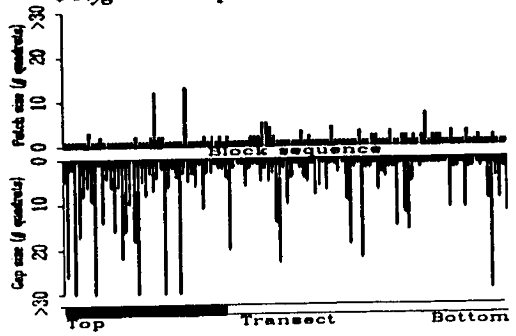
Dryas integrifolia



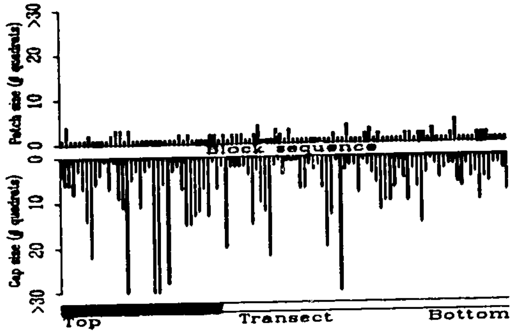
Carex aquatilis



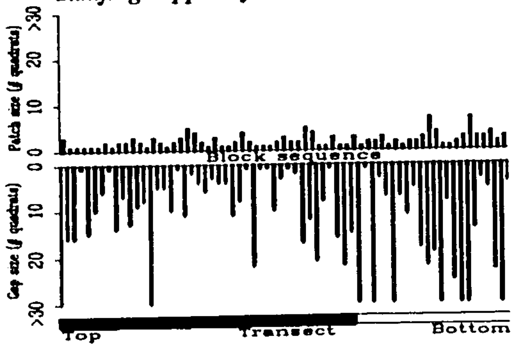
Polygonum viviparum



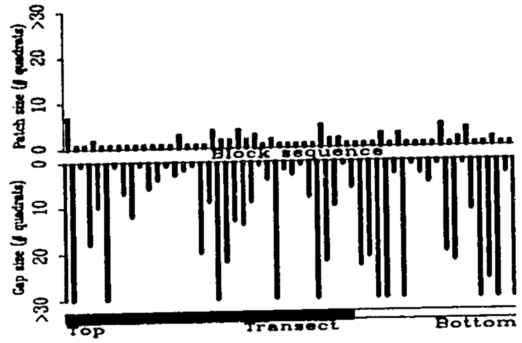
Carex misandra



Saxifraga oppositifolia



Salix arctica



For each individual species, the size of patches or gaps along each transect either remained constant, varied with a distinctive trend or had no trend at all. Species with generally large patches separated by consistently small gaps were less common than species with small patches separated by large gaps. There was only a single species (*Eriophorum triste*) on transects BMS, BRS and OWT and two species (*Carex aquatilis* and *Dupontia fischeri*) on transect CRT that had consistently small gaps between patches. Small patches with generally large gaps, however, were found for two species on transect BMS (*Pleuropogon sabinei* and *Polygonum viviparum*), four species on transect BRS (*P. sabinei, P. viviparum, Salix arctica* and *Juncus biglumis*), five species on transect CRT (*S. arctica, Eriophorum*

scheurchzeri, *Arctagrostis latifolia, Saxifraga cernua* and *Cardamine pratensis*) and five species on transect OWT (*S. arctica, P. viviparum, C. aquatilis, Carex misandra* and *Saxifraga oppositifolia*).

Although all these species had consistent patch or gap sizes, none of the species had both. *Eriophorum triste* had more large patches in the top section on transects BMS and OWT and more large patches in the bottom section along transect BRS. By contrast, *C. aquatilis* and *D. fischeri* on transect CRT and *E. triste* on transect BMS had no pattern to the fluctuation in patch sizes along their transects.

Of the species that had a constant patch size, *S. arctica* (transect BRS, CRT and OWT), *C. pratensis* (transect CRT) and *S. oppositifolia* (transect OWT) did not show a sequential change in the size of gaps along their transects. In contrast, *Juncus biglumis* and *S. cernua* (transect BRS), *C. misandra* and *C. aquatilis* (transect OWT), *P. sabinei* (transects BMS and BRS), *P. viviparum* (transects BMS and BRS), *A. latifolia* (transects BRS and CRT), *S. arctica* (transect CRT) and *E. scheurchzeri* (transect CRT) all showed a trend along their transects.

Juncus biglumis, C. misandra, P. sabinei (transect BMS), *A. latifolia* and *S. cernua* (transect BRS), *C. aquatilis* (transect OWT) and *P. viviparum* (transects BRS and OWT) all have larger gaps or a greater number of large gaps in the top half compared to the bottom half of their respective transects. With *A. latifolia* (transect CRT), *P. sabinei* (transect BRS), and *P. viviparum* (transect BMS) there was either a greater size or number of large gaps near the bottom of the transect. The spacing between patches of *E. scheurchzeri* and *S arctica* on transect CRT were similar in that both had large gaps present at the top and bottom of the transect. However, *S. arctica* also had large spaces between patches in the middle of the transect.

Most of the species that did not have a constant patch or gap size showed a change in the number of patches, or the size of patches, along their transects. *Carex aquatilis* (transect BMS) was present in almost all the quadrats in the top section (few gaps) but was present in small, dispersed patches in the bottom section (more and larger gaps). Both *P. sabinei* and *A. latifolia* were less common in the bottom section of their transects in which they were found (fewer and larger gaps). *Eriophorum scheurchzeri* on transect BRS (Figure 2-6) shifted from larger patches at the top to smaller patches at the bottom of the transect, while the gaps between them increased. The reverse response, from smaller to larger patches, was found with *E. scheurchzeri* on transect BMS. *Carex aquatilis* on transect BRS also showed a shift from small gaps at the ends of the transect to large gaps in the centre.

There were six species that had either an apparent arbitrary fluctuation in the size of their patches and gaps along the transect or did not have consistently small patches or gaps. These species were *J. biglumis* and *S. arctica* on transect BMS, *E. scheurchzeri* and *A. latifolia* on transect BRS and *C. membranacea* and *D. integrifolia* on transect OWT.

Pattern Analysis - Single Species

The results from the 3TLQV analysis are found in Tables 2-3 to 2-6 for the eight species studied on each transect, and are found in their order of frequency. The size of the patterns were shown in terms of number of sample quadrats and are listed within two ranges: 1 - 14 and 15 - 70 quadrats in size.

A. *Pattern Range: 1-14 quadrats in size*

Using the data from the whole transect, the range of the first pattern found at less than 15 quadrats in size was from 4 to 7 quadrats on transect BMS (with five out of eight species having a scale of 6 or 7 quadrats), from 3 to 11 quadrats on transect BRS, from 5 to 11 quadrats on transect CRT, and from 3 to 12 quadrats on transect OWT. The intensities ranged from 7.00 to 20.33 on transect BMS, from 6.62 to 15.81 on transect BRS, from 4.29 to 11.63 on transect CRT and from 7.74 to 21.46 on transect OWT.

Six species were found on more than two of the transects. *E. triste*, *S. arctica* and *C. aquatilis* occured on all four transects, while *E. scheurchzeri*, *A. latifolia* and *P. viviparum* occured on three out of the four transects (Table 2-1). The first scale of pattern for *E. triste* ranged from 3 to 7 quadrats in size for the four transects. *S. arctica* had a similar width in its range (6 to 10 quadrats), but for only three of the four transects. The fourth transect (BRS) showed no scale of pattern for *S. arctica*. Although *C. aquatilis* had a greater range in its first scale of pattern than *E. triste* and *S. arctica*, this was due to a large value on transect OWT. A scale of pattern of 11 quadrats in size was found on transect OWT, while the other three transects had values of 5 or 6 quadrats in size.

Table 2-3. Quadrat Variance (3TLQV) analysis of species from the BMS transect (Sverdrup Pass). The size (# of quadrats) and intensity (in brackets) of patterns found for each species are listed within the range of 1 -14 and 15 to 70 quadrats in size. Analysis was done using data from the full transect (**FULL**), data from quadrats 1 to 500 (**TOP**), and data from quadrats 501 to 1000 (**BOT**). Species are arranged in order of frequency. "--" represents where no scale of pattern was found.

	Size of Pattern					
	Range: 1 - 14 quadrats			Range: 15 - 70 quadrats		
Species	FULL	TOP	BOT	FULL	TOP	BOT
Eriophorum triste	7 (7.00)	9 (6.39)	4 (9.46)	23 (7.22)	25 (5.58)	22 (8.48)
Carex aquatilis	6 (7.39)	5 (5.31)	6 (8.23)	--	69 (9.97)	28 (9.58)
Salix arctica	6 (16.66)	11 (11.22)	6 (16.15)	48 (10.77)	33 (7.13)	49 (14.51)
Eriophorum scheurchzeri	7 (13.79)	6 (14.98)	--	--	44 (3.89)	16 (7.27)
Juncus biglumis	4 (20.33)	--	4 (21.05)	36 (3.91) 67 (8.15)	15 (6.74) 20 (6.08)	25 (13.20) 65 (4.46)
Arctagrostis latifolia	--	10 (4.45)	--	18 (3.96)	--	17 (8.89) 49 (6.20)
Polygonum viviparum	7 (8.25)	6 (11.88)	4 (7.12) 9 (4.87)	24 (5.58)	24 (7.21)	--
Pleuropogon sabinei	--	4 (12.06)	8 (9.17)	24 (9.06)	26 (8.16)	23 (9.70)

Table 2-4. Quadrat Variance (3TLQV) analysis of species from the BRS transect (Sverdrup Pass). The size (# of quadrats) and intensity (in brackets) of patterns found for each species are listed within the range of 1 -14 and 15 to 70 quadrats in size. Analysis was done using data from the full transect (FULL), data from quadrats 1 to 500 (TOP), and data from quadrats 501 to 1000 (BOT). Species are arranged in order of frequency. "--" represents where no scale of pattern was found.

	Size of Pattern					
	Range: 1 - 14 quadrats			Range: 15 - 70 quadrats		
Species	**FULL**	**TOP**	**BOT**	**FULL**	**TOP**	**BOT**
Eriophorum triste	3 (15.09) 11 (6.62)	--	3 (16.64) 9 (9.17)	38 (7.47)	25 (7.08)	43 (7.51)
Eriophorum scheurchzeri	11 (10.38)	3 (26.53)	10 (12.49)	--	26 (6.16) 59 (5.86)	60 (3.63)
Arctagrostis latifolia	5 (12.69)	4 (16.97)	3 (20.80)	--	20 (8.37) 58 (13.83)	66 (14.44)
Carex aquatilis	5 (9.98)	4 (11.42)	--	--	30 (9.46) 60 (8.01)	--
Salix arctica	--	3 (26.84) 11 (13.05)	--	18 (10.62)	--	15 (12.34) 57 (7.96)
Juncus biglumis	8 (8.59)	7 (12.46)	5 (8.85)	20 (4.98) 35 (5.23)	34 (6.36)	17 (6.88)
Pleuropogon sabinei	3 (15.81)	8 (2.93)	3 (20.35)	--	37 (1.12)	39 (6.07)
Polygonum viviparum	6 (8.74)	6 (10.43)	5 (7.39)	46 (5.20)	26 (2.78) 47 (6.98)	40 (2.98)

Table 2-5. Quadrat Variance (3TLQV) analysis of species from the CRT transect (Sverdrup Pass). The size (# of quadrats) and intensity (in brackets) of patterns found for each species are listed within the range of 1 -14 and 15 to 70 quadrats in size. Analysis was done using data from the full transect (FULL), data from quadrats 1 to 500 (TOP), and data from quadrats 501 to 1000 (BOT). Species are arranged in order of frequency. "--" represents where no scale of pattern was found. N/A represents a section of the transect where the species is not found

	Size of Pattern					
	Range: 1 - 14 quadrats			**Range: 15 - 70 quadrats**		
Species	**FULL**	**TOP**	**BOT**	**FULL**	**TOP**	**BOT**
Carex aquatilis	6 (8.63)	10 (7.38)	3 (17.80)	19 (5.11) 60 (4.61)	20 (3.18) 60 (5.94)	--
Dupontia fischeri	5 (11.32)	5 (13.05)	4 (11.40)	32 (5.01)	65 (6.57)	20 (6.97)
Eriophorum triste	5 (11.32) 14 (8.41)	5 (15.60)	3 (18.76) 11 (7.06)	--	15 (5.35)	50 (10.25)
Saxifraga cernua	8 (10.64)	6 (6.53)	10 (6.39)	20 (6.99)	25 (3.15)	26 (4.35)
Eriophorum scheurchzeri	5 (11.63)	--	5 (10.44)	57 (4.41)	53 (4.87)	34 (4.32)
Arctagrostis latifolia	6 (8.02)	3 (11.14)	6 (10.75)	19 (3.65) 47 (2.93)	18 (3.95) 65 (1.55)	21 (3.42) 40 (3.77)
Cardamine pratensis	11 (5.69)	N/A	11 (8.17)	32 (3.40)	N/A	32 (4.75)
Salix arctica	10 (4.29)	6 (6.53)	10 (6.39)	25 (4.54)	25 (3.15)	26 (4.35)

Table 2-6. Quadrat Variance (3TLQV) analysis of species from the OWT transect (Alexandra Fiord). The size (# of quadrats) and intensity (in brackets) of patterns found for each species are listed within the range of 1 -14 and 15 to 70 quadrats in size. Analysis was done using data from the full transect (**FULL**), data from quadrats 1 to 500 (**TOP**), and data from quadrats 501 to 1000 (**BOT**). Species are arranged in order of frequency. "--" represents where no scale of pattern was found.

	Size of Pattern					
	Range: 1 - 14 quadrats			Range: 15 - 70 quadrats		
Species	**FULL**	**TOP**	**BOT**	**FULL**	**TOP**	**BOT**
Eriophorum triste	3 (21.46) 14 (7.74)	5 (11.82)	3 (24.61) 12 (6.09)	50 (3.88)	18 (6.83) 51 (3.91)	28 (5.19)
Carex membranacea	8 (14.53)	8 (13.06)	8 (14.43)	--	24 (3.85)	50 (3.50)
Dryas integrifolia	9 (13.48)	8 (15.64)	7 (12.61)	30 (9.02)	20 (6.11) 34 (9.97)	29 (7.07) 46 (8.98)
Carex aquatilis	11 (9.98)	5 (11.13)	4 (16.51) 9 (11.69)	54 (4.27)	16 (5.94)	37 (7.87)
Polygonum viviparum	--	4 (13.70)	7 (9.94)	33 (5.07) 53 (7.38)	34 (4.95) 61 (7.52)	15 (6.33) 40 (9.02)
Carex misandra	7 (11.11)	7 (10.12)	3 (27.01)	69 (4.50)	--	18 (6.82) 49 (6.41)
Saxifraga oppositifolia	12 (11.40)	11 (10.58)	5 (10.75) 140 (11.19)	68 (3.17)	23 (5.97)	--
Salix arctica	9 (8.00)	11 (7.24)	9 (6.94)	23 (6.66)	22 (6.98) 69 (4.53)	26 (5.91)

The range of the first scale of pattern for *E. scheurchzeri* was from 5 to 11 quadrats in size along transects BMS, BRS and CRT. Both *A. latifolia* and *P. viviparum* did not have values less than 15 quadrats in size on one transect (BRS and BMS, respectively) and showed very similar scales of pattern on the other two transects. *A latifolia* had a pattern at 6 (transect BMS) and 5 (transect CRT) while, *P.viviparum* had a pattern at 6 (transect BMS) and 7 (transect BRS) quadrats in size.

Of all the species that exhibited spatial patterns, *E. triste* was the only species that had two scales of pattern smaller than 15 quadrats in size. These were found on transects BRS, CRT and OWT and in all three cases the intensity of the first scale of pattern was higher than that of the second scale of pattern. The analysis also found that there were only two species along transect BMS (*A. latifolia* and *P. sabinei*; Table 2-3), one species on transect BRS (*S. arctica*; Table 2-4) and one species on transect OWT (*P. viviparum*; Table 2-6) that did not have a scale of pattern less than 15 quadrats in size.

A separate 3TLQV analysis was done on the top 500 sample quadrats and the bottom 500 sample quadrats and then they were compared. This was done in order to investigate whether the detected patterns were consistent along the transects.

All the species showed different scales of pattern in the two sections except *Carex membranacea* on transect OWT (Table 2-6). A scale of pattern was found in both the top and bottom sections for five species on transect BMS (Table 2-3) and BRS (Table 2-4), six species on transect CRT (Table 2-5) and all eight species on transect OWT (Transect 2-6). The difference between the two scales of pattern ranges from 1 to 5 quadrats (10 to 50 cm) on transects BMS and OWT and from 1 TO 7 quadrats (10 to 70 cm) on transects BRS and CRT. There was no apparent inclination for the larger pattern to occur in the top or bottom section for the species found on more than one transect. In addition, the patterns found for these species in each section appeared independent of each other.

There were five species that showed several scales of pattern in the analysis of the top and bottom sections compared to one species in the analysis of the whole transect (Tables 2-3 to 2-6). Some species also, indicated patterns less than 15 quadrats in size for data from the whole transect but not for data from each section (Tables 2-3, 2-4). Only three species did not indicate patterns in the analysis of the whole transect (Tables 2-3, 2-4,2-6) while, seven species did not have a pattern in either their top or bottom sections (Tables 2-3, 2-4, 2-5).

B. *Pattern Range: 15-70 Quadrats in Size*

From the analysis of the whole transect, additional patterns were found between 15 and 70 quadrats in size. For most species, their second scale of pattern occurred within this range. Of those species that had a pattern, the first scale of pattern in this division ranged from 17 to 48 quadrats on transect BMS (Table 2-3), from 18 to 46 on transect BRS (Table 2-4), from 18 to 57 quadrats on transect CRT (Table 2-5), and from 23 to 69 on transect OWT (Table 2-6). The intensities for these same scales of pattern ranged from 3.91 to 10.77 on transect BMS, from 4.98 to 10.62 on transect BRS, from 3.4 to 6.99 on transect CRT and from 3.17 to 9.02 on transect OWT.

S. arctica was the only species present on all four transects that indicated a scale of pattern between 15 and 70 quadrats in size for all the transects. The range of the first pattern in this division was large (18 - 48 quadrats) although the values on transect CRT (25 quadrats) and transect OWT (23 quadrats) were very close. *E. triste* showed a similarly large variation in the pattern found (23 - 50 quadrats) for the three transects that had values between 15 and 70 quadrats in size (transects BMS, BRS and OWT). *C. aquatilis* showed the least amount of similarity between transects. One scale of pattern was found on transect OWT (54 quadrats), two on transect CRT (19 and 60 quadrats), and no pattern was found on transects BMS and BRS.

Those species that were found on the three Sverdrup Pass transects (transects BMS, BRS and CRT), also showed a lack of consistency in the scale of pattern found between transects. *P. viviparum* which had a scale of pattern between 15 and 70 quadrats in size for all three transects, had a range from 24 to 46 quadrats. *A. latifolia* had a pattern on transect BMS at 18 quadrats and on transect CRT at 19 quadrats but did not show any value on transect BRS for this division. A scale of pattern of 57 quadrats in size was found only on transect CRT for *E. scheurchzeri*.

There were six species that did not show a pattern in the 15 to 70 quadrat range compared to four species in the 1 to 14 quadrat range. No pattern was found in the 15-70 quadrat range for *C. aquatilis* and *E. scheurchzeri* on transects BMS and BRS, *A. latifolia* and *P. sabinei* on transect BRS, *E. triste* on transect CRT and *C. membranacea* on transect OWT. In addition, species showing two scales of pattern were also more common in the 15-70 range. Only *E. triste* had two scales of pattern in the 1 to 14 quadrat range, while *J. biglumis* on transect BMS and BRS, *C. aquatilis* and *A. latifolia* on transect CRT and *P. viviparum* on transect OWT all showed two patterns between 15 and 70 quadrats in size.

Six of the eight species had a scale of pattern for both the top and bottom sections of their respective transects between 15 and 70 quadrats in size. The difference between the first scale of pattern found in the top section and that found in the bottom section had a range from 3 to 31 quadrats (30 to 310 cm) on transect BMS, from 4 to 26 quadrats (40 to 260 cm) on transect BRS, from 1 to 45 quadrats (10 to 450cm) on transect CRT and from 7 to 34 quadrats (70 to 340 cm) on transect OWT. Similar to the trend found in the 1 to 14 quadrat range, there was no apparent preference for which section had the larger scale of pattern or how the scales were related between species found on more than one transect.

Eight species showed two scales of pattern in the analysis of the top and bottom sections. Of those species that showed two scales of pattern along the whole transect only *J. biglumis* on transect BRS (Table 2-3) did not indicate two patterns in at least one section. All the species that did not indicate a pattern in the analysis of the whole transect showed a pattern in the analysis of at least the top or bottom sections. Six species did not indicate a scale of pattern in either the top or bottom sections of their transects.

Pattern Analysis - Species Pairs

Table 2-7 shows the mean number of species found in each quadrat for the transects. There was no significant difference between transects or between the top and bottom sections (F-ratio; $P > .05$). Of the eight species studied in the pattern analysis, an average of 3 were found in each quadrat.

The results from the quadrat covariance analysis are in Table 2-8. Only covariance peaks that were greater than 10% of the lowest variance value for either species, were included in the evaluation. Half of the species pairs on transects BRS and CRT and two thirds on transect BMS indicated a pattern (13, 14 and 18 out of 27 possible combinations, respectively), while transect OWT had a scale of pattern indicated for 20 of 27 combinations.

Except for *S. arctica* on transect OWT, all the species that indicated a pattern with more than five of the seven species had an intermediate frequency on their transects (present in 250 to 750 of the quadrats). These included one species on each of the Svedrup Pass transects (BMS, BRS and CRT) and three species on transect OWT (Table 2-8).

E. scheurchzeri on transect BMS showed only negative covariance with six of the species and no covariance with *S. arctica.* On transect BRS, *E. scheurchzeri* showed a covariance with all the species except *A. latifolia,* however, only *P. sabinei* showed positive covariance. *Eriophorum triste* on transect CRT, also indicated a positive covariance with only one species, *A. latifolia,* while a negative covariance with the other five species.

Dryas integrifolia (transect OWT) was the only species that showed covariance with all the species analyzed on its transect. It showed positive covariance with *E. triste, C. aquatilis, C. misandra, S. oppositifolia* and *S. arctica* and negative covariance with *C. membranacea* and

Table 2-7. The mean number (SD) of species per quadrat using only the 8 most common species found along each transect. These values are for data from the complete transect (FULL), data from quadrats 1 to 500 (TOP) and data from quadrats (BOT).

		BMS	BRS	CRT	OWT
Mean (± S.D.)	FULL	3.03 (± 1.04)	2.80 (± .90)	2.63 (± .81)	2.58 (± 1.21)
	TOP	3.04 (± .96)	2.63 (± .79)	2.37 (± .66)	2.52 (± 1.12)
	BOT	3.01 (± 1.14)	2.97 (± .96)	2.89 (± .81)	2.65 (± 1.28)

Table 2-8 . Species combinations that indicate a positive (+ covariance) and negative (- covariance) scale of pattern of less than 15 quadrats in size. Only those covariance values that had strong relationships were considered (covariance value > 10% of the lowest variance value of the two species). For each transect the proportion of species combinations (ratio) that indicate a scale of pattern less than 15 quadrats in size is shown. █ = species present in > 750 quadrats; ░ = species present in < 250 quadrats.

Transect	Species	Species Number		Ratio
		(+) covariance	(-) covariance	
BMS	█1) *Eriophorum triste*	5, 8^{*},4	3^{+}	18/27
	2) *Carex aquatilis*	3	7^{+},4	
	3) *Salix arctica*	2, 5^{+}, 7	1^{+}, 8	
	4) *Eriophorum scheurchzeri*		1, 2^{+}, 5, 6, 7, 8	
	5) *Juncus biglumis*	1, 3^{+}, 6	4, 8	
	░6) *Arctagrostis latifolia*	5	4, 7	
	░7) *Polygonum viviparum*	3	2, 4, 6, 8	
	░8) *Pleuropogon sabinei*	1^{*}	3, 4, 5, 7	
BRS	█1) *Eriophorum triste*	6	2	13/27
	2) *Eriophorum scheurchzeri*	7	1, 4, 5, 6^{+}, 8	
	3) *Arctagrostis latifolia*		4, 7	
	4) *Carex aquatilis*	5	2, 3, 7	
	5) *Salix arctica*	4	2, 6	
	░6) *Juncus biglumis*	1	2^{+}, 5, 7	
	░7) *Pleuropogon sabinei*	2	3, 4, 6	
	░8) *Polygonum viviparum*		2	

+ two scales of pattern found at less than 15 quadrats in size (first pattern at blocksize of 1)

* first scale of pattern at a scale of 1 is negative; second pattern at a scale of 9 is positive

Table 2-8 (continued)

Transect	Species	Species Number		Ratio
		(+) covariance	(-) covariance	
CRT	■1) *Carex aquatilis*	2	3, 6	
	2) *Dupontia fisheri*	1, 4	3, 5	
	3) *Eriophorum triste*	6	1, 2, 4, 5, 8	
	4) *Saxifraga cemua*	2, 7	3, 5, 6	
	░5) *Eriophorum scheurchzeri*		2, 3, 4, 8	
	░6) *Arctagrostis latifolia*	3	1, 4	
	░7) *Caramine pratensis*	4		
	░8) *Salix arctica*		3, 5	14/27
OWT	■1) *Eriophorum triste*	3	2, 4, 6	
	2) *Carex membranacea*		1, 3, 4, 6, 7, 8	
	3) *Dryas integrifolia*	1, 4, 6, 7, 8	2, 5	
	░4) *Carex aquatilis*	3, 5, 8	1, 2	
	░5) *Polygonum viviparum*	4, 6	3, 8	
	░6) *Carex misandra*	3, 5	1, 2, 8	
	░7) *Saxifraga oppositifolia*	3, 8	2	
	░8) *Salix arctica*	3, 4, 7	2, 5, 6	20/27

P. viviparum. *Carex membranacea* on transect OWT indicated no covariance with *P. viviparum* and a negative covariance with the other six species. *Salix arctica* indicated a positive covariance with *D. integrifolia*, *C. aquatilis* and *S. oppositifolia* and a negative covariance with *C. membranacea*, *P. viviparum* and *C. misandra*.

Pattern Analysis - Multiple Species

In the multiscale ordination analysis, the first principal component accounted for 39%, 35%, 32%, and 25% of the variation in transects BRS, CRT, BMS and OWT, respectively. When the eigenvalues were partitioned into the amount that each block size contributed, no peaks were detected for blocksizes less than 15 quadrats for all four transects. This was true also of the second and third eigenvalues as well as in the separate analysis of the top and bottom sections of each transect.

DISCUSSION

The results indicate that the spatial arrangement of species present in high arctic sedge meadows can occur at several scales of pattern. More specifically, at least two scales of pattern at less than 7 m (70 quadrats) were identified for each of the eight major species on each of the four transects.

Pielou (1974) has suggested that the spatial patterns displayed by vegetation are primarily the result of exogenous and/or endogenous influences. Exogenous patterns are the result of differences in habitat and can occur at both small and large scales. Endogenous mosaics resulting from characteristics like plant morphology and plant interactions, occur mainly at small scale. The importance of habitat differences, or exogenous forces, on the distribution and patchiness of the vegetation is shown distinctly by the changes in the patch or gap size along the transects. The effects of the morphological characteristics of plants or clones on the spatial pattern in the meadows find considerable support from the known ecology of arctic vegetation.

In arctic vegetation, the morphology of the plants is an important influence on the vegetation pattern at small scales. Poor environmental conditions and a short growing season have influenced the growth patterns and reproductive strategy of arctic plants. The vegetation of sedge meadows is dominated by long-lived perennials that store most of their biomass below-ground and depend primarily on vegetative reproduction for propagation (Muc, 1975; Maessen *et al.*, 1983; Callaghan and Emmanuelsson, 1985; Henry, 1987; Henry *et al.*, 1990). These adaptations are emphasized differently by the various growth forms present and result in the subsequent small scale morphological character of the vegetation.

The sedge meadow species can be classified into four growth forms: graminoids, forbs, cushion plants and dwarf shrubs. Of these categories, graminoids are the dominant growth form in High Arctic meadows both in their abundance and in their contribution to total biomass (Muc, 1976; Henry, 1987; Bergeron, 1988). Most graminoids rely on vegetative propagation and take several years to reach the flowering stage (Billings and Mooney, 1968; Bliss, 1971; Saville, 1972; Billings, 1987; Henry *et al.*, 1990). When seed production does occur, germination and seedling establishment is low except on disturbed sites (Bliss, 1971; Freedman *et al.*, 1982). The role of sexual reproduction in the spatial pattern of graminoids is therefore, limited to establishing new clones in areas where there are gaps in the vegetation (Callaghan and Emanuelsson, 1985).

Vegetative reproduction is the main influence on the spatial pattern of graminoids and is largely influenced by the dispersal ability and lifespan of individual vegetative clones. Measurements of the distribution of tillers of *C. aquatilis* have found the majority of tillers (65 - 70%) within 1 cm of the parent shoot, with the remaining tillers found at a distance of 15 to 50 cm (Shaver and Billings, 1975; Muc, 1976; Henry 1987). The tillers of *C. aquatilis*, *Eriophorum angustifolium* and *Dupontia fisheri*, were also found to live from 3 to 8 years (Saville, 1972; Allessio and Tieszen, 1975; Shaver and Billings 1975; Callaghan and Emanuelsson, 1985; Henry, 1987). Both the dispersal ability and lifespan of vegetative propagules would therefore, tend to result in vegetative colonies of less than 1.5 m in size.

Of the four species found along the studied transects, only *S. oppositifolia* depends on seed production for establishing new individual (Stewart, 1981; Desrosiers, 1991). *Saxifraga cernua* and *Polygonum viviparum* reproduce by vegetative bulbils and *Cardamine pratensis* reproduces by deciduous buds (Stewart, 1981; Freedman *et al.*, 1982). In the case of *S. cernua*, the dispersal distance of bulbils has been found to be 7.2 6.9 cm on King Christian Island (Grulke and Bliss, 1985). The short dispersal of bulbils, therefore, would suggest that clumps of individuals would result in a small scale of pattern similar to that found in the graminoids.

Cushion plants like *Dryas integrifolia* have very low productivity (Svoboda 1977 ; Henry *et al.*, 1990) and can spread horizontally forming dense mats on the tundra (Callaghan and Emanuelsson, 1985). Other studies have found that the distribution of mats have been strongly influenced by the microtopography in sedge meadows and are found only on the tops of hummocks (Muc, 1976; Henry, 1987; Muc *et al.*, 1989). In our meadows, where the hummocks are found to be less than 1.5 m in size, this would mean that vegetative colonies of *D. integrifiolia* would also be expected to be no larger than 1.5 m.

Dwarf shrubs are stress-tolerators (Grime, 1979) that adjust to the severe conditions of the arctic tundra by growing slowly and extending their lifecycle over many years (Billings and Mooney, 1968; Bliss, 1971). Unlike graminoids, the spatial expansion of dwarf shrubs is dependent on the growth of woody side branches rather than the production of new tillers. They therefore, have a slow spatial expansion due to the energetically expensive production of woody tissue. Dwarf shrubs found in less severe alpine habitats have shown annual shoot growth of 1 to 2 cm in length (Bliss, 1971). In the high arctic where side branches live for a maximum of a few decades (Bliss, 1971), this would result in individual plants that were less than 1 m in size.

Single Species Pattern

One of the objectives of this study was to obtain a measurement of spatial pattern in the vegetation which could be used to evaluate the distribution of different species. Three Term Local Quadrat Variance (3TLQV) was partially successful in doing this by identifying two scales of pattern. However, it was not completely successful because the scales of pattern that were identified cannot be used to describe the actual clone or patch size of the species. Dale and McIsaac (1989) have noted that the scale of pattern represents the average of the patch and gap size. Therefore, species with large patches separated by small gaps can indicate the same scale of pattern as species with small patches separated by large gaps. The result in the analysis was that the first scale of pattern was relatively consistent between species and meadows. To arrive at an accurate indication of patch size, species frequency also needs to be considered.

For the two scales of pattern that were identified, the interpretation of the patch size is different. For the first scale of pattern (<140 cm), the actual size of patches and gaps (how the species are clumped) influences the value of the scale found. Therefore, using the results of the patch/gap size graphs, the first scale of pattern found for the 3TLQV analysis can be interpreted. Three relationships were found along the transects; constant small gaps separated by large patches, constant small patches separated by large gaps and variable patch and gap sizes. In the case of all the growth forms, these relationships can be said to reflect the success of individual species in producing new growth or new propagules.

In the nine graminoid species studied, the variation in patch and gap size indicates variation in the size of clones resulting from vegetative reproduction. The presence of closely spaced large patches indicates that conditions favourable for successful reproduction are present. The occurrence of large gaps between small patches suggests that the plants produced few tillers (low reproductive output) or occur only within specialized microhabitats in the meadows. The third relationship showing a variation in patch size along the transects suggests that there is variation in one or several factors within the meadows that influence vegetative propagation.

Only two graminoid species, *C. aquatilis* and *E. triste*, occurred on all four transects in more than 5% of the quadrats. However, their responses along each transect varied. *E. triste* was the most robust of the two species having large clones on transects BMS, BRS and OWT, while having both large and small clones on transect CRT. By contrast, *C. aquatilis* had large colonies only on transect CRT. The abundance of *C. aquatilis* along transect OWT was low (predominantly small clones) while variable (both small and large clones) on transects BMS and BRS.

The remaining graminoids, although less successful, also showed preferences for different transects. *D. fischeri*, was both abundant (large clones) and successful in establishing itself only on transect CRT. While, *E. scheurchzeri* (transects BMS and BRS), *A. latifolia* (transects BMS and BRS), *J. biglumis* (transect BMS) and *C. membranacea* (transect OWT) are established within individual meadows, but, have variable degrees of abundance as indicated by the presence of both large and small clones. *Juncus biglumis* (transect BRS), *P. sabinei* (transect BRS), *A. latifolia* (transect CRT), *E. scheurchzeri* (transect CRT) and *C. misandra* (transect OWT) occurred both infrequently and in small patches, which suggests that they are existing at the margins of their ecological range or within specialized microhabitats along the transects.

The relationship between the first scale of pattern and the actual patch size found for the forbs is the same for all four species. The forbs occur mostly in small patches (1 to 2 quadrats in size) separated by large gaps. This agrees with what is known about the dispersal ability of bulbils and buds (Grulke and Bliss, 1985) and also the productivity of forbs in sedge meadows. Forbs contribute less to the total aboveground biomass in high arctic meadows (Muc, 1976; Henry, 1987; Henry *et al.*, 1990) because of low rate of establishment (Bell and Bliss, 1980; Freedman *et al.*, 1982) and the higher mortality of seedlings compared to graminoid tillers (Callaghan and Emanuelsson, 1985).

The association between hummocks and the frequency of *Dryas integrifolia* appears to be in agreement with the results of the patch analysis. Besides only occurring in the meadow with pronounced hummock formation (transect OWT), the size of the patches and gaps were found to be variable within specific limits. *D. integrifolia* formed mats larger than one quadrat in size, while being limited by the size and spacing of the hummocks.

The dwarf shrub, *Salix arctica*, showed a consistent scale of pattern on all four transects as well as a close similarity in patch size. Although more frequent on transects BMS and BRS, *S. arctica* generally had small patches separated by large gaps. This is in agreement with what would be expected in dwarf shrubs which have a slow growth rate (Bliss,1971). In addition, Callaghan and Emanuelsson (1985) have suggested that the absence of some age classes of *S. arctica* is due to the detachment and rooting of side-branches. The fractionation of older plants could be important in limiting the size of individual plants and subsequently the size of patches.

The second, larger scale of pattern identified along the transects was different from the first scale in that it is influenced by how the patches and gaps are clumped or grouped rather than how individual plants are clumped. The two scales of pattern also differed in how pronounced and how stable were their patterns. In the comparison of intensity values the second scale of pattern was generally less than the first scale indicating that the second scale of pattern was less pronounced. That the second pattern is due to habitat variation, can be suggested by the lack of consistency or stability of the pattern along the transect. In a comparison of the top and bottom sections there was a greater difference in the values found in the second scale than the first. In addition, there were a greater number of species showing two patterns or not having patterns in the 15 to 70 quadrat range.

The species' patches, as identified by the first scale of pattern, are largely the result of the vegetative output of individual plants or vegetative colonies. By contrast, the "patches" found in the second scale of pattern correspond to areas where the density of species patches are high. The variability in the clumping of patches is probably due to the recruitment of new independent individuals into the habitat conditions present in each meadow. The low germination success (Bliss, 1971; Chapin *et al.*, 1979; Freedman et al., 1982) and high energetic expense of establishing new individuals (Chapin *et al*, 1980) in the arctic helps to explain why there is variability in their distribution.

The interpretation of the results of the second scale of pattern are complicated by two factors. First, there is a lack of consistency in the patterns of the species on the different transects and secondly, the indicated scale of pattern does not represent the "patch" size but the average of the patch and gap size or areas of high and low species patch density. Both of these factors make it difficult to interpret the direct relationship between the species and the transects, even with the results of the patch/gap graphs.

Despite the difficulty in interpreting the second scale of pattern, some trends were obvious in the results. The species found on more than one transect had different patterns on each transect, and also a different relationship between the patterns found in the top and bottom sections. This agrees with the different environmental conditions found on the four transects (Chapter 3). In addition, it suggests that the patchiness is not related directly to the elevation gradient along each transect. If the patchiness was related to the gradient, it would be expected that the relationship between species in the top and bottom sections on different transects, would be the same.

Multispecies Pattern

In previous work it has been noted that interspecific association depends greatly on the scale of the sampling units (Pielou, 1974; Dale and Blundon, 1991). Multiscale ordination analysis was used in this study because it allows the investigation of interactions at different scales of pattern that have already been identified as important in the 3TLQV analysis. The results of the 3TLQV analysis suggested that the first scale of pattern was related to the vegetative growth or reproductive success of individual species. The multiscale ordination analysis at this scale should therefore, give an indication of the relationship between the different species.

The differences in the frequency values on each transects would imply that some form of association (positive or negative) between species is present. For example, *C. aquatilis* and *E. triste* have a greater frequency and larger more consistent patches on different transects and therefore would be expected to be negatively associated where they occurred together. This does not, however, occur on all the transects. Only some of the patterns are shown to be related in the quadrat covariance analysis. The multispecies pattern in the meadows is therefore, probably more complex than what can be derived from similarities in species frequency and patch size.

In the covariance analysis, the lack of association between some of the single species patterns can be partially attributed to the degree of homogeneity in the environmental conditions in the meadows. The second scale of pattern in the 3TLQV analysis suggests that there is some degree of heterogeneity in environmental conditions. We would then expect that if the species in the meadows had very distinctive niches, this variation in environmental conditions would result in a distinctive pattern in the species distribution in the meadows.

For the three transects at Sverdrup Pass (transects BMS, BRS and CRT), less than two thirds of species pairs indicate covariance peaks. The lower number of covariance peaks suggests that many of the species pairs do not occur in alternating phases in the meadows. Vegetative reproduction could be the cause of this characteristic pattern. One of the advantages of adopting a strategy of vegetative reproduction is that the parent plant can subsidise the growth of the new individual. With *C. aquatilis* it has been estimated that the carbon cost of producing a new tiller by sexual reproduction is 10,000 times that of producing a vegetative tiller (Chapin *et al*, 1980). This subsidy helps support and improve the survival of propagules in generally inhospitable microhabitats, and results in a greater spatial distribution. The absence of distinctive relationships between the patches for some of the species on the Sverdrup transects is therefore, probably the result of the environmental conditions having a less pronounced affect on the distribution of species.

By contrast, the quadrat covariance analysis on transect OWT indicates a greater degree of organization and restriction in the species distribution. Three quarters of the possible covariance peaks were found on transect OWT. This was primarily due to the behaviour of species with intermediate frequencies. There were four species on transect OWT that indicated covariance peaks with more than four other species, but only two or one species on the other transects. The greater number of species with distinct relationships between their first scales of pattern suggest that species along transect OWT have more distinct spatial locations.

This spatial organization is most likely due to the microtopography. The inclusion of *D. integrifolia* as one of the four species that indicates more than four covariance peaks on transect OWT corroborates this conclusion. *Dryas integrifolia* is documented as being found exclusively on the tops of hummocks in sedge meadows (Muc, 1976; Henry, 1987; Muc *et al.*, 1989). Having a positive relationship to *D. integrifolia* indicates that the other seven species have a distinct spatial relationship to the hummocks in the meadows.

The purpose of multiscale ordination analysis is to assess species associations at several different scales and the relationship among these associations (Ver Hoef and Glenn-Lewin, 1989). The detection of a scale of pattern of less than 15 quadrats would suggest that the species distribution at that scale was influenced by both consistent and common processes. The results of our study, however, indicated no alternating phases of patches with different species composition in the small scale spatial pattern of the vegetation. The partitioned eigenvalues for all four transects indicated no peaks at less than 1.5 metres in size. Part of the explanation can be attributed to the large habitat breadths of species that was suggested by the quadrat covariance analysis. In the multiscale ordination analysis this variability is compounded when all eight species are considered at once.

The lack of pattern found in the multiscale ordination analysis does not mean that there is an absence of spatial dependency in the vegetation at that scale. Besides the results from the quadrat covariance analysis, Dale *et al.* (1993) also found that the distribution of the species on the same transects are partially associated with each other. They found that quadrats that were close to each other (within 10 quadrats), while not identical, were very similar in their composition. Both these results suggests a greater degree of organization in the meadows than is suggested by the multiscale ordination analysis.

In addition, the accuracy of the multiscale ordination analysis in detecting the degree spatial dependency is further disputed by discrepancies between the quadrat covariance analysis and the values of the principal components. Beschel and Matveyeva (1972), working in arctic sedge-hummock meadows, have suggested that the dispersion in the data accounted for by the principal component axes can be used to indicate the degree of organization in the meadows. Based on the results from the quadrat covariance analysis, transect OWT should show the greatest degree of organization in the multiscale ordination analysis: however, it has the lowest value of the four transects.

The apparent contradictions to the results of the multispecies ordination analysis by the conclusions from some of the other analyses highlights the limitations of the method. In addition, there has been some concern about using presence-absence data in PCA because the variables take only the values of 0 and 1 (Jackson, 1991). We therefore, can only use the results to support the conclusion from the quadrat covariance analysis that the species do not occur in phases characterised by distinct vegetation compositions.

In summary, the results of the single and multispecies analysis suggest that there are different influences on the spatial pattern of species at different scales. Vegetative reproduction is probably an important factor in the small scale patches of individual species, while habitat variation influences the distribution of these patches in the meadows. Distribution of the small patches in the meadows, however, could not be related to their location on the drainage gradient because no consistent relationship was shown. The predominance of vegetative reproduction also influences the relationship between small scale patches. Vegetative propagation seems to be an important factor in creating fewer differences in the spatial dependency of individual species and subsequently, a more homogeneous distribution of the vegetation in the meadows.

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CHAPTER 3

ENVIRONMENTAL INFLUENCES ON THE SPECIES DISTRIBUTION IN SEDGE MEADOW COMMUNITIES

INTRODUCTION

Physical environmental factors are believed to be the most important influences on vegetation patterns in high arctic plant communities (Bliss, 1971; Edlund and Alt, 1989). The strong gradients in environmental conditions, especially soil moisture, structure communities in the arctic landscape.(Muc, 1976; Webber, 1978; Muc *et al*, 1989; Sheard and Geale, 1983b). Sedge meadows occupy the wet end of the soil moisture gradient and are restricted to lowland oases in the Queen Elizabeth Islands (Babb and Bliss, 1974; Henry *et al*, 1986).

Wet soil conditions throughout the growing season is the unifying feature of sedge meadows (Muc, 1976; Sheard and Geale, 1983b; Henry *et al*,1990; Henry, 1994) and result in these meadows having the greatest net production of all high arctic communities (Muc, 1977; Muc *et al*,1989; Henry *et al.* 1990). This high net productivity results in relatively dense plant communities where positive or negative associations among species may also be important in structuring the communities.

Previous studies have attempted to describe the species-environment relationship of vegetation in sedge meadows using criteria, such as varying litter and moss cover (Henry *et al*, 1990), and the presence of hummocks or frost boils (Muc, 1976; Muc *et al*, 1989). Few studies, however, have attempted to use multivariate direct gradient techniques to analyze the relationship between environmental parameters and the structure of sedge meadow communities (Henry, 1994), and there are no studies which have also attempted to incorporate multispecies associations into the investigation.

The environmental variables measured were litter cover, soil moisture, moss cover and microtopography, and were selected as indicators of noted environmental conditions within sedge meadows (Muc, 1976; Muc *et al*,1989; Henry *et al.* 1990). The intention was not to measure all the influential environmental variables but to select a few variables that could be easily measured in each quadrat and were correlated with the most important conditions in the meadows.

Variation in litter cover was measured because it has been attributed to variations in the grazing intensity of muskoxen (Henry *et al.* 1990; Henry, 1994; Henry and Svoboda, 1994). Grazing by large herbivores increases nutrient cycling, elevates nutrients in the soil and decreases relief by eliminating litter and increasing trampling in the meadows (Jefferies *et al.*, 1992; Raillard *et al.*, 1992;

Henry and Svoboda, 1994). In addition, grazing can be an important factor contributing to species diversity (Archer and Tieszen, 1980; Henry, 1987; Jefferies *et al.*, 1992) or increased productivity for some plant species (Chapin, 1980; Henry *et al.*, 1986; Raillard *et al.*, 1992; Henry and Svoboda, 1994).

Soil moisture is an important factor affecting community structure (Billings and Mooney, 1968; Reznicek and Svoboda, 1982; Sheard and Geale, 1983a,b). The species pattern in sedge meadows has been linked to the distribution of soil moisture, the fluctuation of soil moisture and water flow patterns and rates (Beshel and Matveyeva, 1972; Muc, 1976; Henry, 1987; Chapin *et al.*, 1988; Ostendorf and Reynolds, 1993). These variations in soil water influence both the species occurence and productivity in the meadows.

Mosses, as major components of high-arctic sedge meadows, are important as indicators of certain environmental conditions. Soil moisture is positively correlated with moss cover (Vitt and Pakarinen, 1977) and results from studies in other communities suggest that fluctuations in soil moisture are connected with moss distribution patterns (Gignac *et al.*, 1991). The thickness and coverage of moss has also been shown to affect vascular species distribution (Daly *et al.*, 1989) and permafrost depth (Brown, 1977).

Microtopography has been shown to be important in differentiating between types of sedge meadows (Muc, 1976). Some plant species tend to associate with the microhabitats created by the hummocks and hollows and would otherwise be less abundant (Beshel and Matveyeva, 1972; Muc, 1976; Henry, 1987).

Objectives

The objectives of this study were: (1) to determine if some combinations of vascular species occur more or less often together than expected in three arctic sedge meadows; and (2) to determine the relationship between the vegetation in three different meadows and measured environmental parameters using a contiguous quadrat sampling regime along a drainage slope.

Study Site Description

A. *Location*

Work was carried out at two sites on central Ellesmere Island during the summer of 1991. Sverdrup Pass (79° 09'N; 79° 40'W) is located inland in an ice-free corridor running between the east and west coasts of Ellesmere Island, while Alexandra Fiord (78° 53'N; 75° 55'W) is located on the east coast. Sverdrup Pass and Alexandra Fiord also differ in grazing intensity. The Sverdrup Pass site is heavily grazed by a resident herd of muskox (~1.2 animals km^{-2}; Raillard, 1992) while the Alexandra Fiord site is visited infrequently (Henry *et al*, 1986) and therefore, lacks any sign of being grazed.

Two sedge meadows were studied at Sverdrup Pass and one meadow at Alexandra Fiord. The meadows at Sverdrup Pass were found on drainage slopes on the north (Plate 3-1:1) and south (Plate 3-1:2) sides of the valley. The Alexandra Fiord meadow was located on a drainage slope in the northwest corner of the lowlands (Plate 3-1:3). Meadows at Sverdrup pass (Plate 3-2:1,2) had noticeably less litter and microtopographical relief than the meadow at Alexandra Fiord (Plate 3-2:3).

B. *Geology and Soils*

Sverdrup Pass consists of a mixed lithology with the south side of the valley consisting of Precambrian gneiss and granite of Canadian Shield origin and the north side of Cambrian and lower Ordovician subhorizontal beds of limestone and dolomite (Christie, 1967; Bergeron, 1988). Alexandra Fiord also has a mixed lithology of granite, gneiss, pegmatite and dolomitic sedimentary rocks with its soils dominated by granitic material (Christie, 1967; Sterenberg and Stone, 1994; Henry, 1994).

Meadows at both sites have gleysolic static cryosol soils which are similar in texture but differ in the thickness of their organic horizons (Bergeron, 1988; Muc *et al*, 1994; Henry, 1994). Sverdrup Pass meadows had thicker organic layers than meadows at Alexandra Fiord (Henry, 1987). Muc *et al.* (1989) has suggested that the poor development of soils in the Alexandra Fiord lowlands is the result of recent deglaciation (ca. 8500 ybp)

Sverdrup Pass has higher total N and P concentrations in soil water than Alexandra Fiord (Henry and Svoboda, 1994), however, the results from other studies suggest that the nutrient concentrations may be very similar (Murray, 1991; Henry, 1994). Murray (1991) also showed there was no difference in total N and total P concentrations in soil water between dolomitic and granitic meadows at Sverdrup Pass. In addition, the pH of granitic meadows and Dolomitic meadows at Sverdrup Pass were 7.4 and 8.4, respectively. Alexandra Fiord meadows are slightly acidic (pH 5.9-6.3) (Henry, 1987).

Plate 3-1. Photographs showing the north (1) and south (2) slopes at Sverdrup Pass and the Alexandra Fiord lowland (3). The location of the four study transects are also indicated. **A:** transect CRT, **B:** transects BMS and BRS, **C:** transect OWT.

1

2

3

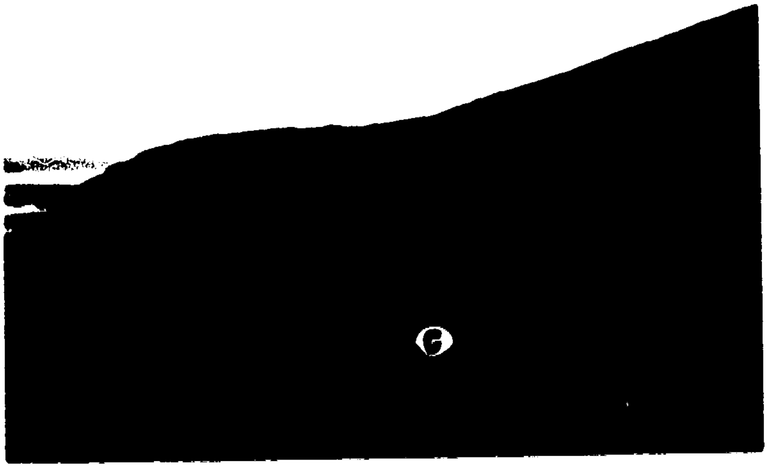

Plate 3-2 Photographs showing vegetation and microtopography in the north meadow (1) and south meadow (2) at Sverdrup Pass and the meadow found at Alexandra Fiord (3).

1

2

3

C. *Climate*

Maxwell (1981) has divided the Canadian Arctic Islands into five climatic regions based on cyclonic activity, sea ice-water regime, broad-scale physiographic features and net radiation. Central and northern Ellesmere Island are located in the northern climatic region (category 5) based on its rugged mountaineous terrain, the highest range in mean annual temperature (> 35° C) and the frequency of summer surface-based temperature inversions ranging from 20% to 40%.

Both Alexandra Fiord and Sverdrup Pass have further been grouped into an intermontane climatic area in central Ellesmere Island by Edlund and Alt (1989). This area is characterized by having the most dense and diverse plant assemblages in the Queen Elizabeth Islands as a result of high summer growing temperatures (mean July temperature > 5° C), reduced cloud cover and increased solar energy input. The reduced cloudiness is the result of diminished penetration into the intermontane system of cold northwesterly air masses.

METHODS AND MATERIALS

Microclimate Measurements

Climate data were collected at both sites using an automatic climate station. The stations measured incoming solar radiation (LiCor pyranometer, 3 m) wind speed (3 m), relative humidity (1.5 m), and air (1.5 m) and soil temperatures (-10 cm). The sensors were sampled each minute and hourly and daily data (means and totals) were stored on an automatic datalogger (CR10, Campbell Scientific Corp.). A standard rain gauge was used to measure precipitation.

Vegetation and Environmental Sampling

At Sverdrup Pass, the north meadow was sampled using two 100 m transects (transects BMS and BRS) while the south meadow was sampled with only a single transect (transect CRT). The meadow at Alexandra Fiord was sampled using a single 100 m transect (transect OWT). Transects BMS, CRT and OWT were all placed running down the drainage slope in the centre of their respective meadows. Transect BRS was located perpendicular to the centre of transect BMS and ran from the edge of the meadows to the centre. All the transects had slopes of less than 10° hence, the overall elevation change was not considered a strong influence on the species distribution for a 100 m transect.

The vegetation was sampled along the 100 m transect in a continuous sequence of 10 cm x 5 cm quadrats (1000 quadrats/transect). In each quadrat the presence or absence of each vascular plant species was noted and a visual estimate of the percent cover by all moss species and total litter, was made. In addition, each quadrat was also classified using a moisture (1-submerged; 2-wet; 3-dry) and a physiognomic (1-hollow; 2-side; 3-hummock) index. Nomenclature for the vascular plant species followed Porsild and Cody (1980).

The microtopography along the transects was measured from a fixed point above the transect using a surveying level. The elevation of the centre of each quadrat was measured and then adjusted by subtracting a running average score calculated for that quadrat. The running average was calculated by taking the average elevation score of 9 quadrats centred around each quadrat. By subtracting a running average the resulting difference in elevation would be due only to microtopographical changes and not due to the slope of the transect.

Less intensive measurements of the depth of the permafrost and fluctuation in water levels were made along a transect adjacent (~ 2m) to each vegetation transect. The depth of the permafrost and the water level was noted every 10 days from July 2 to August 11, 1991. Permafrost measurements were made using a calibrated steel probe every 2 m along the second transect. Water levels were measured in 4 cm diameter plastic pipes that were sunk 10 cm into the ground. Pipes were placed every 2 m adjacent to transect BMS and every 10 m adjacent to transects BRS and CRT. Water level measurements were made at Alexandra Fiord only twice during the summer (July 19 and 28) and therefore were not included in the results.

Data Analysis

Environmental characteristics of the sites and each transect were compared using the statistical package SYSTAT. Weather conditions (incoming solar radiation, relative humidity and air temperature) as well as soil temperature values were compared using a standard t-test. The active layer depth and transformed percent litter and moss cover (arcsine transformation) were compared using ANOVA.

A. *Species Association Analysis*

For the multispecies association analysis the data sets from all four transects were combined and then only the eight most common species (found in >12% of all the quadrats) were used (see Table 3-1). This simplified the analysis and the interpretation of the results, and was also done in order to avoid the problems associated with low expected values in the multispecies association analysis.

Table 3-1. Vascular plant species found along transects at Sverdrup Pass (transects BMS, BRS and CRT) and Alexandra Fiord (transect OWT). The values represent the number of quadrats out of 1000 where the species is present. Listed are all species that have been found in meadows at either of the two sites. "-" represents species that have not been found at Alexandra Fiord or Sverdrup Pass. Species are arranged in order of total abundance along all four transects.

Vascular plants	**Species** Code	**Transects**			
		BMS	BRS	CRT	OWT
Eriophorum angustifolium	E ANG	899	900	264	867
Carex aquatilis	C AQU	417	391	894	205
Eriophorum scheucherii	E SCH	521	457	145	0
Dupontia fisheri	D FIS	0	0	881	-
Salix arctica	S ARC	319	310	56	93
Arctagrostis latifolia	A LAT	229	422	71	22
Juncus biglumis	J BIG	396	166	29	57
Carex membranacea	C MEM	0	4	0	485
Dryas integrifolia	D INT	2	0	0	442
Polygonum viviparum	P VIV	97	76	31	195
Saxifraga cernua	S CER	6	15	256	0
Pleuropogon sabinei	P SAB	150	81	0	-
Carex misandra	C MIS	8	17	0	150
Saxifraga oppositifolia	S OPP	0	0	0	147
Cardamine pratensis	C PRA	0	0	61	1
Saxifraga hirsuta	S HIR	4	3	39	0
Stellaria longipes	S LON	8	1	32	1
Equisetum variegatum	E VAR	0	0	4	37
Pedicularis capitata	P CAP	0	4	0	27
Draba lactea	D LAC	0	0	0	30
Melandrium apetalum	M APE	9	11	0	9
Eutrema edwardsii	E EDW	12	9	0	-
Draba glabella	D GLA	0	0	12	1
Cassiope tetragona	C TET	-	-	-	8
Alopecurus alpinus	A ALP	0	7	0	-
Vaccinium uliginosum	V ULI	-	-	-	5
Carex atrafusca	C ATR	0	0	0	3
Saxifraga foliolosa	S FOL	0	0	0	0
Luzula arctica	L ARC	0	0	0	0

Multispecies association analysis was used to determine whether the presence of one or more species increased or decreased the probability of finding other species in the same location. The method tested for the co-occurrence of all eight species in one statistical test using the complete independence model (Fienberg, 1970). The initial stage of the analysis consisted of constructing a multidimensional contingency table for each transect and then taking the average value of the four transects for each corresponding cell. The analysis of the contingency table (Dale *et al.* 1991), indicated the cells that contributed the most to the overall significance of the test statistic. The final statistical result was adjusted to deal with spatial autocorrelation which was a factor in the data, because they were not collected in randomly-placed quadrats but in a continuous sequence of quadrats. The deflation factor to deal with spatial autocorrelation was found by analyzing each of the four transects separately following the method outlined by Dale *et al.* (1991). The highest deflation factor from the analysis of each transect was used to adjust the test statistic of the combined data set.

B. *Ordination Analysis*

The weighted averaging methods, correspondence analysis (CA) and canonical correspondence analysis (CCA), were used because of preliminary work using detrended correspondence analysis (DCA). The first ordination axis was found to be close to 4.0 standard deviation (s.d.) units in length, which ter Braak (1987a) suggests is the point above which CA or CCA should be used instead of PCA (principle component analysis) or RDA (redundancy analysis). Both CCA and CA were run using the program CANOCO version 2.1 on a mainframe computer (ter Braak,1987b).

Canonical correspondence analysis (CCA) was used to examine the relationship between species, samples and the most important measured environmental variables for the combined data set of all four transects (n=4000 quadrats). CCA is a multivariate direct gradient method where the axes are constrained to be linear combinations of the supplied environmental variables (ter Braak, 1987b). It was used on the combined data because it is better than indirect gradient methods (e.g. CA) for revealing the true relationship of species (Palmer, 1993).

Correspondence analysis was used separately on each transect so that a plot of the ordination position to real sample position could be done. This has been termed an ordination 'trace' (Whittaker *et al.*, 1979; Olsvig-Whittaker *et al.*, 1983) and has been used to evaluate micro-scale changes in species composition. CA was used instead of DCA because there was no distinctive "arch effect" in the analysis which warranted the use of DCA.

Untransformed species presence/absence scores were used in both the CCA and CA, with rare species (species abundance < frequency of commonest species/5) being downweighted following the method outlined by ter Braak (1987b). This was done to decrease the influence of rare species in the analysis.

The final ordination results for CA were correlated with litter cover, moss cover, microtopography, the moisture index and the orientation index. Only percent litter cover, percent moss cover and the moisture index were used in the CCA because they were found to be the only environmental variables to significantly influence the separation of the species scores ($t > 1.98$) in preliminary analysis using CA on the whole data set.

The scaling used in the CCA of the combined data set had species scores as weighted means of sample scores. The scaling for the correspondence analysis of each transect used sample scores as weighted means of the species scores.

RESULTS

Table 3-1 lists all the species that were found along the four transects. Twenty of the species were present in greater than 2.5% of the quadrats on at least one transect. Of these species, eleven were considered to be common (in >25% of the quadrats). Only six of the common species were found along all four transects (*Eriophorum triste*, *Carex aquatilis*, *Salix arctica*, *Arctagrostis latifolia*, *Juncus biglumis* and *Polygonum viviparum*). The five remaining common species (*Eriophorum scheurchzeri*, *Dupontia fisheri*, *Carex membranacea*, *Dryas integrifolia* and *Saxifraga cernua*) were either not normally found in meadows at Alexandra Fiord or Sverdrup Pass or were not found in the sample quadrats measured (see Henry, 1987 and Bergeron, 1988).

Environmental Conditions

There was no significant difference between sites of the incoming solar radiation, air temperature and relative humidity in the summer of 1991 (Table 3-2). Soil temperature was found to be higher at Alexandra Fiord than at Sverdrup Pass, while wind speeds were significantly higher at Sverdrup Pass for the July sampling period.

Table 3-2. Mean July weather conditions (±SD) for the summer of 1991 at the Alexandra Fiord lowland (A.F.) and Sverdrup Pass (S.P.).

	JULY 1991	
	A.F.	S.P.
Incoming Solar Radiation ($w\ m^{-2}\ d^{-1}$)	240 ± 70	220 ± 80
Air Temperature (° C)	7.0 ± 2.4	7.7 ± 3.4
Soil Temperature (° C)	9.4 ± 1.4*	6.6 ± 1.7*
Relative Humidity (%)	74.0 ± 8.8	70.4 ± 13.6
Windspeed (m/s)	1.6 ± .6*	5.4 ± 1.8*

* significant difference between sites (t-test, $p < 0.05$)

Table 3-3 shows the average values and standard deviations for the measured environmental variables. Transect OWT at Alexandra Fiord had a deeper active layer depth, higher percent litter cover, a lower percent moss cover and a greater variation in microtopography than the three transects at Sverdrup Pass. Transects BMS, BRS and CRT differed only in percent moss cover. Although not statistically significant, transect BRS (65.8 ± 42.5) had a lower moss cover than transects BMS (86 ± 29.6) and transect CRT (98.8 ± 8.3).

Soil moisture was found to vary both between transects and along each transect. Table 3-3 shows the mean water fluctuation along transects BMS, BRS and CRT. The transect in the south meadow showed less fluctuation in its water levels (1.6 cm) than the two transects in the north meadow (4.8 and 3.4 cm respectively). In addition, transect CRT was also found to have a greater proportion of its vegetation submerged than transects BMS, BRS and OWT (Figure 3-1) at the time that the quadrats were sampled. Submerged areas were evenly distributed only on transect OWT. The submerged areas along transects BMS, BRS and CRT were both larger and had a clumped distribution.

Species Association Analysis

The results of the multispecies association analysis of the eight most abundant species in the combined data set are given in Table 3-4. The combination of the presence of *C. aquatilis* and *D. fischeri* and the absence of the other six species, occurred significantly more often than expected. In addition, the combination of *C. aquatilis* and *D. fischeri* also occurred significantly more often when either *A. latifolia*, *S. arctica* or *E. scheurchzeri* was also present in the quadrat.

In the analysis, *C. membranacea* occurred alone at a significantly high frequency. It also occurred more often than expect with only one species, *E. triste*. By contrast, *E. triste*, in its association with other species, always occurred with more than one other species. *E. triste* occurred with *E. scheurchzeri* in combination with either one (*A. latifolia*) or two (*A. latifolia* and *J. biglumis*, *S. arctica* and *J. biglumis* or *S. arctica* and *A. latifolia*) other species significantly more often than was expected.

The results from the multispecies association analysis showed that the absence of all eight of the species in one particular quadrat happened very infrequently (Table 3-4). It also indicated that three out of the eight species did not occur by themselves. *J. biglumis*, *S. arctica* and *C. aquatilis* were all found to occur alone significantly less often than would be expected by chance.

Table 3-3. Mean (± SD) active layer depths, litter cover, moss cover, microtopographical measurements and the mean fluctuation in water levels in July, along each transect found at Sverdrup Pass (BMS, BRS and CRT) and at Alexandra Fiord (OWT). The running average was found by calculating the average value of 9 quadrats centred around each quadrat.

	BMS	**BRS**	**CRT**	**OWT**
Maximum Active layer depth (cm)*	42.2 ± 4.5	43.2 ± 4.7	42.9 ± 4.1	56.0 ± 7.8
Litter cover (%)*	13.8 ± 9.1	11.6 ± 8.4	10.4 ± 8.8	45.9 ± 30.4
Moss cover (%)*	86.6 ± 29.6	65.8 ± 42.5	98.8 ± 8.3	37.5 ± 40.1
Average difference between the slope of the transect (running average) and the elevation of each transect (cm, n = 1000)	0.0 ± 1.1	0.0 ± 1.22	0.0 ± .94	0.0 ± 3.2
Mean range of water levels during July	4.8 ± 2.8►	3.4 ± 1.5♦	1.6 ± 0.9♦	---

* Significant difference among transects (ANOVA; $P < 0.001$)

► Calculated from 50 values (every 2 m along transect)

♦ Calculated from 10 values (every 10 m along transect)

Figure 3-1. Profiles of the study transects at Sverdrup Pass (**BMS**, **BRS** and **CRT** transects) and Alexandra Fiord (**OWT** transect) showing areas that were submerged (shaded areas) during time of vegetative sampling. The profile shows the change in the relative elevation (cm) along the transects (quadrat sequence).

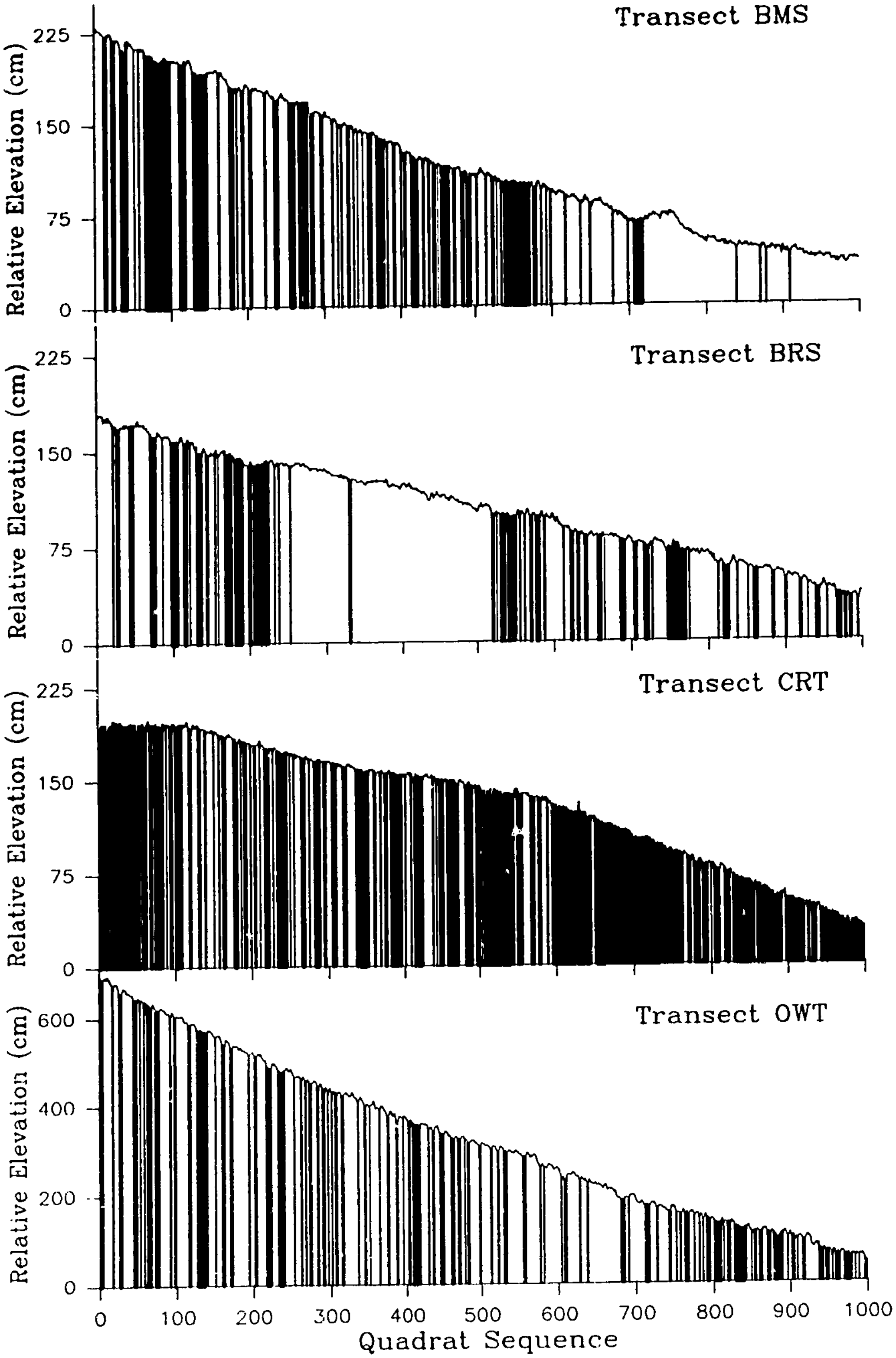
Transect BMS
Transect BRS
Transect CRT
Transect OWT
Relative Elevation (cm)
225
150
75
0
600
400
200
0
100
200
300
400
500
600
700
800
900
1000
Quadrat Sequence

Table 3-4. Combinations of the eight most abundant plant species found in the total data set from all four transects that are significantly high and significantly low in frequency. Combinations are indicated by black squares in species cells where cells are ordered left to right by species abundance. The deflation factor for the analysis of the data set was 1.3.

High Frequency

Carex aquatilis	*Dupontia fischeri*	*Carex membranacea*	*Eriophorum triste*	*Eriophorum scheuchzeri*	*Salix arctica*	*Arctagrostis latifolia*	*Juncus biglumis*
		■					
		■	■				
■	■						
■	■					■	
■	■				■		
■	■			■			
			■	■		■	
			■	■		■	■
			■	■	■		■
			■	■	■	■	

Low Frequency

Carex aquatilis	*Dupontia fischeri*	*Carex membranacea*	*Eriophorum triste*	*Eriophorum scheuchzeri*	*Salix arctica*	*Arctagrostis latifolia*	*Juncus biglumis*
							■
					■		
■							
■				■			
	■		■				
	■		■				■
	■		■			■	
	■		■		■		
	■		■	■			
	■	■	■				
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■		■	■	■			
■	■	■	■				
■	■		■			■	
■	■		■		■		

C. aquatilis and *E. scheurchzeri*, without the other six species, occurred significantly less often than expect. Similarly, so did the combination of *D. fischeri* and *E. triste*. *D. fischeri* and *E. triste* were also present infrequently in combination with other species. This was found when *D. fischeri* and *E. triste* were present in the same quadrat with either *J. biglumis*, *A. latifolia*, *S. arctica*, *E. scheurchzeri* or *C. membranacea*.

In the analysis, the occurrence in a quadrat of only *C. membranacea*, *E. triste* and *E. scheurchzeri*, and the combination of these three species with addition of *C. aquatilis*, happened less often than expected. The combination of *C. aquatilis*, *D. fischeri* and *E. triste* with either *C. membranacea*, *A. latifolia* or *S. arctica* was also found to occur less frequently than expected.

Ordination Analysis

Figure 3-2 shows the ordination biplot derived from the CCA of the combined data set. The sum of the canonical eigenvalues was 0.41 (Table 3-5) with the first two axes accounting for 95.7% of the variation in the species-environment biplot. In addition, the environmental variables used in the analysis explained 60% of the amount of variation in the species matrix.

Table 3-5 also includes the species-environment correlations which are the correlations between a specific species axis and its equivalent environmental axis. A high correlation value was found for the first ordination axis (0.74). While not strictly statistically significant (ter Braak, 1987b), a t-test at the 5% significance level of the canonical coefficient indicated that both litter cover (t=4.91) and moss cover (t=-3.21) strongly influenced the first ordination axis (Table 3-6). The second axis was strongly influence by the moisture index used (t=-2.53).

The ordination biplot (Figure 3-2) shows a good separation of the three meadows. The relationship that the transects have to percent litter cover, percent moss cover and increasing soil moisture (hydric conditions) is determined by their location relative to the environmental arrows. Transects that are positively correlated with an environmental parameter have their sample means located in the general direction of that environmental arrow. The correlations are interpreted as being stronger the further the sample means are from the origin (ter Braak, 1987a).

Transect OWT showed a positive relationship with high litter cover while the Sverdrup Pass transects (BMS, BRS and CRT) were correlated with less litter cover. High percent moss cover was found to characterize transect CRT while transect OWT showed a negative relationship with moss

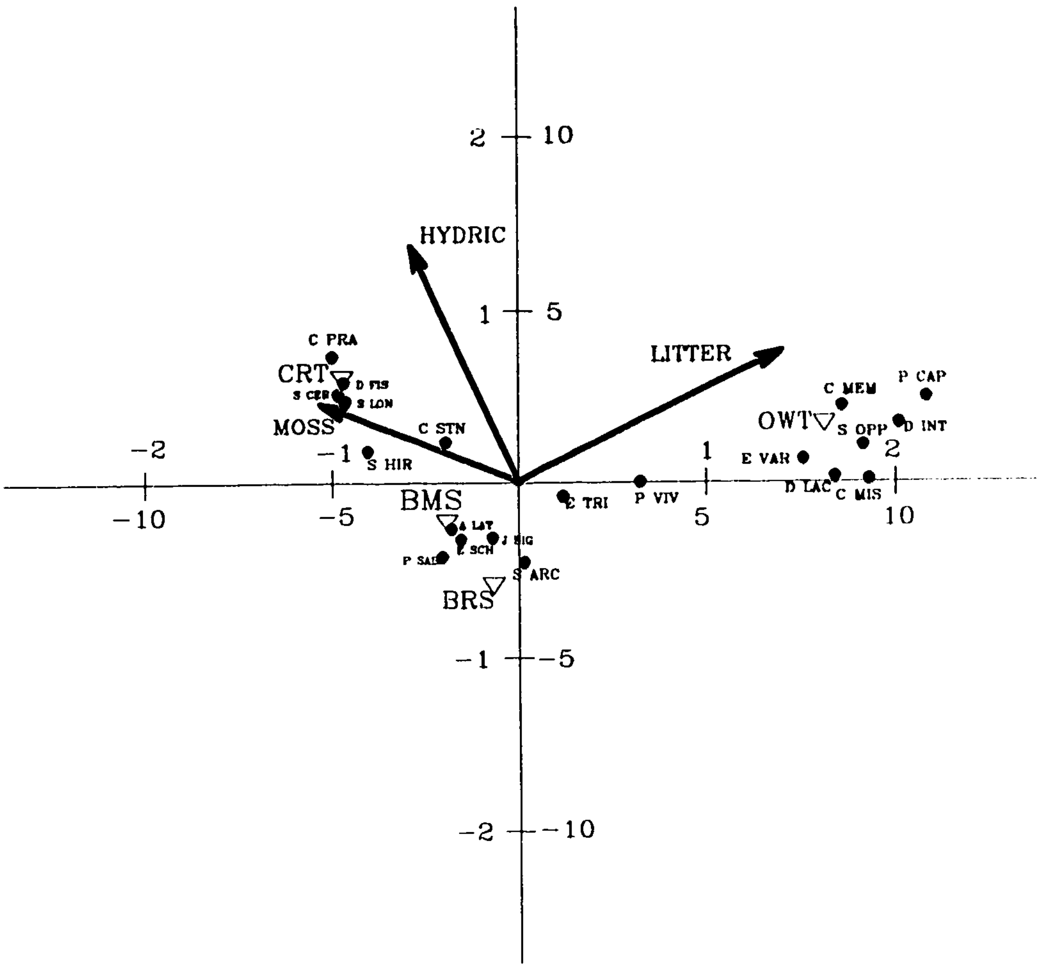


Figure 3-2. Ordination diagram of species, mean sample scores for each transect (BMS, BRS, CRT and OWT) and environmental variables based on canonical correspondence analysis of sedge meadow vegetation data. The environmental variables are represented by arrows that point in the direction of an increase in percent litter cover (LITTER), percent moss cover (MOSS) and an increase in soil moisture (HYDRIC). Species codes found in Table 3-1. Environmental scale bottom (axis 1), right (axis 2). Species scale top (axis 1), left (axis 2).

Table 3-5. Summary statistics for the CCA ordination of the combined data from Sverdrup Pass (BMS, BRS and CRT) and Alexandra Fiord (OWT).

	Axis 1	Axis 2	Axis 3
Eigenvalue	0.31	0.09	0.02
Species environment correlation	0.74	0.42	0.28
Species-environment relation	74.4	95.7	100.0
Variation in species matrix accounted for by environmental variables used			60%
Sum of canonical eigenvalues (after fitting covariables)			0.41

Table 3-6. Canonical coefficients and correlations of environmental variables with the first two axes of the CCA

Variable	Canonical coefficients (t-values)[a]		Correlations	
	Axis 1	Axis 2	Axis 1	Axis 2
Litter cover	0.882 (4.91)	0.668 (1.78)	0.863*	0.386
Moss cover	-0.564 (-3.21)	0.360 (0.98)	-0.591*	0.230
Moisture index	0.279 (1.58)	-0.936 (-2.53)	0.388	0.748*

[a] absolute t-values for canonical coefficients >2.3 show strong relationships but are not strictly statistically significant (ter Braak, 1987).

* Significant correlation ($P < 0.05$).

cover. Both transects BMS and BRS were not strongly influenced, either positively or negatively, by moss cover. Soil moisture was most strongly correlated with transect CRT, and soil samples from transect CRT were more hydric than samples from the other transects.

Figure 3-2 also shows the species scores for those species found in greater than 2.5% of the quadrats along any of the transects. Those species that were found on all four transects appear the closest to the centre in the ordination plot and therefore had the weakest relationships to the environmental variables measured. *E. triste*, and especially *P. viviparum*, were more likely to occur as litter cover increased (positive relationship), while *C. aquatilis*, *A. latifolia* and *J. biglumis* were slightly more likely to occur as litter cover decreased (weak negative relationship). *S. arctica* was not influenced by the amount of litter cover.

The frequency of *C. aquatilis*, and to a lesser extent *A. latifolia*, increased with increasing moss cover. *E. triste*, *S. arctica* and *P. viviparum* showed a decrease in their occurrence with an increase in moss cover. *J. biglumis* was not influenced by the amount of moss cover present.

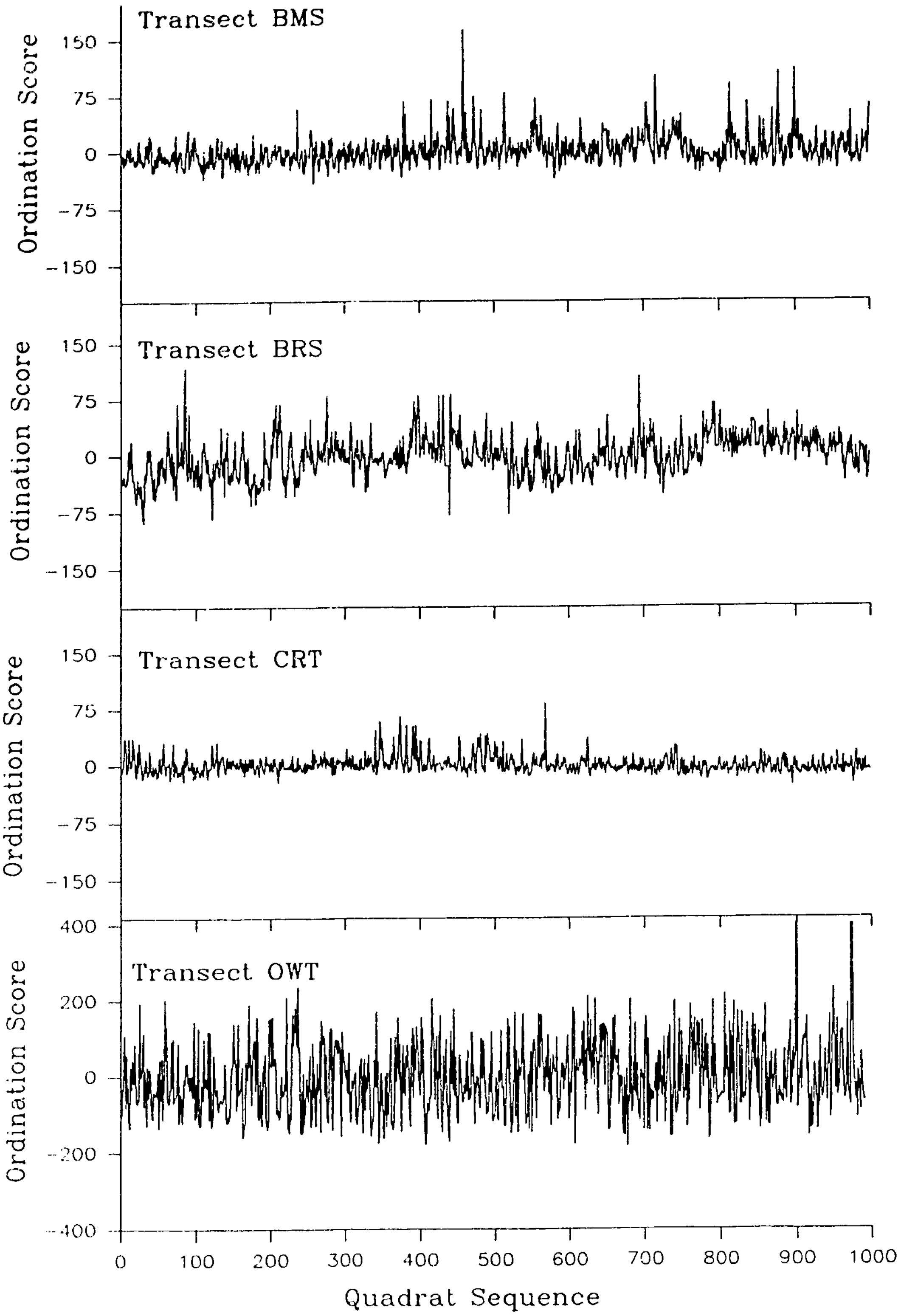
The relationship of four of the six species to an increase in hydric conditions (an increase in surface water and soil moisture) was the same as that found for increasing moss cover. *C. aquatilis* was more common in wetter areas while, *S. arctica*, *E. triste* and *P. viviparum* were more common in drier areas. *J. biglumis* occurred more often in drier areas, and *A. latifolia* did not appear to be influenced by the soil moisture conditions measured.

The remaining species in the ordination biplot had their distributions restricted to certain transects and were found to occur close to the positions of the mean sample scores for that transect. *C. membranacea*, *D. integrifolia*, *P. capitata*, *S. oppositifolia*, *C. misandra*, *E. variegatum* and *D. lactea* were all exclusively found, or had their highest frequency of occurrence, on transect OWT. They occur in the same area of the ordination plot as the Alexandra Fiord transect, and have the same relationships to the environmental variables.

A similar relationship to environmental variables was found for species that were more common at Sverdrup Pass. *P. sabinei* occurred in quadrats with less litter cover, a greater amount of moss cover and less standing water. These conditions were associated with transects BMS and BRS, where *P. sabinei* was most common. The five species that were present mainly on transect CRT (*S. cernua*, *S. hirsuta*, *S. longipes*, *C. pratensis* and *D. fisheri*) had the same relationship to the environmental variables as the average sample scores from the transect. They occurred in quadrats with high moss cover, low litter cover and a greater amount of standing water.

Figure 3-3 shows the ordination position on the first axis for each strip transect against its real sample position. Fluctuation in the ordination trace indicates a change in species composition along each transect. All four transects showed differences in the species composition of adjacent

Figure 3-3. Correspondence analysis trace of the four sample transects (BMS, BRS, CRT and OWT). Axis 1 is the sample sequence on the transect; Axis 2 is the sample ordination score on the first CA ordination axis.


Transect BMS
Transect BRS
Transect CRT
Transect OWT
Ordination Score
150
75
0
-75
-150
400
200
0
-200
-400
0
100
200
300
400
500
600
700
800
900
1000
Quadrat Sequence

quadrats but, no major change in vegetation from the top to the bottom ends of their respective transects. Although, transects BRS and OWT did show a oscillating pattern overlaying the change in adjacent sample scores.

Transect OWT showed a greater separation in adjacent samples in the ordination trace than the other three transects, while transect CRT had the least separation in adjacent sample values. By contrast, all four transects had very similar eigenvalues (Table 3-7) indicating a similar degree of separation in the species scores along the first ordination axis. Low correlations were found for all transects between the species axis and the environmental axis defined by the measured environmental variables (Table 3-7).

DISCUSSION

All of the species found in greater than 2.5% of the quadrats on at least one of the transects were shown to be associated with wet meadows in previous studies (Muc, 1976; Webber, 1978; Sheard and Geale, 1983a; Edlund and Alt, 1989; Muc *et al*, 1989; Henry, 1994). Their distribution is not however, continuous throughout the range of wet meadows studied. Muc (1976), for instance, found that frost-boil meadows and hummocky meadows were dominated by *Carex aquatilis*, *Salix arctica*, *Eriophorum triste*, *Polygonum viviparum* and *Arctagrostis latifolia*, while in the wetter meadows only *Carex aquatilis*, *Arctagrostis latifolia* and *Eriophorum triste* were prominent. Similar changes in dominance were found by Sheard and Geale (1983a) and Webber (1978) over the range of meadows they studied.

The species association and the canonical correspondence analysis provided some indication of which environmental factors affect the prominence of different species in the wet meadows studied. Using both analyses the eight most common species could be divided loosely into three groupings. One grouping contained *C. aquatilis* and *D. fisheri*, a second grouping contained *J. biglumis*, *E. scheurchzeri* and *S. arctica* and third grouping contained *E. triste* and *C. membranacea*. Overlap in the groupings was found between groups one and two and groups two and three mainly as a result of the high frequency of *E. triste* and *C. aquatilis* in the quadrats. Both species are prominent in most major types of wet meadows in the High Arctic (Sheard [illegible], 1983a; Bliss and Svoboda, 1984; Bergeron, 1988; Edlund and Alt, 1989 ; Muc *et al.*, 1989; Henry, 1994) and probably occur with the other common species in the study meadows because of their apparently wide environmental tolerances. *Eriophorum triste*, for example, showed no real difference in shoot density in both grazed and ungrazed meadows (Henry and Svoboda,1994) which could help to explain its occurrence with both *C. membranacea* and the species in group two.

Table 3-7. Summary statistics for the CA ordination of the transects from Sverdrup Pass (**BMS**, **BRS** and **CRT**) and Alexandra Fiord (**OWT**).

	Transect	Axis 1	Axis 2	Axis 3
Eigenvalue				
	BMS	0.35	0.24	0.23
	BRS	0.33	0.25	0.24
	CRT	0.27	0.27	0.25
	OWT	0.30	0.28	0.26
Species environment-correlation				
	BMS	0.255	0.388	0.266
	BRS	0.352	0.174	0.234
	CRT	0.181	0.077	0.202
	OWT	0.145	0.320	0.190
Species-environment relation *				
	BMS	21.7	57.1	73.1
	BRS	53.5	63.5	80.9
	CRT	29.3	34.4	68.0
	OWT	6.6	36.9	46.9

* these represent % variation in species data accounted for by the measured environmental variables

The species groups were also located in the same ordination space as the transects they were most commonly found in. This is because the location of sample scores is highly influenced by the relationship of their species to environmental variables in the ordination (ter Braak, 1987a). Transects CRT and OWT which have the greatest difference in species composition, therefore, are the farthest apart in the ordination space. The two transects in the north meadow at Sverdrup Pass (BMS and BRS) have similar species compositions and similar locations in the CCA diagram.

Although this separation of the transects along the first ordination axis was found to be due to litter and moss cover, the distribution more appropriately represents a gradient of grazing intensity. It has been suggested that grazing intensity can influence the amount of litter and moss cover found in sedge meadows. Henry (1987) and Raillard *et al.* (1992) have suggested that high litter cover at Alexandra Fiord is a direct result of the absence of periodic grazing by muskox. An increase in grazing intensity results in an increase in moss cover probably because of more rapid recycling of nutrients and a more open canopy (Henry, 1987; Henry and Svoboda, 1994). The absence of grazer results in the accumulation of litter which influences the productivity of mosses by altering the water regime in the meadows. The highest productivity of mosses has been found in areas which have a constant water source which is maintained at a constant level through the growing season (Vitt and Pakarinen, 1977). The hummocks formed by the accumulation of litter at Alexandra Fiord establish more variable water conditions in the meadow resulting in a constricted moss distribution. In addition, the litter cover provides a very poor substrate for the establishment of new mosses because it does not remain wet enough during the growing season (Henry, 1987).

The importance of grazing intensity in distinguishing the Sver [illegible] and Alexandra Fiord sites was also seen more indirectly in the floristic composition and oth [illegible] acteristics of the study sites. *Dryas integrifolia*, *Cassiope tetragona* and *Vaccinium uliginosum* are intolerant of grazing (Bliss and Svoboda, 1984; Henry and Svoboda, 1994) and occur only at Alexandra Fiord while, some more tolerant graminoid species are more common at the Sverdrup Pass site. *Carex aquatilis* is probably the best example of the graminoids. In experiments using clipping to simulate grazing, an increase in leaf growth (compensatory growth) was found (Raillard, 1992; Henry and Svoboda 1994), suggesting that grazing may stimulate productivity under certain conditions.

The lack of grazers in arctic sedge meadows can create different environmental conditions by affecting microtopography and soil temperature. It has been suggested that the large variation in the microtopography in the meadows at Alexandra Fiord was partly the result of the formation of hummocks caused by the accumulation of litter and the absence of trampling by muskox (Henry, 1987; Henry and Svoboda, 1994). The presence of hummocks increases the occurrence of species that are found typically in more mesic rather than hydric sites or are absent from areas where periodic flooding occurs (Beschel and Matveyeva, 1972; Muc, 1977; Henry, 1987; Henry, 1994). The difference in species composition at Alexandra Fiord, especially the prominence of *D. integrifolia* and *C. membranacea* is the result of this greater microtopographical relief.

Soil temperature is an important factor affecting productivity in arctic communities. Higher soil temperatures increase root growth, the decomposition of organic matter, the uptake of soil nutrients and water by roots, the release of nutrients from frozen soil horizons and the depth of the active layer (Bliss, 1971; Chapin, *et al. 1979*, Ryden, 1981; Billings, 1987).

The difference in soil temperature shown at Sverdrup Pass and Alexandra Fiord is related to the increase in litter and the decrease in moss cover due to the lack of grazing. Henry (1987) has suggested that the hummocks formed by the litter increase the soil temperature because the inclined sides will receive more direct sunlight and the air spaces between the litter traps warm air. The almost continuous moss cover at Sverdrup pass has the opposite effect by decreasing the depth of the active layer (Henry, 1994). Brown (1977) has shown that a thick surface organic layer can insulate the soil resulting in lower soil temperatures.

The second axis in the ordination was defined by a moisture gradient and was the most important factor for separating the meadows at Sverdrup Pass. The south meadow was found to be wetter than the north meadow probably as a result of a greater retention of water in pools and slower drainage. The larger amount of soil moisture available on transect CRT would also explain the higher moss cover in that meadow. The amount of soil moisture and the fluctuation of water levels are important factors effecting the distribution and occurrence of mosses (Vitt and Pakarinen, 1977; LaFarge-England, 1989; Gignac *et al.*, 1991). The groupings identified by the species association analysis on the most common species also indicates a moisture gradient. *Carex aquatilis* and *D. fisheri* tend to occur in wetter, more submerged areas than *E. scheuchzeri* (Sheard and Geale, 1983a), *S. arctica*, *J. biglumis* (Muc, 1976; Bergeron, 1988) and *C. membranacea* (Henry, 1987).

Although litter cover, moss cover and moisture were important environmental variables, there was still 40% of the variance in the species distribution not accounted for by the CCA analysis. Some of this variance could be due to an earlier snowmelt at Alexandra Fiord (Henry, pers. comm.) or to the differences found in soil N and P concentrations (Henry and Svoboda, 1994). Both could be contributing factors to differences in productivity and diversity between the sites. These factors, however, are only site specific. Differences in species composition between quadrats on the transect and also between the meadows at Sverdrup Pass are probably not greatly influenced by these factors.

Most likely the variation in the species distribution that is not accounted for by CCA is related to parameters that influence the distribution within individual meadows. A low correlation between the environmental axis and the species axis in the correspondence analysis of each transect indicated that none of the environmental variables measured seemed to explain the distribution of species along the transects.

Litter was mainly used as an indicator of grazed versus ungrazed areas and it is unlikely that muskox grazing patterns would exclude some areas within a meadow. In addition, it is doubtful that these ungrazed areas would exist for a long enough period of time to change the species composition.

Moisture and moss cover, while important for differentiating meadows, are probably not as important at influencing the distribution of vascular plants within the meadows. One of the reasons for placing transects running down the meadows was to test the hypothesis that there were differences in the properties of the water table at the top and bottom of the drainage slope. However, the ordination traces did not show any major change in the distribution of vascular species between the two ends of the transects. If the position along the drainage slope is important, it must occur at a larger scale than that measured.

The vegetation in the meadows is, in some sense, an expression of the long term environmental conditions in the habitat, therefore, differences in moss cover and moisture would have to be constant for extended periods of time in order to influence the distribution of vascular plants along the transects. This probably does not occur along the Sverdrup Pass transects. Due to the low microtopography in the north meadow, the existing fluctuation in water levels probably precludes the establishment of areas that retain distinctive water regimes. In the south meadow, where the water fluctuation was less, the majority of the transect was submerged. With less variation in the water conditions of the meadow, moisture becomes less important as a factor differentiating the vegetation along the transect.

Since the measured environmental variables do not appear to explain all the species distribution that occurs in the meadows, other factors must be involved. Two possible influences might be the reproductive strategy of the predominant vegetation and interactions between species. The vegetation in the High Arctic is dominated by long-lived perennials that depend primarily on vegetative reproduction for propagation (Billings and Mooney, 1968; Bliss, 1971; Saville, 1972; Billings, 1987; Henry *et al.*, 1990). The dispersal of vegetative propagules is therefore, an important factor in determining the spatial distribution of species. Vegetative reproduction also has a competitive advantage over sexual reproduction in the Arctic because it allows plants to grow into unoccupied microsites while still receiving an energetic subsidy from the parent plant (Chapin *et al.*, 1980). In doing this, the plants are able to grow in microsites where they normally would not be found. This was probably why microtopography was not significant in my analysis. Although microtopography was probably important for some species (notably *D. integrifolia* and *C. membranacea*), it probably was not important to a majority of species.

From the pattern shown of submerged quadrats, the ordination trace and the variance in the microtopography, it appeared that hummock-hollow microhabitats were present along transect OWT. This physical structure, however, may not be important for the majority of species in the meadows because their vegetative growth allows the species to invade the slightly wetter and dryer microhabitats.

Callaghan an Emanuelsson (1985) have discussed interactions between arctic vascular plants in terms of positive and negative relationships. The aggregation of plants can have a positive benefit for the species involved by providing shelter from wind exposure, an increase in local temperature, an organic rooting substrate and an increase in moisture retention. Negative interactions, like competition, occur as space decreases and resources become more abundant. Both interactions can therefore, influence the distribution of the vascular species in the meadows. One species that might be important in this regard could be *Dryas integrifolia*. Carlsson and Callaghan (1991) have suggested that evergreen dwarf shrubs can play an important part in influencing plant distributions by providing shelter for some species.

In summary, grazing intensity and soil moisture are important factors influencing the distribution of species in High Arctic sedge meadows. Variation in these environmental parameters between meadows showed that certain groups of species have very distinct associations. The distribution of species within meadows, however, was less conclusive and other factors, besides those measured must be important in the arrangement of species.

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CHAPTER 4

SUMMARY AND SYNTHESIS

Vascular plant species were shown to be non-randomly arranged along all four study transects. At least two scales of pattern were found for the measured species at less than 7 metres in size. The first scale of pattern for all the species was shown to be 10 to 150 cm in size and was relatively consistent along the transects and between species. The second scale of pattern usually occurred between 150 and 700 cm in size and corresponded to the size of clumps of patches. This pattern was more variable showing different scales for each species, irregularity along each transect and inconsistent patterns for species on more than one transect.

The consistency shown in the first scale of pattern between species and transects suggested that it was primarily due to biological factors. The environmental factors that were measured appeared to be important for determining species composition and frequency in the meadows, but did not seem to effect the minimum patch size. This suggested that the species had a common characteristic which effected their spatial coverage, like vegetative reproduction.

In general, the distribution of vegetation in each meadow did not occur in patches with certain species compositions, although some species pairs did indicate specific relationships. Of the possible 35 species pair combinations on each transect, less than two thirds of the pairs in the two Sverdrup Pass meadows and three quarters of the pairs in the Alexandra Fiord meadow showed an association with the smallest scale of pattern. Some spatial orientation of the different species therefore, does seem to exist within the study meadows.

A better understanding of the importance of microtopography in the Alexandra Fiord meadow was also shown by the relationship between the spatial patterns of species and species occurrence. The occurrence of hummocks in meadows has often been suggested as a factor that increases species diversity (Beschel and Matveyeva, 1972; Muc, 1976; Henry, 1987). Implicit in this idea is that there is an increase in structuring of the vegetation with species occurring in specific microhabitats. The multispecies pattern, however, does not corroborate this assumption. There is no distinct separation of species into alternating phases. In addition, the most common species all indicate a positive covariance with *Dryas integrifolia* which is often used as an indicator of differences in soil moisture on hummocks (Beschel and Matveyeva, 1972; Muc, 1976; Henry, 1987). The microhabitat differences related to the hummocks are probably not an important factor influencing the distribution of the common species and therefore, not an important factor in distinguishing between quadrats along the transects.

The parameters that best distinguished between the Sverdrup Pass and Alexandra Fiord sites were moss and litter cover. These two variables were shown to have an inverse relationship, which Henry (1987, 1994) has attributed to differences in grazing intensity. The accumulation of litter as a result of a lack of recent grazing at Alexandra Fiord (Henry *et al*, 1986) has been thought to limit the productivity of mosses by effecting the availability of water through the development of hummocks and a dry substrate (Henry, 1987; Henry and Svoboda, 1994).

The plant-herbivore interaction that seems to differentiate the two study sites is a common natural disturbance in many grassland communities (Pickett and White, 1985). Although a direct comparison of the two sites cannot be done based on disturbance or grazing intensity due to other site differences (e.g. coastal versus inland locations), some comparison to other grasslands can be made. Unlike more southern grasslands, differences in species diversity (McNaughton, 1979; Collins and Barber, 1985) and the spatial pattern of the vegetation (Belsky, 1986) were not found between the study sites. The increase in microhabitat diversity caused by an increase in disturbance is probably balanced by the increase in microhabitat diversity caused by litter accumulation. In addition, High Arctic meadows are dominated by vegetatively reproducing individuals unlike short and mid-grass communities. Belsky (1986) found when grazing was eliminated in the short and mid-grass communities in the Serengeti, the spatial pattern of the vegetation changed due to a shift from short sexually-reproducing species to tall vegetatively reproducing species.

The water regime seemed to be the most important factor differentiating the two meadows at Sverdrup Pass. The south meadow was associated with stable water levels and a higher water table that resulted in most of the transect being submerged. Water levels in the north meadow varied through July and there was less extensive accumulation of water along the two transects.

Groups of species were shown to be associated with the conditions in each of the meadows. Some species were present or prominent on only a few transects while, the more common species tended to occur in specific combinations within quadrats. These species combinations indicated that there were certain properties associated with individual quadrats which either promoted or inhibited the occurrence of different species. Variation in litter cover, moss cover and soil moisture are probably important parameters influencing this distribution, however, they appear to be more important at influencing the occurrence of species within meadows rather than there spatial arrangement.

Litter cover, moss cover and soil moisture were found not to be important factors explaining the differences in species composition between quadrats found on each transect. This could be the result of only sampling for one summer or the result of short transects. For the length of the transect used these parameters might not show enough spatial variation to influence the arrangement of species.

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