PLANT DISTRIBUTION AND COLONIZATION IN EXTREME POLAR DESERTS, ELLESMERE ISLAND, CANADA

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THESIS ABSTRACT

Polar desert vegetation (with usually less than 5% vascular plant cover) represents 15.1% of the arctic tundra biome area, yet its composition and distribution are poorly known. The Canadian High Arctic contains 75.6% of the polar deserts of the world. They are characterized by very cold and extremely short growing seasons and minimal summer precipitation. This thesis investigates the vascular species richness and distribution based on the survey of 82 sites on central Ellesmere Island, Canada. In addition, it addresses fundamental questions regarding three major variables potentially limiting plant community development: the availability of 'safe sites'; the abundance of viable seeds; and the limited time for plant establishment since the site's deglaciation.

The minimum sampling area of this sparse vegetation was measured to be 10-25 m^2. Vascular species richness ranged from 2-22. Four key vascular species: *Saxifraga oppositifolia*, *Papaver radicatum*, *Draba subcapitata* and *Draba corymbosa* occurred on 60-100% of the sites. Some species were restricted to a specific substrate, either granite or carbonate. Bryophyte and lichen cover was frequently < 0.1% and < 5% respectively. Environmental variables measured explained a large portion of the vegetation variation (more than 67%). Elevation was the most important variable. Vegetation on low elevation sites was more abundant and diverse. Four vegetation groupings reflecting plant abundance, plant diversity and substrate type were distinguished with a two-way indicator species analysis (TWINSPAN).

Plant distribution on a dolomitic plateau was contagious and plants tended to grow near protective boulders. Along two altitudinal gradients, flower buds were produced almost every year by *Papaver radicatum*, but flower and fruit production varied depending on site conditions and yearly summer climate. Germinable seed banks were found even in extremely poor sites.

This study demonstrates the diversity of polar deserts in central Ellesmere Island. Reproduction by seeds on such sites is common although its success depends on local climate which varies greatly from year to year. Recruitment of new seedlings is rare although vacant 'safe sites' and seeds are available. Ground surface dessication may partly interfere with this process. The findings of this work suggest that recruitment is restricted to short periods when conditions are more favourable.

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CHAPTER 1:

GENERAL INTRODUCTION

1.1 VEGETATION IN POLAR DESERTS

The presence of plants growing in an environment which is extremely cold and dry (both conditions known to impede plant growth) may, at first, be surprising. Vast expanses of the High Arctic appear bare, yet these landscapes do support persistent, although meagre, vegetation which includes both vascular and non-vascular species. Bliss *et al.* (1973) described polar deserts as vegetation with minimal lichen and bryophyte abundance and low vascular plant cover, less than 5%. Worldwide, approximately 850 000 km^2 (an area equivalent to France and Italy together) are covered by this resilient vegetation (Bliss and Matveyeva, 1992). More than 90% of these deserts are found in Canada and Greenland (75.6% and 15.0%, respectively; Bliss and Matveyeva, 1992). To this day our knowledge of the vegetation of these deserts is rather scarce, and our understanding of patterns of plant colonization of remote barren landscapes is even more limited. With climatic warming and the reduction of glaciated areas, profound changes are likely to take place in polar regions which will affect these marginal habitats.

As the northernmost island in Canada, Ellesmere is the largest of the Queen Elizabeth Islands (Figure 1.1) and half of its deglaciated area is covered by polar deserts (Bliss *et al.*, 1973). A number of vegetation studies have characterized the flora, plant communities and net primary productivity of the more floristically diverse polar oases on Ellesmere Island (*e.g.* Bergeron and Svoboda, 1989; Svoboda and Freedman, 1994), but only a few studies have described polar desert vegetation (*e.g.* Maycock and Fahselt, 1992; Bliss *et al.*, 1994). The purpose of my research was to conduct a thorough survey of

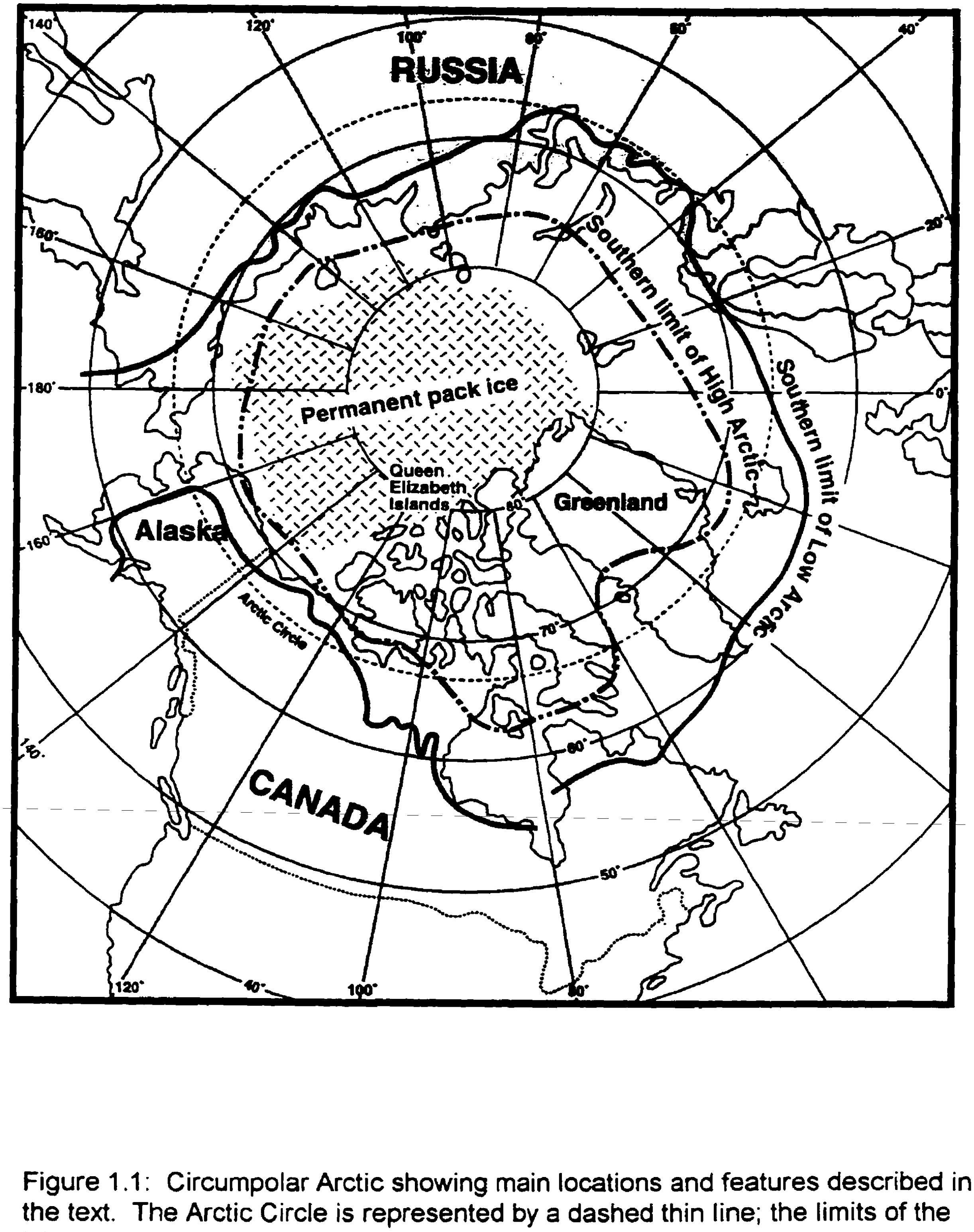

Figure 1.1: Circumpolar Arctic showing main locations and features described in the text. The Arctic Circle is represented by a dashed thin line; the limits of the High and Low Arctic are shown by thick lines. Modified from Bliss and Matveyeva (1992).

vegetation in central Ellesmere Island in order to describe the plant communities and to investigate colonization of polar deserts by plants.

1.2 BACKGROUND INFORMATION

1.2.1 Glacial history

In a distant past, during the Tertiary Era, temperate conditions allowed the growth of swampy forests at 80°N (Francis, 1988; McIver and Basinger, 1988; Thurston *et al.*, 1989). Evidence is mounting that forests were present at similar latitudes up to the very beginning of the Pleistocene (2 million y BP; Bennike and Böcher, 1990; Matthews and Ovenden, 1990; Whitlock and Dawson, 1990; Böcher, 1995). However, almost all traces of these forests now have been erased. During the Pleistocene epoch (2 million y BP until 10000 y BP), successive glaciations have carved the landscape of the northern hemisphere (*e.g.* Plate 1.1). The Laurentide Ice sheet covered most of northern, central and eastern North America during the last glaciation (Fulton and Prest, 1987), which was called 'Wisconsin' in North America and 'Würm' in Europe (Ives, 1974). The idea of an 'Innuitian Ice Sheet' over the Queen Elizabeth Islands has been put forward by Blake (1970) but more recent evidence suggests that the glaciation of the Queen Elizabeth Islands was more complex and that the ice sheet was probably partitioned into smaller ice masses in that region (England and Bradley, 1978; Hodgson, 1985; England and Bednarski, 1986). The glacial maximum of the late Wisconsin stade was approximately 18000 y BP, and its retreat at the southern margin around 10000 y BP, has been used to define the beginning of the present interglacial, the Holocene (Ritchie, 1993).

Minimum estimates on the initial emergence for northern Ellesmere are 10000 to 8100 y BP (Bradley, 1990). The rapid amelioration of climate in early Holocene forced the retreat of the glaciers more rapidly in the south-eastern part of the Island than in the North (Blake, 1986). In central Ellesmere (79°N),

Plate 1.1: Aerial photograph of the eastern end of Sverdrup Pass, 79°09'N, Ellesmere Island. The deglaciated valley ends in Flagler Bay; to the right small ice caps cover the uplands; glacier outlets descend into Beitstad Fiord and Hayes Fiord. Photograph # T508L-41, Energy, Mines and Resources Canada, July 1959.

which became our study region, glacial retreat near Irene Bay (west coast) started around 8820 y BP and on the eastern flank of Sverdrup Pass around 7340 y BP (Hodgson, 1985). On Hazen Plateau (82°N) glaciers were still within a few kilometres of their maximum position until *ca.* 6200 y BP (England 1978; England and Bednarski, 1986).

There are indications of more open sea ice conditions around Ellesmere in early Holocene (Stewart and England, 1983; Williams *et al.*, 1995). These conditions would support productive systems at these northernmost latitudes during this period (Bradley, 1990) and would be associated with vegetation expansion from glacial refugia (Brassard, 1971; Dahl, 1987) or of reinvasion from the South (Nordal, 1987). The mid-Holocene is also the period of maximum expansion of the boreal forest to the north (Ritchie, 1984; Payette and Morneau, 1993), and this period (4000-5000 y BP) is referred to as the Hypsithermal (Fredskild, 1985; Ford, 1993, p. 215).

During the last 3000 years, however, the climate has been cooler than in the early Holocene and glaciers have re-advanced (Bradley, 1990). The most recent cooling period, the Little Ice Age (LIA, 150-350 y BP; Bray, 1968) may have been the coldest period of the Holocene and some glaciers advanced to their post-glacial maximum positions (Bradley, 1990). Presently, most glaciers are receding (Bradley, 1990; Slaymaker and French, 1993), and some are uncovering plants or entire plant communities which grew at the sites 300-800 years ago (Bergsma *et al.*, 1984; Havström *et al.* 1995; Jones, 1997). Analyses of subfossil material of *Cassiope tetragona* showed that plant communities were killed suddenly by the advance of glaciers and climate estimates suggest that the mean temperature approximately 400 years ago was 0.7°C lower than that at present (Havström *et al.*, 1995).

1.2.2 Origin of arctic flora

From where and when did the present arctic species originate? Even today, this question cannot be answered fully (Ritchie, 1993). Generally, the species now present in the Arctic are believed to have evolved from species of the nemoral flora, in alpine regions during the Tertiary Era (Löve and Löve, 1974). During this period the earth was much warmer than that at present and there were no regions that experienced truly arctic climatic conditions (Murray, 1995); forests covered the entire northern hemisphere. High mountains, however, were vegetated by stunted cold-tolerant species and these are thought to have radiated into the northern regions (Löve and Löve, 1974; Murray, 1995).

Advances in the study of paleodistribution of plants (pollens, algae and macrofossils, *e.g.* Matthews *et al.*, 1986; Gajewski *et al.*, 1995) and animals (mostly insects, *e.g.* Böcher, 1995) bring very convincing evidence that diverse vegetation types were present at high latitudes during the early Quaternary Period, prior to the Pleistocene glaciations (Matthews and Ovenden, 1990; Whitlock and Dawson, 1990; Bennike and Böcher, 1990). Ritchie (1993) argues that the arctic vegetation of Canada has existed for more than four million years. At Meighen Island (at 80°N), in the Canadian High Arctic, Matthews (1987) found fossils of *Saxifraga oppositifolia*, *Dryas integrifolia* and *Oxyria digyna* in formations dating from the late Pliocene. These species were found with remnants of coniferous forest woodland species (Matthews, 1987). These findings and the work of Funder *et al.* (1985) and Böcher (1995) in northern Greenland indicate the presence of forest-tundra communities at the Pliocene-Pleistocene transition (*ca.* 2-3 million y BP) in what we presently call the High Arctic.

Were all these species eliminated from high latitudes by past glaciations? Did plants reinvade the northern latitudes from the narrow tundra zone preserved at the southern limit of the ice margin (Sauer, 1988, p. 157)? These questions have long been and are still being debated (Hadač, 1963; Löve and

Löve, 1974; Dahl, 1987; Nordal, 1987). Two theories are generally considered: the Tabula Rasa and the Nunatak theories (Ives, 1974; Dahl, 1987; Nordal, 1987; Crawford and Abbott, 1994). The Tabula Rasa describes the extermination of all highly organized land plants and animals in polar regions during glaciation. This implies that reinvasion of plants originated from more southern latitudes (Nordal, 1987). On the other hand, the Nunatak theory suggests that some species survived in ice-free areas north of the southern limit of Pleistocene glaciers, in coastal refuges or on mountain tops. Accordingly, the present vegetation would include species that evolved and survived in the Arctic (Gjaerevoll, 1963; Dahl, 1987).

Plant geographical distributions have been used to distinguish floristic groups around the world (Takhtajan, 1986). The abundance of arctic species with circumpolar distribution suggests that many taxa established in the high latitudes prior to the glaciations (Hadač, 1963; Hultén, 1971). The large number of endemics at the species level in the floras of arctic regions (Takhtajan, 1986) was often used as an argument, especially in Scandinavia, supporting the survival of isolated populations in refugia during the glacial episodes (Rönning, 1963; Ives, 1974). But recently Nordal (1987) reported that in view of the rapid rates of evolution and of possible long-distance dispersal, survival in refugia is not essential to the explanation of endemism in Scandinavia. Caution should be taken when generalizations are derived exclusively from floristic plant geography since gaps in plant distribution may depend on a number of factors (*e.g.* inadequate field sampling; Ritchie, 1984 and 1993; McJannet *et al.*, 1993).

Information based on the geology and the geomorphology of northern regions is also important to the understanding of plant distribution (Ives, 1974; Ritchie, 1993). The increasing knowledge on the position of glacial limits (*e.g.* Hodgson, 1985; England, 1986) and on the sea level drop during glaciation and isostatic rebound after deglaciation (Hodgson *et al.*, 1994) suggests that, in addition to a corridor between the Cordilleran and Laurentide ice sheet during the mid-Wisconsin break and an emergent Bering Platform (Murray, 1987; Elias, 1996), there were land masses free of ice at the height of the last glaciation in the High Arctic. These areas may have served as refugia, particularly for the hardy high arctic flora (Brassard, 1971; Fredskild, 1985). The climate during the Pleistocene interglacials was warmer than today (Matthews *et al.*, 1986), maybe as much as 4-12°C in the Arctic (Slaymaker and French, 1993), favouring vigorous plant growth during these episodes. The repetitive expansions and contractions of the glaciers were responsible for numerous additions and subtractions to the flora promoting the establishment of a new floristic mix on the treeless tundra (Murray, 1987).

Studies of distribution of pollen and macrofossils from lake sediments in Northwest Greenland (78°N, Fredskild, 1985) and, from peat profiles on the Fosheim Peninsula, Ellesmere Island (80°N; Garneau, 1992) and on Novaya Zemlya, Russia (74°N; Serebryanny and Tishkov, 1994) demonstrate that relatively diverse and abundant vegetation developed rapidly following ice retreat. Fredskild (1985) describes species-rich pioneer vegetation (consisting of herbs and Pteridophytes) establishing following ice retreat. Although this pioneer vegetation could not be dated precisely, the transition to a *Salix* dominated community happened around 7500 y BP approximately 1000 y after the ice retreated. Such pioneer plant communities are more likely to have developed from regional rather than from distant (*e.g.* at the southern margin of the Wisconsin ice sheet) seed and propagule sources.

The last word has not been said yet about this fascinating topic. New information is gathered every year that adds details to the historical mosaic or sometimes redraws a significant portion of it. Murray (1995) summarizes well our present understanding: "The arctic flora of North America has its origins in the preadapted survivors of the arctic Tertiary forests to which were added 1) Pleistocene migrants from Asia, 2) plants that returned during interglacials and in post-glacial time from unglaciated areas south of the continental ice sheets, 3) in-situ survivors of Quaternary glaciation in northern refugia, and 4) the newly evolved taxa of Pleistocene and Holocene age."

1.2.3 Arctic, tundra biome and vegetation zones

Delimitation of the Arctic: Another controversial topic in northern studies is the definition of the Arctic, of its boundaries, and of its subdivision into climatological, vegetational and other zones. My intentions here are simply to define the terms and the vegetation zones used in this thesis, not to review the extensive literature on the subject.

The first delimitation of the Arctic that comes to mind is the Arctic Circle. at 66°32'N (Figure 1.1). It is the latitude at which at least one day every year has 24h without sunset and one day 24h without sunrise. This latitude depends on the tilt of the earth (21°58'-24°36') which slowly changes with the periodicity of 40400 years (Embleton and King, 1968; p. 25). However, this precisely formulated geographical definition of the arctic region is of little practical use for ecologists. Major parts of the world which experience extremely cold climate, are underlain by permafrost and covered by tundra vegetation, are below the Arctic Circle (in Canada). In contrast, forests in Eurasia, Alaska and Yukon extend far above the Arctic Circle (Figure 1.1).

Climatically, the Arctic refers to the northern circumpolar regions. In Canada this region is called the Arctic Ecoclimatic Province (Ecoregions Working Group, 1989). Table 1.1 shows some climatic data for Canadian weather stations from the cool temperate to the arctic province. Potential insolation, frost-free period, temperature and number of thawing degree-days (TDD) decrease with increasing latitude. Young (1971) and later Edlund and Alt (1989) have associated the distribution of vascular plants with mean July isotherms. For example, the northern limit of tundra woody plants (*e.g. Salix arctica* and *Dryas integrifolia*) and sedges corresponds to the regional mean July isotherm of 3°C (Edlund and Alt, 1989) and to the arctic floristic zone 1 of Young (1971). The 10°C mean July isotherm has often been used to mark the southern limit of the arctic region in North America. Large water bodies (*e.g.* Hudson Bay

Table 1.1: Summary of annual climatic conditions (normals 1951-1980) and annual mean radiation at Canadian weather stations from temperate to high arctic conditions. TDD represents thawing degree-days (above 0°C). Source: Atmosphere Environment Services (1982) and † Rouse (1993).

Station	Latitude (N)	Longitude (W)	Mean temperature (°C)		TDD	Period in days	Annual total precip. (mm)	†Potential insolation (W/m^2)
			Annual	July		Frost-free		
Arctic province								
Alert, NWT	82°30'	62°20'	-18.2	3.6	202	27	154.4	175
Resolute, NWT	74°43'	94°59'	-16.6	4.1	249	45	131.4	187
Baker Lake, NWT	64°18'	96°00'	-12.2	11.0	878	90	234.6	217
Boreal province								
Churchill, Man.	59°45'	94°04'	-7.2	11.8	1151	107	402.3	242
Temperate province								
Winnipeg, Man.	49°54'	97°14'	2.6	19.6	2770	170	525.3	283

in Canada) influence the climate and mean July isotherms are not parallel with the latitudes (Figure 1.1).

Biologically, the southern limit of the arctic tundra is now generally associated with the northern limit of the treeline (Aleksandrova, 1980; Murray, 1987; Bliss and Matveyeva, 1992). In North America, the treeline corresponds relatively well with the 10°C mean July isotherm and with the boundaries of the continuous permafrost (Stonehouse, 1989), in Eurasia the relationship is less evident. The treeline may be most closely associated with the median position of the Arctic Front in summer (Barry, 1967; Larsen, 1971; Scott, 1992). The forest-tundra transition zone, just south of the treeline, is sometimes called the Subarctic (Rousseau, 1952; Aleksandrova, 1980; Sirois, 1992). It belongs to the Subarctic Ecoclimatic Province (Ecoregions Working Group, 1989) and represents the northern limit of the boreal biome or Taiga (Bliss and Matveyeva, 1992).

***Tundra biome and vegetation zones*:** The 'tundra biome', as defined during the International Biosphere Program (IBP), refers to "... areas with permafrost, or areas where the temperature is too low, or precipitation and wind too great for a natural forest vegetation, or where in the time for normal regeneration the area has not recovered from razing by man, fire or animals" (Wielgolaski, 1972). This definition includes regions in high mountains (alpine tundra) as well as regions in the Arctic (arctic tundra) and in Antarctica (antarctic tundra). Tundra covers more than 5% of the continents, slightly less than temperate grasslands, but its total annual energy fixation represents only one quarter of this more productive treeless vegetation (Table 1.2).

The arctic tundra biome is vast (7.6×10^6 km^2), covers a variety of landforms and is exposed to a range of climatic conditions promoting the development of distinct vegetation types. The Russian literature is extensive on this subject and Russian authors subdivide the tundra into zones based mostly on floristic and geobotanical characteristics (*e.g.* Gorodkov, 1935; Tikhomirov,

Table 1.2: Land area and net primary production (above- and belowground) of some major vegetation zones of the world. Modified from Lieth (1975).

Vegetation unit	Area (10^6 km^2)	Net primary productivity			Total annual energy fixation (10^{18} cal)
		Range g/m^2/year	Approximate mean	Total production (10^9 t)	
Tropical rain forest	17.0	1000-3500	2000	34.0	139.4
Warm temperate mixed forest	5.0	600-2500	1000	5.0	23.5
Boreal forest	12.0	200-1500	500	6.0	28.8
Chaparral	1.5	250-1500	800	1.2	5.9
Temperate grassland	9.0	100-1500	500	4.5	18.0
Tundra	8.0	100-400	140	1.1	4.8
Deserts	8.5	0-10	3	-	0.1
Others	88			48.4	205.6
Total for continents	149.0		669	100.2	426.1

1960; Aleksandrova, 1960 and 1980; Yurtsev, 1994). Non-Russian researchers divide the arctic tundra into zones based more on climatic and/or edaphic criteria (*e.g.* Young, 1971; Edlund, 1983; Edlund and Alt, 1989). According to Russian authors, the 'Polar desert zone' (Aleksandrova, 1988) or 'High Arctic tundra subzone' (Yurtsev, 1994) is very narrow, limited to the northernmost Russian Islands, the northern tip of Svalbard and Greenland, and the northwestern margin of the Canadian Arctic Archipelago. This would correspond to the bioclimatic zone 1 (herb zone) described by Edlund and Alt (1989). According to this classification, the sparse vegetation observed in most of the Canadian Arctic Archipelago is a depauperate arctic tundra vegetation, due to elevation (Aleksandrova, 1988). In this 'Polar desert zone' the plant cover is discontinuous but on moist, better developed soils 'High Arctic tundras', characterized by a rather high cover of bryophytes, lichens, blue-green algae with scattered cushion plants, are common (Yurtsev, 1994).

In this thesis, I adopted the zonation described by Bliss and Matveyeva (1992) that subdivides the Arctic into High and Low Arctic (Table 1.3). This relatively simple classification is based mostly on density of plant cover and physiognomic characteristics (presence or absence of erect shrubs), and it recognizes a mosaic of vegetation types within each zone (Table 1.3). The delineation between the two zones approximates the 8°C July isotherm in Canada, whereas in Eurasia it is closer to the 4°C July isotherm (Maxwell, 1992). The Low Arctic has longer and warmer growing seasons and more available moisture than the High Arctic (Table 1.1 and 1.3). It encompasses the continental regions above the treeline and the southern-most tip of Baffin Island, Greenland and Novaya Zemlya (Figure 1.1). Colder and dryer conditions of the High Arctic are found in the Canadian and Russian Arctic Archipelago, Svalbard and the northern one-half of Greenland; included also are the Boothia and Melville Peninsulas in Canada, the northern tip of Taymyr Peninsula in Russia and areas around Barrow in Alaska (Figure 1.1).

Table 1.3: Classification of arctic vegetation and general climatic values associated with each zone, according to the North American and Eurasian tradition. Modified from * Bliss and Matveyeva (1992) and from ** French and Slaymaker (1993): [a]Queen Elizabeth Island; [b] Tundra, southern areas; [c] Arctic treeline.

North America* (Bliss, 1975, 1979)		**Eurasia*** (Gorodkov, 1935; Chernov and Matveyeva, 1979)		Climatic values typical of vegetation zones**	
				Mean July Temperature (°C)	Duration of thaw season (days)
ARCTIC TUNDRA BIOME					
High Arctic	**Polar desert** (herb-cryptogam)	**Polar desert Zone**	**Polar desert** (cryptogam-herb)	5	75[a]
	Polar semi-desert (cryptogam-herb, cushion-plant-cryptogam, mire)	**Tundra Zone**	**Arctic tundra** (dwarf-shrub-herb) **Typical tundra** (sedge-dwarf-shrub, polygonal mires)	10	90-120[b]
Low Arctic	**Tundra** (low-shrub-sedge,tussock-dwarf-shrub, mire)		**Southern tundra** (low-shrub-sedge, tussock-dwarf-shrub, mire)	10-13	120-145[c]
BOREAL BIOME					
Taiga	**Forest-tundra**	**Taiga**	**Forest-tundra**	13-15	150-170
	Taiga		**Taiga**	15-18	180-210

In the Low Arctic, low-shrub (*Betula*, *Salix*), dwarf-shrub, cottongrass tussock and wet sedge-moss tundras dominate. Most of the biomass and deposited carbon reserve (90%) are found in this more productive zone (Table 1.4). In the High Arctic, low erect shrubs are absent and the dominant species are cushion plants (*Dryas integrifolia*, *Saxifraga oppositifolia*), prostrate shrubs (*Salix arctica*) and rosette species (*e.g. Saxifraga, Draba, Minuartia*; Bliss and Matveyeva, 1992). The High Arctic represents 35.4% of the ice-free arctic land area (Table 1.4). Plant productivity there is low, and the total standing crop corresponds to less than 9% of the total arctic carbon reserve (Table 1.4).

High arctic vegetation. This classification distinguishes three vegetation types in the High Arctic (Table 1.4), mires, polar semi-deserts (with vascular plant cover from 5 to 20%) and polar deserts (vascular plant cover < 5%; Bliss *et al.*, 1973; Bliss and Svoboda, 1984). The latter two types cover extensive areas (33% of the arctic biome) whereas the high productivity mires (140 g/m^2/year) are scattered on only 2.4% of the arctic land area (Table 1.4). These mires are generally found in 'complex' (Bliss, 1977) with the polar deserts and semi-deserts and they are more common in the southern portion of the High Arctic (Edlund and Alt, 1989; Figure 1.2). High arctic mires are dominated by *Carex stans* and are generally found in arctic oases (Freedman *et al.*, 1994).

In polar deserts and semi-deserts, plant diversity is low and small rosette forbs, cushion plants and few grasses (especially *Puccinellia* spp. and *Phippsia algida*) account for most of the low productivity (1 and 35 g/m^2/year respectively; Table 1.4). Polar deserts have a low standing crop (0.046 kg/m^2; Table 1.4) compared to the polar semi-deserts (2.19 kg/m^2) where bryophytes and lichens are more abundant and may bring the total plant cover > 50% (Bliss *et al.*, 1973).

Table 1.4: Total and relative area, annual net primary production (NPP) and above ground carbon reserves (Total C) of major arctic vegetation types. O.M. indicates organic matter content. Modified from Bliss and Matveyeva (1992); * calculated assuming the world vegetation standing crop is 550 x 10^{15}g according to Eswaran *et al.* (1993).

	AREA		NPP g/m^2	STANDING CROP		
VEGETATION TYPE	Land area $10^6 km^2$	Proportion of biome (%)		O.M. (kg/m^2)	Total C (10^{15} g)	Proportion of biome (%)
Low Arctic	**3.616**	**64.6**			**23.707**	**91.0**
Tall shrub	0.174	3.1	1000	6.20	0.475	1.8
Low shrub	1.282	22.9	375	4.10	2.316	8.9
Tussock, sedge-dwarf shrub	0.922	16.5	225	8.40	3.142	12.1
Mire	0.880	15.7	220	43.31	17.129	65.7
Semi-desert	0.358	6.4	45	4.01	0.645	2.5
High Arctic	**1.984**	**35.4**			**2.353**	**9.0**
Mire	0.132	2.4	140	23.36	1.358	5.2
Semidesert	1.005	17.9	35	2.19	0.978	3.8
Polar desert	0.847	15.1	1	0.046	0.017	0.06
Total Arctic		Proportion of world				Proportion of world*
Land plus ice	**7.567**	**5.1%**				
Ice-free land	**5.600**	**3.8%**			**26.06**	**4.7%**

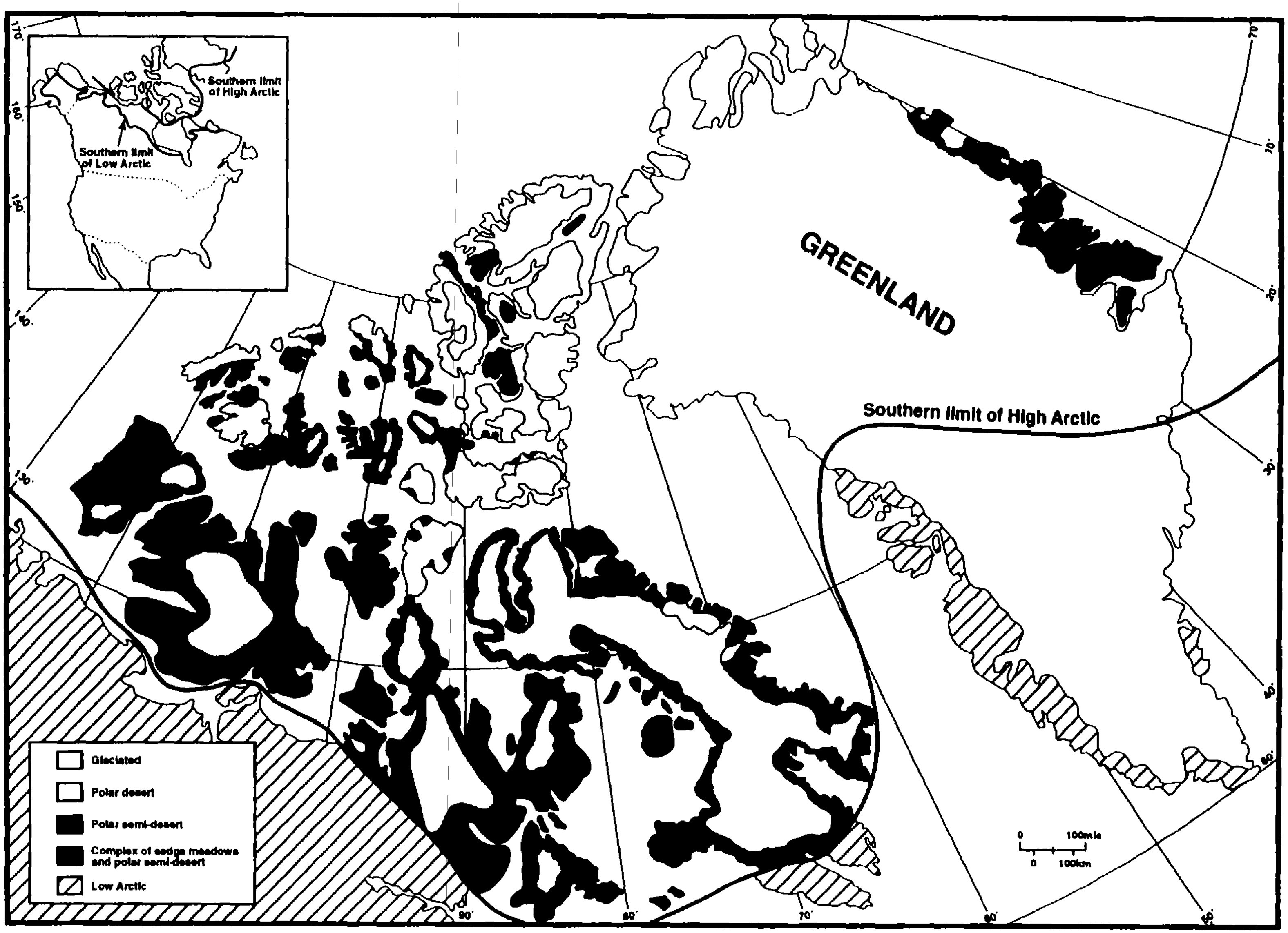

Figure 1.2: Delineation of major vegetation types within the North American High Arctic. Modified from Bliss (1977).

1.2.4 Polar deserts

According to the definition presented above (vascular plant cover < 5%), polar desert vegetation is mostly found in North America (75.6% in Canada and 15.0% in Northern Greenland; Bliss and Matveyeva, 1992). The low representation in the Eurasian region is mostly due to the paucity of ice-free land at the northernmost latitudes (small islands covered in large part by glaciers; Aleksandrova, 1988), and also to the absence of land at very high latitudes in Eurasia (*i.e.* above 75°N; Figure 1.1). It is also important to note that due to higher precipitation (which promotes a more abundant and diverse vegetation, especially bryophytes) and despite cold summer temperatures (Matveyeva, 1994), many Russian 'polar deserts' have higher plant cover and belong, in fact, to the polar semi-desert vegetation type (Bliss and Matveyeva, 1992).

Climate. Far from being uniform, climatic conditions in the High Arctic are affected by mountains, large land masses, proximity to frozen or to open water and by the reflectivity of the land-ocean surface (Maxwell, 1992). For example, mean summer temperatures range from 0.2°C in northernmost Greenland to 5°C on southern Banks Island and annual precipitation is highest on the eastern side of Greenland than elsewhere (Table 1.5). It is also important to note that most of the climatological data available come from low elevation coastal weather stations; inland weather patterns have to be, in large part, extrapolated (Maxwell, 1981).

Overall, the North-American high arctic macroclimate, is characterized by cold and dry conditions, with mean July temperatures around 3-5 °C, annual precipitation 100-150 mm (Maxwell, 1981) and the number of degree-days above 0°C 250-300 (Edlund and Alt, 1989). The majority of the precipitation falls as snow, being highest in the southern regions of the High Arctic and on the eastern side of the Queen Elizabeth Islands (Maxwell, 1981). The western

Table 1.5: Climatic data for high arctic stations. Modified from Bliss and Matveyeva (1992) and from Bay (1992). Mean summer temperature is mean of month of July and August (see Bay, 1992); most values are 10-year averages.

Station (latitude)	Mean temperature °C		Precipitation annual (mm)	Degree-days above 0°C
	Annual	Summer		
USA				
Barrow, AK (71°)	-12.1	3.0	100	288
Canada				
Sachs Harbour, NWT (72°)	-13.6	5.0	103	458
Resolute, NWT (75°)	-16.4	3.6	136	222
Eureka, NWT (80°)	-19.3	4.6	58	318
Alert, NWT (82°)	-18.2	3.6	154	202
Greenland				
Edderfugle Øer, NW (74°)	-10.9	3.0	-	238
Daneborg, NE (74°)	-9.9	3.6	286	285
Thule Air Base, NW (76°)	-11.6	4.2	163	348
Danmarkshavn, NE (76°)	-12.4	3.0	192	237
Station Nord, N (81°)	-17.1	2.3	227	222
Kap Moltke, N (82°)	-15.7	4.2	<25	305
Kap Morris Jesup, N (83°)	-19.0	0.2	-	70
Russia				
Cape Zhelaniya (76°)	-8.3	2.0	128	134
Cape Chelyuskin (78°)	-13.9	1.4	113	117
Max:	-8.3	5.0	286	458
Min:	-19.3	0.2	25	70

margin of the Queen Elizabeth Islands is particularly cold due to the proximity of the ocean ice pack (Figure 1.1).

Polar desert vegetation is most frequently found in the northern part of the High Arctic (Edlund and Alt, 1989; Figure 1.2). It is predominant on exposed, wind swept sites where the snow accumulation is minimal, and on upland sites that are colder due to temperature altitudinal lapse rate (Maxwell, 1981), with short growing seasons. In other studies, few microclimate measurements have been made directly in polar desert vegetation. Climate of upland sites was compared with that of nearby lush and diverse lowlands on Devon Island (Truelove Lowland; Courtin and Labine, 1977; Gold and Bliss, 1995) and Ellesmere Island (Alexandra Fiord; Batten, 1987). Labine (1994) compared the climate of the Alexandra Fiord oasis with polar desert sites near the coast and above the lowland (*ca.* 500 m a.s.l.). Overall, mean temperatures of the polar desert sites were lower, snowmelt was later (by 2 weeks on Devon Plateau; Courtin and Labine, 1977) and re-freeze was earlier (1 week) than in the lowland. Soils warmed up very little during these cold and short growing seasons (Courtin and Labine, 1977). Aleksandrova (1970) defined polar deserts in Russia as areas north of the 2°C mean July isotherm which, according to Courtin and Labine (1977), is too low for the southern limit of high arctic polar deserts.

Vegetation. The physical environment of the High Arctic presents numerous constraints for plant growth, reproduction and establishment (Billings, 1987). However, the Arctic is not uniformly harsh and Murray (1987) warns us not to oversimplify the conditions plants face by assuming a predictable harshness in that environment. Arctic vegetation is well adapted to low temperatures and short growing seasons (Chapin and Shaver, 1985), but polar desert species must also tolerate severe seasonal aridity and extremely limited nutrient supply (Aleksandrova, 1988). According to Bliss and Matveyeva (1992), a small group of approximately 20 vascular species is found on polar deserts; the most common are the cushion plant *Saxifraga oppositifolia*, the small herbs *Papaver radicatum*, *Draba subcapitata*, *Draba corymbosa* and *Minuartia rubella* and the grass, *Puccinellia angustata*. Reproduction by seeds prevails in these unpredictable habitats (Murray, 1987).

In addition to a reduction in floristic diversity, a gradation in vigour and a delay in phenology can be observed between neighbouring polar desert sites and along altitudinal gradients (Chapter 6).

1.3 PLANT COLONIZATION

1.3.1 Characteristics of colonizers

The High Arctic offers vast areas of bare ground to colonization by cyanobacteria, algae, fungi, lichens, mosses and vascular plants. Few flowering plants appear to be able to establish in the polar deserts. What are the characteristics necessary for such organisms to be successful?

Colonization is the first step that every organism must succeed at, in bare as well as in already vegetated habitats (Bazzaz, 1986). Therefore, at one point in its life every organism is a colonizer. For colonization to be successful, a viable seed must meet germination requirements (Fowler, 1985) and the young plant must be able to continue development to the stage of a reproductive adult (Grubb, 1986). The term colonizer, however, is frequently used to refer to those species which disperse over relatively long distances and establish in unoccupied (or partially occupied) habitats (Bazzaz, 1986).

Colonizers that enter intact vegetation, where they were previously unknown, and dominate or displace species within it are sometimes called 'invaders' (Barrett and Richardson, 1986; Bazzaz, 1986). Such species have, so far, been uncommon in arctic tundra, although some 'alien' species are establishing populations near human installations and utilizing, as dispersal corridors, the disturbance created by transportation corridors in the north

(Forbes, 1992). Increasing human activity and climate change may provoke increases or shifts in resource availability that could promote such species invasion (Fox and Fox, 1986), especially in the continental tundra. The remoteness and extreme climatic conditions in the High Arctic, however, make the concern about alien species invasion less pressing. Parts of the polar landscape have been only recently released from ice and primary succession is still occurring (Svoboda and Henry, 1987; Jones, 1997).

Colonizers of primary successions are confronted with two main obstacles, 1) dispersal to a site lacking a buried seed pool and 2) establishment in infertile, often dry sites (Chapin, 1993). Depending on the nature of the newly released habitats, seed source may be local (*e.g.* glacier gravel; Walker *et al.*, 1986) or more distant (*e.g.* volcanic islands; Fridriksson, 1987). Most species which colonize these empty habitats produce numerous, light and wind-dispersed seeds (Fenner, 1987; Stöcklin and Bäumler, 1996). They have minimal dormancy requirements; generally germinating rapidly rather than entering the seed bank (Chapin, 1993). These characteristics contrast with those of species establishing after disturbance, which often spring from a buried seed bank (Fenner, 1987; McGraw *et al.*, 1991). Most of the pioneers of primary successions are long-lived, often slow growing, iteroparous perennials (Gray, 1993), whereas species of secondary succession are short-lived (often annual). They reproduce rapidly, sometimes vegetatively (Loveless and Hamrick, 1984; Bazzaz, 1986).

In addition to an efficient mode of dispersal, pioneer species of primary successions frequently have to tolerate extreme edaphic and climatic conditions (Gray, 1993). Since recently deglaciated sites offer only very coarse soils generally low in nutrients, seedling mortality is frequently high. Water availability is essential for germination and establishment (Stöcklin and Bäumler, 1996).

Microbiota are the primary colonizing group of organisms in most virgin landscapes (Wynn-Williams, 1993). Rocks and lithosols are colonized by phototrophic, chemolithotrophic and heterotrophic microbes which promote weathering and stabilize particle substrata (Wynn-Williams, 1993). Following this initial colonization, cryptogams and vascular plants can establish. Nitrogen-fixing prokaryotes, mostly non-symbiotic organisms, allow higher plants to overcome the chronic nitrogen deficiency in the tundra (Getsen *et al.*, 1997). Lichens have chemical and biological interactions with rocks and soils, whereas mosses may contribute indirectly to physical weathering by penetrating cracks in rocks (Walton, 1993). Vascular plants can invade bare soils as rapidly as mosses and lichens (Cooper, 1939), and sometimes lichens actually take longer to establish (Worsley and Ward, 1974; Fahselt *et al.*, 1988). In the High Arctic, where lichen growth is particularly slow, vascular plants in bloom can be found in areas where the rocks are still almost completely free of lichen (*cf.* Chapter 3). Fahselt *et al.* (1988) estimated a mean time period of 80 years before lichen colonization initiation occurred on bare rock surfaces in Sverdrup Pass, Ellesmere Island.

Woody species are important colonizers in the low arctic (Walker *et al.*, 1986; Chapin, 1993) and alpine (Vetaas, 1994; Stöcklin and Bäumler, 1996) landscapes that have recently become ice-free. Symbiotic nitrogen fixation may be considered to be advantageous in bare habitats, but, partly due to their large seeds, nitrogen-fixers are rarely the first to colonize such sites (Chapin, 1993; Gray, 1993). However, N-fixers (*e.g. Alnus spp.*) become rapidly important in the developing plant communities (Chapin *et al.*, 1994), and tend to be strong competitors (Walker, 1993).

In the High Arctic, seed production is infrequent and seedling establishment rare (Bell and Bliss, 1980). Seedlings of woody species are particularly rare and herbaceous plants are more frequently found on recently deglaciated sites (Jones, 1997). Bliss and Gold (1994) demonstrated the important role of cyanobacteria as nitrogen fixers (mostly *Nostoc* spp.) along a high arctic coastline. However, symbiotic interactions between N-fixing organisms and vascular plants are still poorly know in the High Arctic. The most common forms of such interactions (*i.e.* leguminous-rhizobial symbiosis and root-thickening of graminoid species) are found only in the more diverse and productive plant communities and are rare in the High Arctic (Getsen *et al.*, 1997). The typical woody plants in the tundra (*e.g. Salix* spp., *Dryas integrifolia*) are not symbiotic N-fixers, but they make use of ectomycorrhizal associations to alleviate nitrogen scarcity in arctic soils (Getsen *et al.*, 1997).

Mycorrhizal interactions were documented for a number of prevalent vascular species at Alexandra Fiord, Ellesmere Island (Kohn and Stasovski, 1990). Ectomycorrhizae were found associated with species frequently dominant in polar semi-deserts: *Cassiope tetragona, Dryas integrifolia, Kobresia myosuroides*, *Salix arctica* and *Saxifraga oppositifolia*. Ericoid mycorrhizae were found on roots of *Carex nardina*, *Vaccinium uliginosum*, *Silene acaulis* and also *Cassiope tetragona*.

A number of species, however, appear to be non-mycorrhizal, for example, *Eriophorum scheuchzeri* common in the wet meadows, the cushion plant *Saxifraga tricuspidata* and the herb *Draba lactea* (Kohn and Stasovski, 1990). *Draba corymbosa* and *Papaver radicatum* were also non-mycorrhizal and these species are common on poorly vegetated sites.

In the high arctic polar deserts and semi-deserts, a small group of forbs and a few grasses and wood rushes (*e.g. Phippsia algida*, Grulke, 1995; *Luzula confusa*, Jones, 1997) are the most common vascular colonizers. They all produce a relatively large number of seeds (Savile, 1972; Bell and Bliss, 1980; Grulke and Bliss, 1985; Jones, 1997) and are among the most tolerant vascular species (Bliss and Peterson, 1992). Species with a combined stress tolerator and ruderal strategy (S/R *sensu* Grime, 1979) thus appear the best adapted to colonize bare polar desert sites.

1.3.2 Succession in the tundra biome

The concept of succession was developed mostly for temperate regions. In the Arctic, the relevance of this concept has been questioned (*e.g.* Griggs, 1934; Raup, 1951). Churchill and Hanson (1958) reviewed the literature and concluded that directional changes, both successional and retrogressional, occur in arctic and alpine area. Detailed studies of vegetation establishment and its changes in the regions formerly glaciated have demonstrated that succession has occurred (Larsen, 1971; Nichols, 1976; Ritchie, 1984) and continues to occur in the alpine and arctic tundra (Cooper, 1939; Walker *et al.*, 1986; Matthews and Whittaker, 1987; Vetaas, 1994; Jones, 1997). Most of the work done in the Arctic has been on primary succession following recent glacial retreat. Studies of secondary succession following natural or anthropogenic disturbances, especially in the High Arctic, are relatively recent (Babb and Bliss, 1974; Forbes, 1993 and 1996).

Connell and Slatyer (1977) proposed three models of succession: the facilitation, tolerance and inhibition models. All three models suggest strong influence of biotic interactions on successional processes. The facilitation model implies that the first established species favourably condition the environment for the later-arriving species; a typical example of the facilitation model is the primary succession. The tolerance model was proposed for not too severe environments where the species most efficient at utilizing limited resources become established and outlive the early colonizers. Finally, the inhibition model implies that the first species to occupy the space dominate the habitat (disregarding the relative competitivity of the species). A slow replacement occurs naturally in disturbances created by the death of individuals and, over time, long lived species become dominant.

Matthews and Whittaker (1987) reviewed the numerous studies done near the Storbreen glacier in Norway. They concluded that a functional model of plant succession should incorporate environmental changes. They stress that the environment changes rapidly on recently deglaciated lands. These authors suggest that the decline of pioneer species may be related more directly to the changes in environmental conditions than to biotic interactions as proposed by Connell and Slatyer (1977). After a number of field experiments, Chapin *et al.* (1994) concluded that no one single mechanism can account fully for primary succession and that the importance of different mechanisms will depend on resource availability and environmental severity.

Field studies in primary succession are numerous in the low arctic tundra and in the alpine tundra. The species and the environmental conditions there are very different from what occurs in polar deserts. Matthews and Whittaker (1987); Bliss and Peterson (1992); Miles and Walton (1993) and Chapin *et al.* (1994) have given detailed information on the subject.

High arctic primary succession. Svoboda and Henry (1987) proposed that depending on the resistance of the environment, three models could be developed (Figure 1.3). These models may not be restricted to the High Arctic, as Bliss and Peterson (1992) demonstrated, but they are very relevant for polar desert vegetation. In low resistance environments, as those described by Connell and Slatyer (1977), the succession would be directional and replacement would occur in time (Figure 1.3A). In severe environments there would be gradual increase in plant abundance but not to the point that species would be replaced ('directional non-replacement succession'; Figure 1.3B). Finally in extreme habitats (as in polar deserts), some species may establish and maintain their presence (*e.g.* species 'a'; Figure 1.3C), whereas most others would be unsuccessful (*e.g.* species 'b,c,d'; Figure 1.3C). The community would reach a state of 'non-directional non-replacement succession' (Figure 1.3C).

In addition to the environmental constraints, time is also an important element in these models. Svoboda and Henry (1987) proposed an index of relative successional potential (RSP): $\mathrm{RSP} = \mathrm{Y}n \times i\mathrm{Y} \times j\mathrm{DG}$, where $\mathrm{Y}n$ represents the number of years since deglaciation; $i\mathrm{Y}$ is the fraction of the year

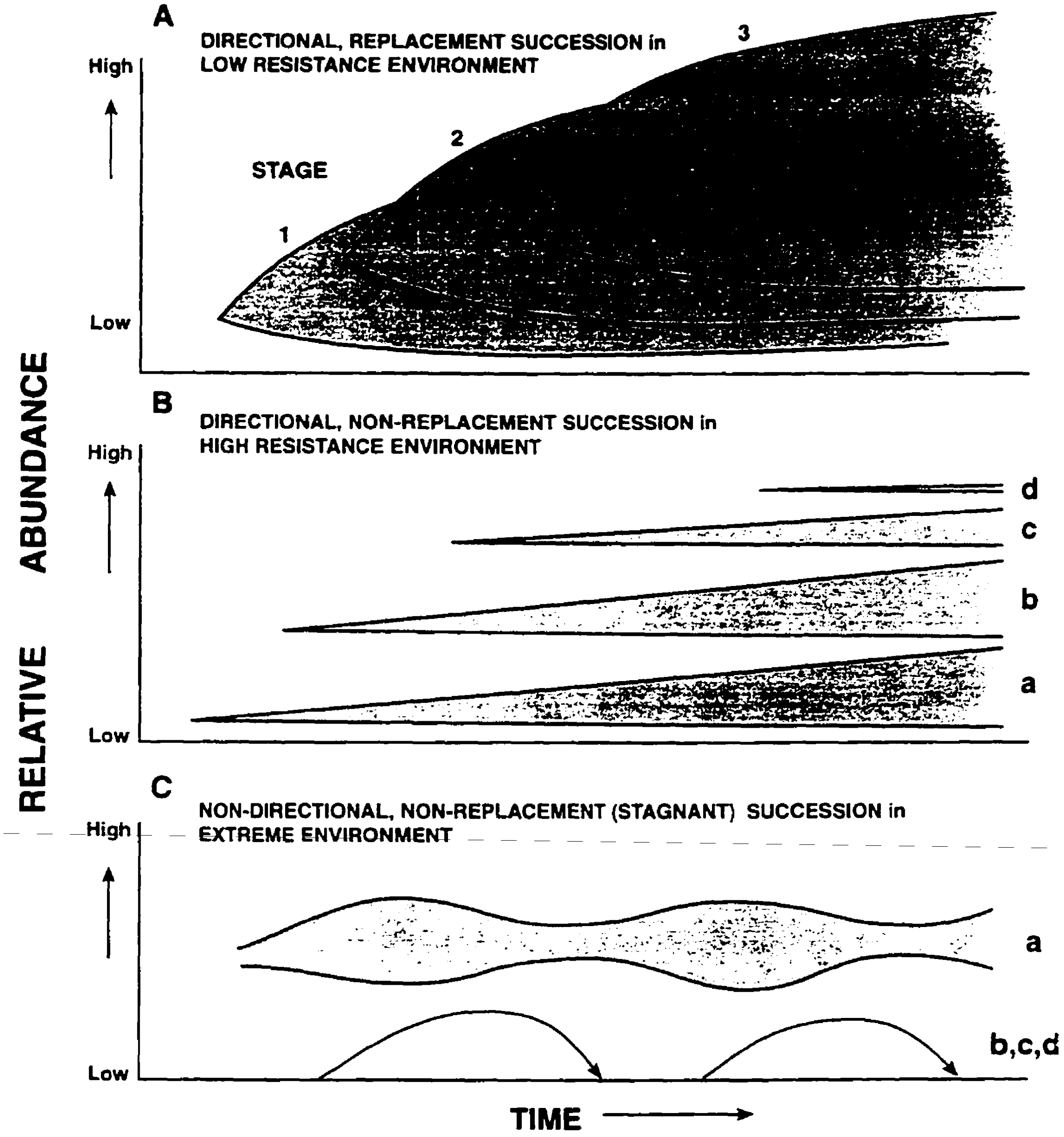

Figure 1.3: Schematic representation of succession models Directional, replacement succession in a low resistance environment (A); Directional non-replacement succession in a high resistance environment (B) and Non-directional, non-replacement succession in an extremely resistant environment (C). Modified from Svoboda and Henry (1987).

representing the growing season; and *j*DG is the ratio of the mean thawing degree-days of the growing season and the optimal value for that vegetation type. Young sites and cold sites would have the lowest RSP compared to older and warmer sites. Bliss and Peterson (1992) proposed a simplification to this equation to reflect only the favourableness of the present climate. They called their index 'IPS' index of potential succession: IPS = *i*Y x TDD, where *i*Y is as in the previous equation; and TDD represents the growing season thawing degree-days.

In the less stressful habitats of the High Arctic, a gradual replacement of early successional species has been described in coastal habitats (Bliss and Gold, 1994) and at the margin of a retreating glacier (Jones, 1997). These correspond well to the model suggested by Svoboda and Henry (1987). According to Bliss and Peterson (1992), in polar semi-deserts, succession has not been studied in detail, but evidence from various sources indicate that the slow build-up of plants on such sites corresponds to the second model of succession presented by Svoboda and Henry (1987; Figure 1.3B). Cryptogam crusts of lichens, cyanobacteria, and mosses would establish prior to the vascular plants in the semi-deserts (Bliss and Peterson, 1992).

In extreme polar deserts, few species would establish new individuals and many plants would not be able to maintain themselves on the site resulting in a non-directional, non-replacement succession (Figure 1.3C). It is expected that very little plant growth would take place, except where more moisture is available and cyanobacteria and cryptogamic crusts can develop (*e.g.* snow flush communities; Bliss and Peterson, 1992). Colonizers of extremely inhospitable sites have particularly low relative growth rates (Chapin, 1993). No studies have investigated succession in the polar desert. It has been suggested that in addition to the environmental constraints limiting plant survival, a low seed rain and few 'safe sites' may limit plant community development in polar deserts (Svoboda and Henry, 1987; Walker, 1995).

1.4 OVERALL OBJECTIVES

The present vegetation of the High Arctic grows in a periglacial environment; it is still under glacial influence and the ground is permanently frozen. As much as 38% of the total land area of the High Arctic is still covered by glaciers (Bliss and Matveyeva, 1992). It has also been affected by recent cold climatic anomalies (the latest was the Little Ice Age, A.D. 1550 to 1850; Bray, 1968) during which glaciers and persistent snow patches increased in size and destroyed the underlying plant communities. Today, 43% of the deglaciated High Arctic is covered by polar desert vegetation, where lichen and moss cover are minimal and vascular plant cover is less than 5%. The vegetation of these vast areas is poorly known and the primary objectives of my work were to sample and describe the vegetation of polar deserts across a broad geographical range, and to study the species composition and abundance in relation to environmental characteristics.

Secondary objectives were to investigate the extent to which polar desert sites typically have limited plant cover because they are relatively young (in an early stage of succession) and if there were indications of the development of richer plant assemblages over time. Svoboda and Henry (1987) suggest a 'non-directional non-replacement' model for succession in extreme environments where only a few species survive while others may invade repetitively without permanent establishment. This theoretical model applies particularly well to polar desert vegetation, but two important premises of this hypothesis have not yet been investigated; the availability of 'safe sites' (favourable collecting places where propagules can successfully establish; Harper, 1977) and the magnitude of the meagre seed rain (supply of propagules, produced on site or imported from distant sources).

Three possible hypotheses which account for the limited plant cover and low species diversity in these polar deserts can be outlined as follows:

1) Polar deserts have extremely low plant cover because there are only a few 'safe sites' available for colonization. Those sites, where conditions are suitable for plant establishment, have all been colonized.

2) There is insufficient quantity of viable seeds available, either through seed set on site or through seed import, to fill the available safe sites.

3) The slow rate of colonization has not yet allowed the establishment of extensive plant assemblages and cover. It is possible that these areas are still in an early stage of succession after deglaciation.

Three studies that contribute to the general knowledge of plant communities, population dynamics and species response to multi-year environmental variation will be used to examine these three hypotheses. The detailed study of the spatial distribution of plants in relation to microtopography will be used to estimate the likelihood that availability of 'safe sites' is limiting to community development in polar deserts. Direct measurements of seed banks have provided information on the availability of seeds in these habitats. Long term microclimate measurements and phenological studies on 13 sites along two altitudinal gradients will give important information necessary to determine the 'relative successional potential' (RSP; *sensu* Svoboda and Henry, 1987) and the 'index of potential succession' (IPS; *sensu* Bliss and Peterson, 1992).

This multifaceted study of the geographical and altitudinal distribution of polar desert plant communities, and of their relationship with substrate and climate characteristics, has been used to formulate a theory of the limits of vascular plant tolerance and the rate of plant colonization after deglaciation in the Canadian High Arctic.

1.5 ORGANIZATION OF THE THESIS

1.5.1 Outline of thesis chapters

In order to address questions on the distribution of plants and plant communities in diverse polar landscapes, the exploration of a wide range of sites was important. It was also critical to select the most efficient sampling method since vegetation was scarce and sites could be visited only briefly.

In Chapter 2, I have addressed the problem of sampling in sparse, low cover vegetation. I have established the minimum sampling area required in polar desert vegetation stands to record vegetation. I also developed and tested a cover-abundance scale that is easy to use and is more precise than the usual scales. This approach was used in the survey of the polar desert sites presented in Chapter 3.

In Chapter 3, I have presented and discussed the species diversity and abundance found in a total of 82 polar desert sites across the central portion of Ellesmere Island, Canada. The importance of environmental and spatial factors and a relationship of 'vegetated' (*i.e.* with vascular plants) and 'bare' sites with environmental characteristics (elevation, soil chemistry and texture) have also been studied by using several multivariate techniques. This large scale survey, the first of such a magnitude which has been attempted, draws attention to plant diversity found at various polar desert sites as well as to the importance of key factors (the elevation and the substrate).

Chapter 4 and 5 explore two of the three aspects thought to be limiting to plant establishment in polar deserts: the availability of vacant 'safe sites' (*sensu* Harper, 1977) and the abundance of viable seeds. Chapter 4 describes microscale distributional pattern of plants in relation to microtopography. It also deals with the question of plant clumping to test if this is due to intrinsic or extrinsic factors. This study allowed me to determine if vacant suitable sites for plant establishment existed, and enabled me to quantify the importance of this factor on plant community development in a polar desert stand. Chapter 5, provides data on germinable seed banks at 14 sites. This study was the first of its kind attempted in polar deserts. The presence of viable seeds in soils of such extreme sites suggests that seed availability is not as limiting as previously thought. Information extracted from these two chapters is also valuable to assess the probable time frame for some studied polar desert sites since they became ice-free.

Chapter 6 presents an analysis of the flowering phenology and standing crop of one of the major polar desert species, *Papaver radicatum*, along two altitudinal gradients over four growing seasons. The relationship between annual climate patterns and the *Papaver* growth and phenology are analyzed in the context of climate change. The range of conditions measured in this study provides valuable information that contributes to the interpretation of the large scale distribution of plants in polar desert by quantifying microclimate variation and plant performance. The controlling role of temperature and growing season length on tundra vegetation are generally recognized, but rarely can it be measured concurrently at such a broad range of sites.

Chapter 7 synthesizes the results of Chapters 2 to 5. The information pertinent to the successional models was combined to compare the successional potential of some polar desert sites with other published results and to assess the relevance of the succession model proposed by Svoboda and Henry (1987).

Finally, seven Appendices complement the work.

1.6.2 List of publications

Three chapters of this thesis have been already published (Chapter 2, 5 and 6). Chapters 3 and 4 will be submitted for publication in refereed journals following the thesis defense. Except for Chapter 2, where I am the sole author, my supervisor, Dr. J. Svoboda was or will be a co-author. The contribution of additional co-authors is listed below in relation to the appropriate article. Only minor modifications of the published papers were made to standardize and improve the flow of the thesis.

CHAPTER 2: Lévesque, E. 1996. Minimum area and cover-abundance scales as applied to polar desert vegetation. Arctic and Alpine Research **28**:156-162.

CHAPTER 3: Lévesque, E., and J. Svoboda. Plant communities of the polar desert on Ellesmere Island. Ready to be submitted.

CHAPTER 4: Lévesque, E., A.P. Kwiecien, and J. Svoboda. Microscale distribution of plants and microtopography in a polar desert site, central Ellesmere Island, Canada. Ready to be submitted.

Part of the development of the vegetation and microtopography maps of a polar desert plateau was an undergraduate honours thesis project of A.P. Kwiecien carried out under my guidance. I expanded on his work to perform more complex analyses on the spatial distribution of plants.

CHAPTER 5: Lévesque, E., and J. Svoboda, 1995. Germinable seed banks from polar desert stands, central Ellesmere Island, Canada. Pages 97-107 *in* T.V. Callaghan, U. Molau, M.J. Tyson, J.I. Holten, W.C. Oechel, T. Gilmanov, B. Maxwell, B. Sveinbjörrnsson, editors. Global change and arctic terrestrial ecosystems. Ecosystems research report 10, European Commission, Luxembourg.

An expanded version of this paper was translated to Russian and published in Botanicheskii Zhurnal (Botanical Journal of the Russian Academy of Science). I thank Dr. N.V. Matveyeva from the Komarov Institute in St-

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Petersburg (Russia) for her enthusiasm, encouragements and expert translation and editing of this article .

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CHAPTER 6: Lévesque, E., G.H.R. Henry, and J. Svoboda, 1997. Phenological and growth responses of *Papaver radicatum* along altitudinal gradients in the Canadian High Arctic. Global Change Biology, In Press.

Dr. G.H.R. Henry provided the multi-year microclimate data that was used to extrapolate site-specific information that I collected in 1990. I also consulted with him on the statistical approaches and on the presentation of the manuscript.

CHAPTER 2:

MINIMUM AREA AND COVER-ABUNDANCE SCALES AS APPLIED TO POLAR DESERT VEGETATION

2.1 ABSTRACT

Polar desert vegetation with 5% cover or less was measured on terraces and a plateau surrounding Sverdrup Pass (79°N), central Ellesmere Island, NWT, Canada. The aim of the study was to determine the most efficient method for plant diversity and cover assessment in extremely sparse polar desert plant communities. Minimum area was measured based on, independently, the nested plot and the random quadrat techniques in five polar desert stands. The Species Diversity:Area relationship (S/A) was best described by the Fisher logarithmic model. The minimum area determined for the stands ranged from 10 to 25 m^2. The total vascular species diversity among the sites varied from 6 to 22. Cover values, precisely measured by the grid-quadrat technique, were transformed to four abundance scales: Braun-Blanquet, Domin-Krajina, and two further refinements of Domin-Krajina scale. These modifications were designed to increase the resolution in the low-cover portion of the scale, and substantially improved the accuracy of the cover determination, with only a 10 to 25% proportional overestimation. The author suggests that the use of a modified Domin-Krajina abundance scale in a stratified random sampling of an area at least equal to the minimum area. This allows for a more expedient, yet still adequately accurate, assessment of the extremely low cover of vegetation and

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ensures that minute plants will not be overlooked or their cover grossly overestimated.

2.2 INTRODUCTION

Polar deserts and semi-deserts represent more than 95% of the ice-free land area of the Canadian High Arctic (Bliss *et al.*, 1973). Expensive logistics, short-growing seasons, and inaccessibility of many sites make large-scale assessments of vegetation diversity and abundance a difficult task. Many remote sites might be visited only once and then for only a few hours. To ensure that vegetation data collected from such sites are accurate, yet obtained in an affordable time, great care has to be given to the choice of the assessment method.

Depending on the aims of the study, the presence or absence of the various species can be an adequate descriptor of the local vegetation. But for some investigations the assessment of cover and biomass, or of importance values of the species present may be necessary. In polar deserts, it is not unusual to find a few large plants of *Saxifraga oppositifolia* among several hundreds of tiny *Draba* sp. individuals (*cf.* Chapter 4). In such a case, the frequency estimates would suggest that *Draba* is the dominant species and the importance of the few *Saxifraga* individuals, which often represent most of the site's biomass, could be underestimated.

Only a few studies have been done on sampling approaches in the High Arctic. For examples, Wein and Rencz (1976) compared the accuracy and efficiency of various sampling methods used in studies of arctic vegetation, and Jonasson (1988) discussed the advantages of the point intercept method for the estimation of plant biomass. Wein and Rencz (1976) concluded that the most efficient techniques of plant cover assessment in the high arctic tundra were color-positive slides and the point intercept method. Unfortunately, in the case of extremely sparse polar desert vegetation both recommended techniques are impractical. Minute plants are difficult (if not impossible) to locate and correctly identify on slides even when projected on a screen. The point intercept method would also be impractical on such sites, because the interception of tiny individuals would be rare and would require thousands of measurements. Our field experience shows that the quadrat technique is still the best tool for determination of cover in polar desert vegetation.

As in many other plant communities, it is difficult to decide how many replicates and how large an area should be sampled to obtain a reasonably accurate data set. Wein and Rencz (1976) stated that polar deserts are 10 times more variable than wet meadows and suggest that more than 100 quadrats (0.25 m^2) per stand are needed to achieve acceptable accuracy of plant cover. Matveyeva (1988) proposed a total of 16 m^2 as a minimum area for the frequently occurring species in a frost boil landscape of the Russian polar desert. The minimum area of polar desert vegetation has not been systematically assessed before.

Abundance scales have been used extensively to describe vegetation in reasonable time and with little disturbance (Mueller-Dombois and Ellenberg, 1974; Londo, 1976). van der Maarel (1979) discusses the possible transformations of a number of scales to optimize the numerical treatment of such data. In his analysis, using both the classification and ordination approaches, van der Maarel (1979) obtained the best description of the vegetation when he used data with an intermediate weighting of presence and dominance. Of concern is the difficulty of transforming and interpreting the low cover values that are often only roughly estimated by the most commonly used scales. This is especially critical in the case of polar deserts where the estimation of cover of numerous yet minute and sparse individuals can be so time consuming that an insufficient area ends up being sampled, or only presence or absence of species is attempted.

In this paper, I address the technical aspects of the field sampling of a very sparse polar desert vegetation. As a first step, the minimum area necessary for accurate sampling of polar desert stands of central Ellesmere Island was determined, to establish a reference that could be used when sampling an area with a sparse, low cover vegetation. In addition, I present a new modified cover-abundance scale. This scale allows a more expedient cover estimate than could be obtained by the standard quadrat technique, and a more precise estimate of cover than the traditional cover-abundance scales would yield at the low cover end of these scales.

2.3 METHODS

2.3.1 Study sites

Sverdrup Pass (79°08'N, 81°27'W), a 75-km-long deglaciated east-west valley, is a polar oasis in central Ellesmere Island, NWT (Figure 2.1). This atypically 'lush' valley is bordered by extensive polar desert slopes and uplands. On the south side are granitic outcrops and moraines, topped with the Beitstad ice cap, whereas dolomitic scree slopes, cliffs and plateaus and the Benedict ice cap are on the north side. A total of 75 vascular plant species were identified in the Pass (Bergeron and Svoboda, 1989) of which less than 30 species are common to the moraines and 5 to 10 species to the uplands. These are predominantly perennial herbs (*e.g.*, *Saxifraga oppositifolia*, *Papaver radicatum*, and a few *Draba* species), grasses and sedges (mostly *Poa abbreviata*, *Puccinellia bruggemannii*, and *Carex nardina*) and woody species (*Salix arctica* and *Dryas integrifolia*). Five polar desert stands with approximately 5% vascular plant cover or less were selected on step-like terraces and a plateau at Sverdrup Pass (Table 2.1). Three were on a granitic north-facing substrate (G1 at 347 m; G3 at 443 m; and G4 at 461 m a.s.l.) and two on a dolomitic south-facing substrate (D2 at 336 m; and D6 at 765 m a.s.l.). Each stand had different vegetation and habitat characteristics which represented a range of typical polar

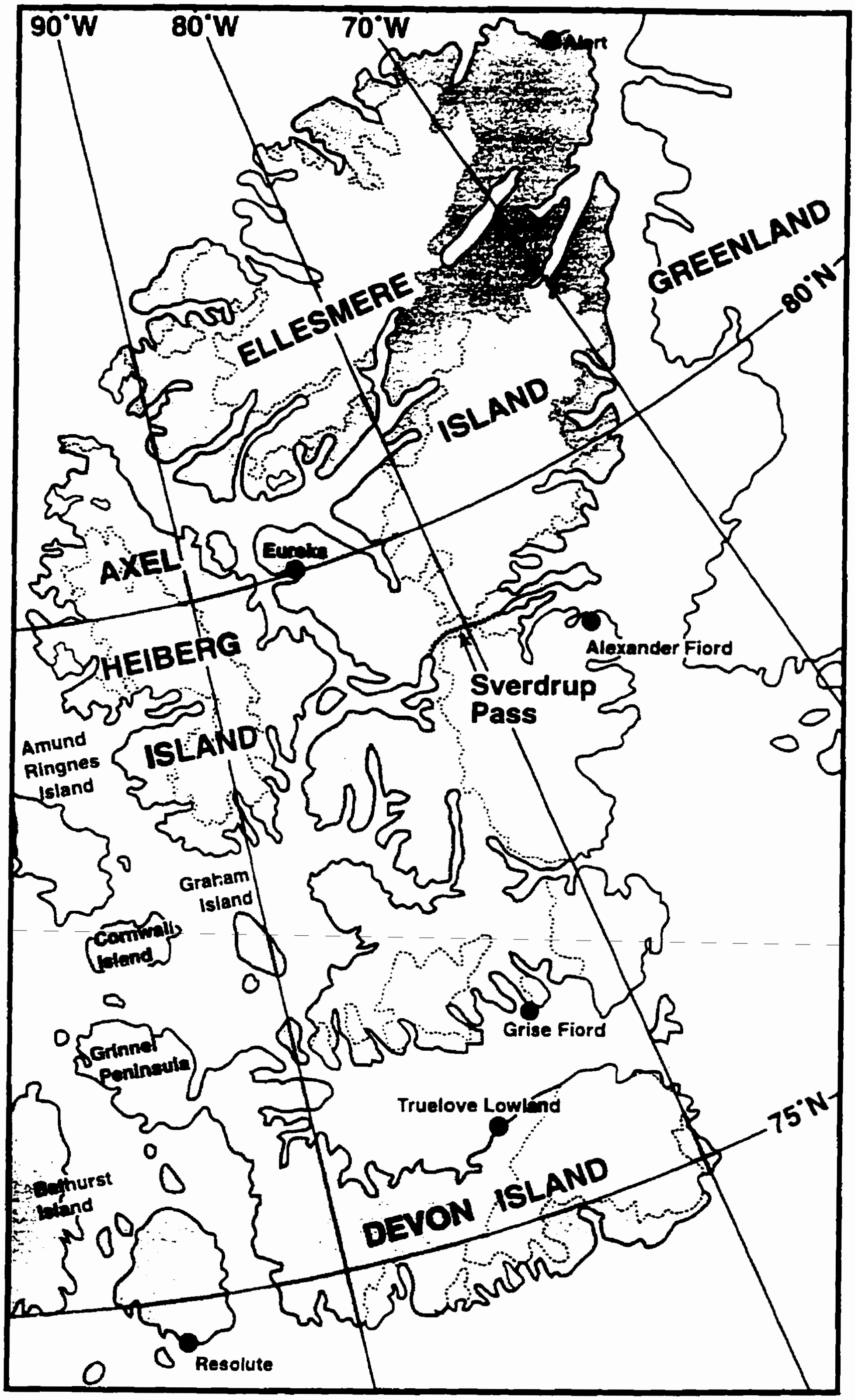


Figure 2.1: Location of study site in the central portion of Sverdrup Pass, Ellesmere Island (79°08'N, 81°27'W). Modified from Svoboda and Freedman (1994).

Table 2.1: Habitat characteristics of the five polar desert sites studied in Sverdrup Pass, Ellesmere Island.

Site	Altitude (m a.s.l.)	Habitat	Cover (%)[a]		Major species
			a	b	
Granitic sites					
G1	347	Granitic N-facing moraine	6.69	6.72	*Saxifraga tricuspidata*
G3	443	Near snow bed, good soil	5.70	5.74	*Carex nardina* + *Poa arctica*
G4	461	Flat plateau mixed gravel	7.23	7.26	*Salix arctica* + *Dryas integrifolia*
Dolomitic sites					
D2	336	Flat and exposed dolomitic gravel	0.32	0.33	*Puccinellia bruggemannii* + *Dryas integrifolia*
D6	765	Poorly sorted polygons, dolomitic rock and gravel	0.16	0.19	*Draba subcapitata* + *Saxifraga oppositifolia*

[a] Total plant cover of the site excluding (a) and including (b) the bryophyte and macrolichen cover (%).

desert situations in that area. The contribution of bryophytes and macrolichens to the total plant cover was minimal in all cases (Table 2.1).

In stands G1 and G3, numerous granitic boulders created pockets suitable for the accumulation of sandy soil and thus these stands were better suited for plant growth. In addition, stand G3 was wind protected from east winds by a small ridge. Late melting snow along this ridge was a source of a continuous moisture supply during the first half of the growing season. As a result, this stand had the largest species diversity of the five stands studied (Plate 2.1). In close proximity to G3, stand G4 was located on a large terrace covered by a mixture of dolomitic and granitic gravel. This rather homogenous stand was characterized by the presence of sparse but large individuals of *S. arctica*, *S. oppositifolia*, and *D. integrifolia* (Table 2.1; Plate 2.2).

Although the dolomitic stands were south-facing, they were more exposed to wind, had lower surface temperature (substrate with higher heat capacity and higher albedo than on the granitic stands) and consequently had shorter growing seasons (Lévesque *et al.*, 1997). Flowering occurred later and leaf development and stem elongation were inferior in those dolomitic stands than in the slightly darker and warmer granitic stands (see an example for *Papaver*, Lévesque and Svoboda, 1992). Both stands D2 and D6 had very limited plant cover (< 1%). Stand D2 was close to the valley bottom. This windswept stand had very few boulders and cracks which would offer protection to plants (Plate 2.3), whereas D6 was situated on a plateau characterized by frost-shattered rocks and frost boils (Table 2.1; Plate 2.4). Small herbs were the most common life form here in contrast to D2 which also had grasses and cushion plants.

2.3.2 Plant cover measurement

Plant cover in 30 randomly placed 50 cm x 50 cm quadrats with a 5 cm x 5 cm grid was measured using direct determination of area, in the five polar desert stands described above in summer 1990. In order to determine the

Plate 2.1: Site G3 showing the relatively high cover of *Carex nardina/Kobresia myosuroides*; this site was part of the studied granitic altitudinal gradient at Sverdrup Pass, Ellesmere Island.

Plate 2.2: Site G4 of the altitudinal gradient with large *Salix arctica* and *Dryas integrifolia* plants growing in a mixed substrate of dolomitic and granitic gravels, Sverdrup Pass, Ellesmere Island.

Plate 2.3: Site D2 of the dolomitic altitudinal gradient at Sverdrup Pass, Ellesmere Island.

Plate 2.4: Site D6 at the top of the dolomitic altitudinal gradient, a large wind swept dolomitic plateau on the north side of Sverdrup Pass, Ellesmere Island.

precise cover for each species, an additional 10 cm x 10 cm 'reference quadrat' with a 0.5 cm x 0.5 cm grid was overlaid on the 50 cm x 50 cm quadrat whenever a plant smaller than the 5 cm x 5 cm grid was present. This allowed determination of the individual species cover with 0.01% precision. The nomenclature of vascular species generally follows Porsild and Cody (1980), exceptions are specified in Appendix 1.

2.3.3 Minimum area determination

Mueller-Dombois and Ellenberg (1974) define the 'minimal area' as the smallest area on which a community's species composition is adequately represented. These authors suggest that this concept can be used to determine the size of the area to be sampled when variations in species diversity as well as when quantitative variation of species abundance need to be studied. More recently, Barkman (1989) defined the methodological minimum area as the size of sample plots necessary to get a representative picture of the phytocoenosis. The term minimum area will be used in this paper to refer to the methodological minimum area, as defined by Barkman (1989), in the context suggested by Mueller-Dombois and Ellenberg (1974) to help determine the minimum size requirement for plant community sampling.

To find the minimum area, a series of nested plots was used in stands G1, G4, and D6 in 1991 and in G3 and D2 in 1993. Starting with 25 cm x 25 cm plots, a list of the vascular species present was compiled. The plot size was doubled repetitively and the area enlargement followed a spiral. Newly encountered species were added to the list until no additional species were found in two consecutive plot sizes (Mueller-Dombois and Ellenberg, 1974). The number of species (S) was then plotted against the plot size or area (A) and against the log of A.

Although commonly used, the nested plot technique has been criticized for having a number of shortcomings, namely, for the sampling procedure, the limited range of sample plot sizes, the insufficient number of observations per plot size and the dependence between nested quadrats (Dietvorst *et al.*, 1982; Barkman, 1989). To avoid these objections, two sites (G4 and D6) were resampled in 1993 using the method suggested by Barkman (1989). Quadrats of increasing sizes were randomly placed in the stand: 10 quadrats of 0.125, 0.25, and 0.50 m^2; five quadrats of 1, 2, 4, and 8 m^2; two quadrats of 16, 32, and 64 m^2; and one quadrat of 128 m^2. The number of species recorded within replicates for each plot size was averaged, and as before, S was plotted against the area and the log of A. Due to bad weather conditions during the sampling of D6, only three replicates of 4 m^2, 2 of 8 m^2, and one of 32 m^2 were sampled.

A number of equations have been presented to describe the general relationship between increasing species number with increasing area sampled (Arrhenius, 1921; Gleason, 1922, 1925; Fisher *et al.*, 1943; Goodall, 1952, 1961; Dahl, 1960; Preston, 1962). Barkman (1989) evaluated three models describing the Species diversity:Area relationship (S/A): two are logarithmic relations (Goodall-Dahl and Fisher) and one is an exponential relation between S and A (Arrhenius-Preston; Table 2.2). According to Hopkins (1955), Barkman (1968, cited by Barkman, 1989) and Royackers and Rothuizen (1975, cited by Barkman, 1989), the Fisher model describes best the S/A of most plant communities. However, in his more recent paper Barkman (1989) suggested that species-poor systems might be better described by the Goodall-Dahl relationship. Since the present data set was composed uniquely of species-poor stands, the performance of the three models was assessed and compared to test the validity of Barkman's suggestion. The best-fit curves were constructed, using SigmaPlot 4.1 (1991), to accommodate the three models for each site and sampling method. The source of variation was calculated using the regression and residual sums of squares, and the nonlinear regression was tested with an F statistic (Zar, 1984). The derivatives of these equations are presented in Table 2.2.

Table 2.2: Theoretical models and derivative of the relationship between species number (S) and plot size (A).

Model	Equation	Derivative
Goodall-Dahl	$S = p * \log (A+1)$	$\frac{dS}{dA} = \frac{p * \log e}{A+1}$
Arrhenius-Preston	$S = k * A^{z}$	$\frac{dS}{dA} = z * k * A^{z-1}$
Fisher	$S = a * \ln (1 + \frac{c*A}{a})$	$\frac{dS}{dA} = \frac{a*c}{a + c*A}$

Where p, c, a, k and z are constants. Modified from Barkman (1989).

The analysis of the S/A is also critical for the relevance of the minimum area estimate. Traditionally, the point of maximum curvature of the curve was used to determine minimum area. However, this point was assessed visually and thus was dependent on the ratio of the axes used (Cain, 1938). Every S/A graph may then have more than one point of maximum curvature. Since these points can only be visualized one at a time on a nonlogarithmic scale (Barkman, 1989), it is impossible to use this technique reliably. As discussed previously, the relationship between species and area can be described by a continually increasing function. The point of interest, where an increase in area yields a minimal increase in new species (*i.e.* where the slope starts to flatten), can not be easily described mathematically. Kilburn (1966) suggests to use the derivative of the curve, substituting a predetermined slope for dS/dA in order to calculate the optimum area to be sampled. Inevitably, the slope values chosen will vary from one community to the next and even for the purposes of the study. Kilburn (1966) suggests that an arbitrary standard sampling point could be determined by using a predetermined slope as a criterion.

The need for such a criterion is recognized widely and has been discussed in the literature (Dietvorst *et al.*, 1982; Barkman, 1989). In this study, to determine the size of methodological minimum area, I will use three criteria. First, the point along the curve at which a 10% increase in total sampling area yields only 10% more species (Cain, 1938; Mueller-Dombois and Ellenberg, 1974). To get an even more conservative estimate, the slope of a 5% increase in total species number for a 10% increase in area was calculated for each site. The minimum area was then obtained by resolving the derivative when dS/dA was replaced by the slope at 10% and at 5%. The third criterion was the area at which 80% of the species present on the site had been sampled. This was determined by resolving the Fisher equation when Y equals 80% of the total species diversity. The first method has the advantage of referring to the rate of species increase in relation to area and does not imply a prior knowledge of the total flora as does the second method (Barkman, 1989).

2.3.4 Application of cover-abundance scales

To compare and test the suitability of the abundance scales, the cover data obtained from exact quadrat readings were transformed into class values for the four abundance scales. Two of these scales were the original Braun-Blanquet and the Domin-Krajina scales as presented by Mueller-Dombois and Ellenberg (1974), and two were Domin-Krajina scales that I modified to increase resolution at the low percentage end of the scale (Table 2.3). For example, a plant having a measured cover of 0.4%, was assigned a value of 1 in the Braun-Blanquet scale, of 2 in the Domin-Krajina scale, of 1 in the modified scale-A and of 2, in the modified scale-B (Table 2.3). Each site's total plant cover estimates were then calculated by using class mid-point values for each species within each quadrat. Class mid-point assumes a symmetrical distribution of plant size frequencies within each class by giving the mean value of the class to any plant within the class. In the previous example, the corresponding class mid-point values are 2.5, 0.5, 0.25, and 0.35% for the four scales respectively. The percentage of proportional overestimation was calculated by dividing the difference between the measured cover and the estimated cover by the measured cover value.

To demonstrate the applicability of the cover-abundance scale in the field, in 1993, the cover of each species in 10 randomly placed 50 cm x 50 cm quadrats was first assessed using the modified scale A and then measured using the fine reference quadrat to a 0.01% precision in four of the five polar desert stands (G3, G4, D2 and D6).

Table 2.3: Cover percentage and corresponding values in cover-abundance scales

Measured Cover (%)	Cover-Abundance Scales			
	Braun-Blanquet Scale[a]	Domin-Krajina Scale[a]	Modified Domin-Krajina Scale-A[b]	Modified Domin-Krajina Scale-B[b]
0 - 0.2	1	2	1	1
0.2 - 0.5				2
0.5 - 1			2	3
1 - 2		3	3	4
2 - 5			4	5
5 - 10	2	4	5	6
10 - 25		5	6	7
25 - 33	3	6	7	8
33 - 50		7		
50 - 75	4	8	8	9
> 75	5	9	9	10
100		10		

[a] Mueller-Dombois and Ellenberg (1974); [b] modified by the author.

2.4 RESULTS AND DISCUSSION

2.4.1 Minimum area

A total of 391.75 m^2 (D6) and 435.75 m^2 (G4) was sampled by random quadrats, and a total of 64 m^2 (G1 and D6) and 128 m^2 (G3, G4 and D2) was sampled using the nested plot technique. The vascular species richness was low in the five polar desert stands: 14, 22, and 12 species for G1, G3, and G4; and 9 and 7 species for D2 and D6 stands, respectively (Table 2.4). The increase in diversity in relation to the increase of the area sampled is presented in Figure 2.2. The use of the two different sampling techniques gave very similar curves for both the G4 and D6 stands. Rare species are more likely to be encountered when sampling a larger area. For example, one small specimen of *Saxifraga cernua* and one of *Minuartia rubella* were found on D6 during the random quadrats sampling.

When the best-fit curves were constructed by using the data, in all cases, the Fisher relation produced a regression with the smallest unexplained portion (minimal Residual Sums of Squares) and thus with the largest F value (Table 2.5; all the P-values were very small, << 0.01). The Goodall-Dahl model, contrary to what was expected, did not describe more adequately the S/A relationship in these species-poor sites. In fact, even the exponential model of Arrhenius-Preston (suggested to be more appropriate for large heterogeneous areas; Barkman, 1989) generated smaller residual sums of squares than the Goodall-Dahl model. Figure 2.3 illustrates the type of fit obtained by the three models on the G1 data set.

The Fisher model equation and derivatives were thus used to determine the minimum area of the studied sites based on their respective coefficients and the three criteria (Table 2.6). The 10% criterion was the slope of a line from the origin to a point where 10% increase in species corresponds to the 10% increase in area. This is where m (the slope) equals the total number of species

Table 2.4: Species presence in the five polar desert sites studied in Sverdrup Pass, Ellesmere Island. [1] indicates very rare species on this site.

	Site				
Species	G1	G3	G4	D2	D6
Draba alpina	x				
Potentilla pulchella	x				
Stellaria longipes		x			
Cassiope tetragona		x[1]			
Melandrium affine		x			
Festuca hyperborea		x			
Luzula arctica		x			
Poa arctica		x			
Saxifraga cernua		x[1]			x[1]
Saxifraga caespitosa		x			
Saxifraga tricuspidata	x	x			
Erysimum pallasii	x	x			
Carex misandra	x	x			
Carex nardina/Kobresia myosuroides	x	x	x		
Draba cinerea	x	x	x		
Draba oblongata	x	x	x		
Poa abbreviata	x	x	x	x	
Dryas integrifolia	x	x	x	x	
Minuartia rubella	x	x	x	x	x[1]
Saxifraga oppositifolia	x	x	x	x	x
Draba subcapitata	x	x	x	x	x
Papaver radicatum	x	x		x	x
Draba corymbosa		x	x	x	x
Puccinellia bruggemannii		x	x	x	
Braya purpurascens			x	x	
Salix arctica			x		
Phippsia algida					x
Species Richness	14	22	12	9	7

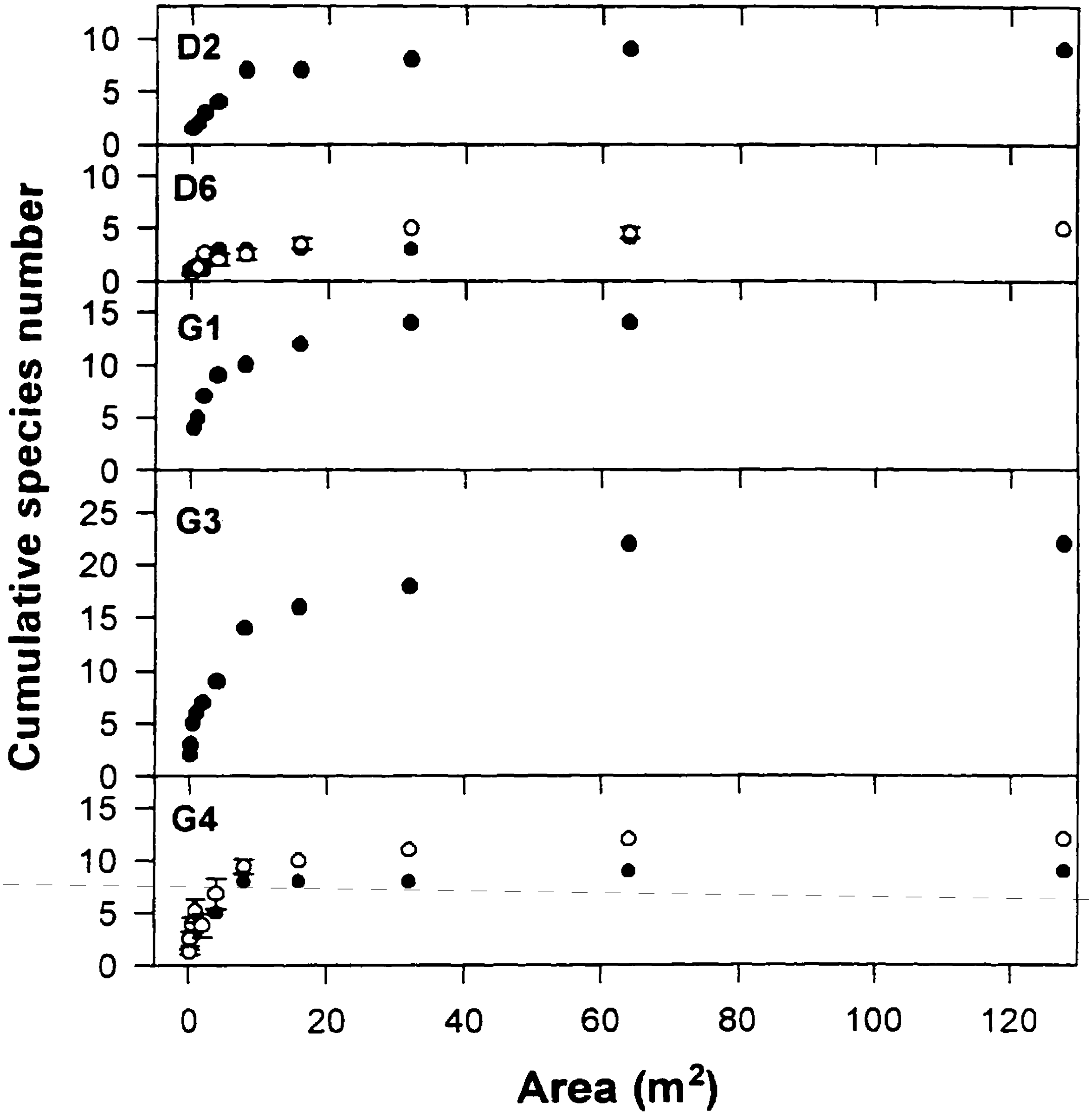


Figure 2.2: Vascular plant species diversity (Cumulative species number) as a function of the plot size (m^2) sampled in five polar desert plant communities: two stands at dolomitic sites (D2 and D6) and three stands at granitic sites (G1, G3, and G4), in Sverdrup Pass, Ellesmere Island. Sampling with the nested plots technique (●); random sampling with quadrats (○): error bars represent the standard error.

Table 2.5: F values from the evaluation of the Species-to-Area relationship using the three models for the five polar desert sites studied in Sverdrup Pass, Ellesmere Island.

Site	Regression DF	Residual DF	Goodall-Dahl	Fisher	Arrhenius-Preston
Granitic sites					
G1[a]	1	8	188	3442	749
G3[a]	1	9	424	1833	626
G4[a]	1	9	134	698	427
G4[b]	1	9	141	818	384
Dolomitic sites					
D2[a]	1	9	309	768	365
D6[a]	1	8	110	231	195
D6[b]	1	9	174	450	388

[a] Species diversity was sampled using the nested plot technique and [b] using the random quadrats technique. $p << 0.001$ for all sites and all models.

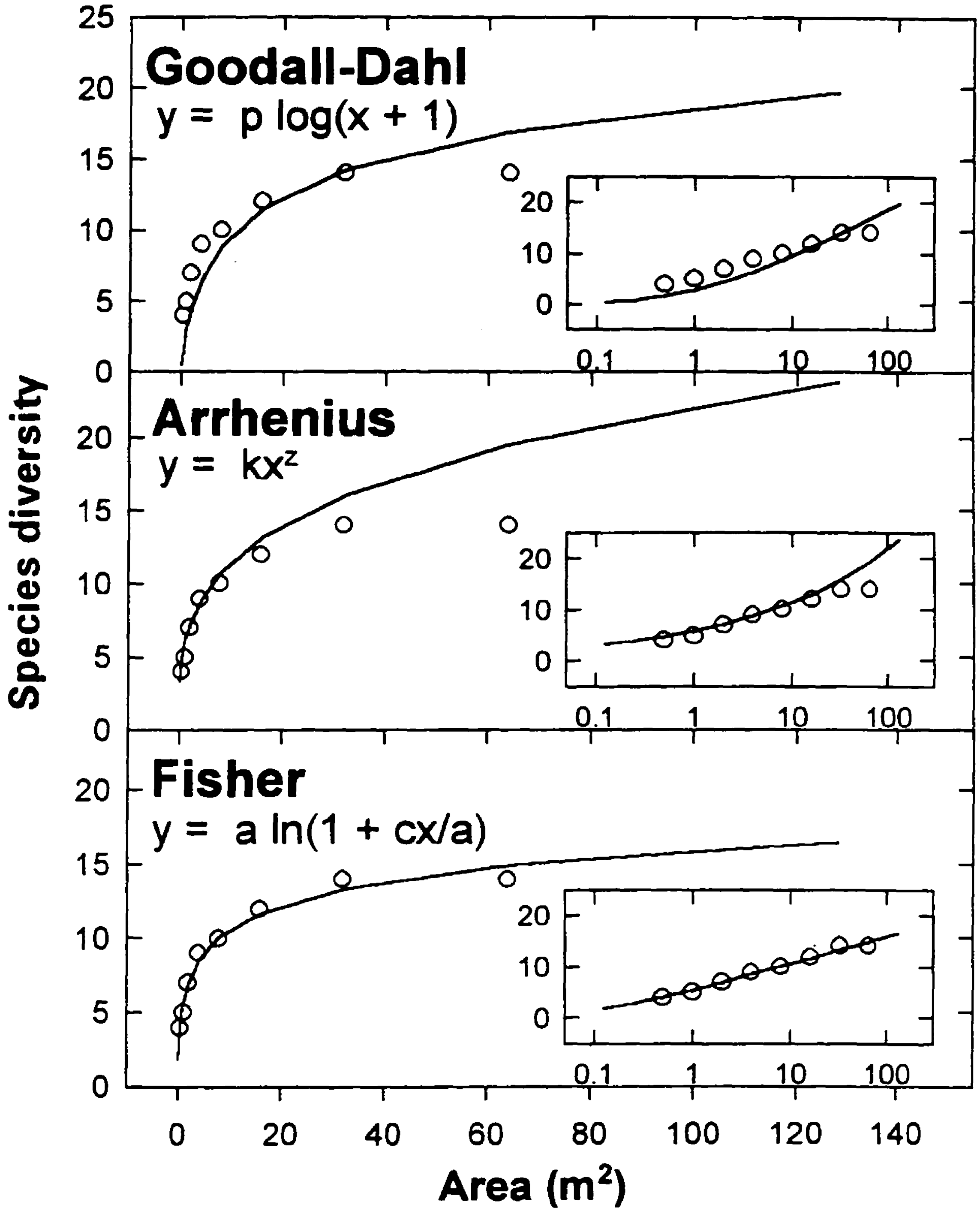


Figure 2.3: Species diversity:Area relationships (S/A) and best-fit curve established for the Goodall-Dahl, Arrhenius, and Fisher models for the polar desert site G1, sampled with nested plots technique. The inserted diagrams show the relationship of species diversity with the log of the area.

Table 2.6: Methodological minimum area (m^2) in five polar desert sites studied in Sverdrup Pass, Ellesmere Island.

Sites	Equation Coefficients		Minimum Area (m^2)		
	a	c	10%[c]	5%[c]	80%[c]
Granitic sites					
G1[a]	2.32	22.44	10.5	21.1	12.8
G3[a]	3.70	15.12	10.5	21.3	28.2
G4[a]	1.29	21.45	9.1	18.3	15.9
G4[b]	1.76	22.65	9.3	18.7	18.1
Dolomitic sites					
D2[a]	1.56	6.84	10.9	21.9	22.8
D6[a]	0.62	4.95	9.9	19.8	21.7
D6[b]	0.72	8.27	9.3	18.7	22.4

[a] Species diversity sampled using the nested plot technique and [b] using the random quadrats technique. [c]The minimum areas were calculated from the Fisher Model of the Species-to-Area relationship (see Table 2.3) using the equation coefficients (a and c) and three discriminating criteria: 10% and 5% species increase per 10% increase in area sampled and 80% of total species diversity.

sampled, divided by the area at which that diversity was first measured. The 5% increase slope was calculated the same way, based on half the species sampled, divided by the same total area. The 80% criterion was the point at which the Fisher equation equals 80% of the total number of species found on the site.

At 10 and 5% accuracy levels, the calculated minimum area was similar for all the sites studied (Table 2.6). The largest minimum area was estimated for the D2 site and the smallest for the G4 site (10.9 vs 9.1 m^2 at 10% slope, and 21.9 vs 18.3 m^2 at 5% slope respectively). There was more variation in the area determined using the 80% of the total flora criterion, with site G3 having the largest estimate (28.2 m^2) and site G1 the smallest (12.8 m^2; Table 2.6). The minimum area estimate seemed more sensitive to the total number of species present at a site when this last criterion was used but, overall, the homogeneity of the distribution of plants had more influence on the size of the minimal area. The sampling method used did not noticeably influence the minimum area. Using either criterion, the more thorough random quadrat sampling confirms that in polar desert stands, sampling of 10 to 25 m^2 is necessary to represent adequately the species composition of a plant community.

After an extensive sampling of a range of arctic vegetation types along a latitudinal gradient of the Taimyr Peninsula in Russia, Matveyeva (1995) recommends sampling of 5 m x 5 m area in heterogenous communities and 3 m x 3 m in homogeneous communities. These areas were found sufficient to encompass the dominant species as well as rarer species with a high fidelity (Matveyeva 1995, pers. comm.). Matveyeva's conclusions, achieved independently yet empirically in very different community types, support the finding of this study which recommends the use of 10-25 m^2 minimum area for sparsely vegetated stands.

2.4.2 Cover measurements

The vascular plant cover of the five sites, as precisely measured by the quadrat technique and as transformed into four abundance scales, are presented in Table 2.7. The cover accuracy of the transformed values increased with the use of the modified scales. Use of the original Braun-Blanquet scale resulted in up to 600% proportional overestimation, and of the Domin-Krajina scale in up to 100%. Transformations to modified Domin-Krajina scales A and B generated cover values much closer to the directly measured ones, resulting in an overestimate of only 25 to 36%. The lower the vegetation cover (as in D2 and D6 stands), the more inaccurate were the transformed values, especially with unmodified scales. For vegetation stands with larger individuals representing most of the total cover (as in G4) the discrepancy between the directly measured cover and that obtained by the application of the scales was smaller. This was related to the use of the class mid-point to extrapolate the total cover which assumes a normal distribution of points within each class. The closer the distribution of sizes per class is to the normal curve, the better the estimate. In scattered vegetation typical of polar deserts, the distribution is skewed towards the lower end of the scale (Figure 2.4), which explains the better estimates produced with the modified scales.

The field testing of the modified Domin-Krajina scale A showed that the correspondence between its cover assessment and results obtained by direct measurements using the fine grid quadrat was very good. Out of the 40 quadrats sampled, 104 species-quadrat combinations were measured. Of these subjective applications of the modified scale only two were incorrectly assessed, and these were borderline cases at the class limit (Figure 2.4). This scale may therefore be reliably used in the field. Using this technique, in 3-4 hours, I was able to assess the cover in more than 60 quadrats (50 cm x 50 cm) compared to only 20-30 when measured by the precise grid-quadrats cover technique.

Table 2.7: Total vascular plant cover from five polar desert sites studied in Sverdrup Pass, Ellesmere Island.

	Mean Cover (%)				
Sites	Measured in the field[a]	Braun-Blanquet[b]	Domin-Krajina[b]	Modified Domin-Krajina-A[b]	Modified Domin-Krajina-B[b]
Granitic sites					
G1	6.7	13.1 (96)	8.3 (24)	7.5 (12)	7.4 (11)
G3	5.7	13.9 (144)	7.4 (29)	6.4 (12)	6.1 (8)
G4	7.2	10.1 (40)	7.9 (10)	7.5 (4)	7.4 (3)
Dolomitic sites					
D2	0.3	1.6 (398)	0.6 (78)	0.4 (36)	0.4 (18)
D6	0.2	1.4 (600)	0.4 (100)	0.3 (25)	0.2 (10)

[a] Cover accurately measured by grid-quadrat technique in the field; [b] Cover calculated from the field data using the class mid-point value for the two traditional and the two modified Abundance Scales. Proportional overestimation in parentheses.

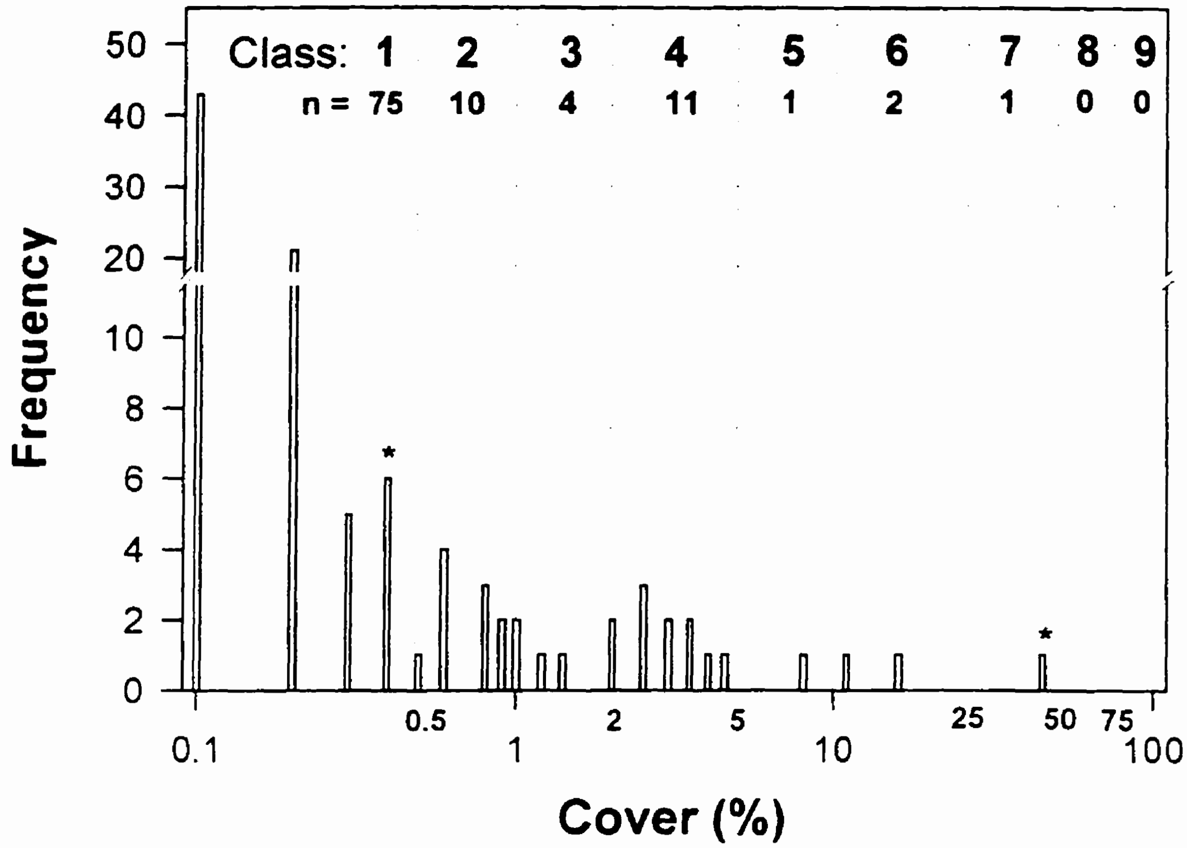


Figure 2.4: Frequency distribution of the total of 104 plants encountered in 40 quadrats, per size-class, as first assessed by the modified Domin-Krajina scale A and then re-measured by the grid-quadrat technique in the same quadrats (50 cm x 50 cm; n = 40). Each asterisk indicates where one individual had been erroneously assessed in a higher class than it belonged.

2.5 CONCLUSIONS

Expediency (speed of obtaining an adequate data set) is a major concern in large scale polar vegetation studies. Plant cover assessment by the use of the modified Domin-Krajina scale A (Table 2.3) in situations with very low plant cover is therefore recommended. Although the finer B-scale (10 cover classes) led to higher accuracy, the extra effort in obtaining the data may not be justified by the marginal gain, except in particular studies where there is a need to measure plant cover with high precision. In this case, however, the effort would be comparable to the application of the direct cover measurement technique.

For cover and frequency measurements in polar deserts, stratified random sampling seems to be the most appropriate approach. The minute size of plants in these extreme environments requires a meticulous survey of every quadrat or plot. A larger number of smaller, randomly placed quadrats *(e.g.* at least 40-60, 50 cm x 50 cm quadrats) allows for more objective, reliable and manageable estimates than the survey of fewer larger plots. The total area covered by the quadrats should be at least equal to the calculated minimum area to adequately document the species diversity and that of plant cover.

CHAPTER 3:

PLANT COMMUNITIES OF THE POLAR DESERT ON ELLESMERE ISLAND

3.1 ABSTRACT

Polar deserts, with < 5% plant cover, are often considered barren, *i.e.* devoid of plants. In fact polar deserts support a persistent vegetation. After a survey of 82 sites, a complete analysis of the environmental characteristics of 45 'vegetated' and 13 'barren' (no vascular plants) upland sites on Ellesmere Island, 80° N, Canada, revealed no differences between the barren and the vegetated sites using Multivariate Discriminant Analysis (MDA) of soil characteristics (pH, P, K, Ca, organic matter and texture) and microtopography (stoniness and roughness). Although not statistically significant, elevation was the single most important factor which distinguished the two groups of sites.

A TWINSPAN classification of 38 of the vegetated sites using 39 vascular species revealed distinct groupings. The first axis reflected differences in species abundance while the second axis showed differences in rock types (carbonate *vs* granite). A constrained ordination analysis (CCA) explained 67% of the variance. Partial CCAs were used to partition the variance into five predictors (geographical location, 5%; elevation, 5%; biological, 11%; soil chemical, 13%; and soil physical variables, 16%), and in two-way (8%) and three-way (9%) interactions. Elevation was again the most important predictor of species distribution along the first axis which explained 14.1% of the variance. Time availability for community development (since snow/ice release) and plant

In collaboration with Josef Svoboda

density (indicating establishment success), determined in large part the observed distributions.

3.2 INTRODUCTION

Permanently frozen ground and large expanses covered by glaciers indicate that the polar regions are still under glacial influence. Half of Ellesmere Island, the northernmost island in Canada, is covered by permanent ice sheets (Bliss *et al.*, 1973; Plate 3.1); remnants of past glaciations. Clearly visible 'lichen kill' zones (Plate 3.2) are common in this mountainous landscape and indicate where permanent snow and ice had been lying until relatively recently (Bergsma *et al.*, 1984). Vascular plants, bryophytes and lichens are becoming established as ice retreats (Maycock and Fahselt, 1992; Jones, 1997) but, even so, the majority of the landscape exhibits sparse plant cover.

Today's climate in the High Arctic is cold and dry (Maxwell, 1981) and growing seasons are short (Edlund and Alt, 1989). Vegetation at these high latitudes has interested botanists since the earliest expeditions in the 1800's. Simmons (1907) had produced the first flora of 'Ellesmereland' early in the 20th century. However, the interior of most islands remained very poorly known (Simmons, 1913, p. 26) until relatively recently. Intensive botanical research was first conducted in the more productive high arctic oases (Bliss, 1977; Freedman *et al.*, 1994) and coastal lowlands where animal and human activities were more extensive (Barrett and Teeri, 1973; Forbes, 1993). Botanical interest has increased and research has now begun to focus on the ecology of these simple, marginal ecosystems (Bliss and Svoboda, 1984; Aleksandrova, 1988; Bliss *et al.*, 1994; Gold and Bliss, 1995).

The vast extent of poorly vegetated high arctic landscapes in North America have been described as polar deserts (*i.e.* with vascular plant cover < 5%) and polar semi-deserts (vascular plant cover from 5 to 20%; Bliss *et al.*, 1973; Bliss and Svoboda, 1984). Polar deserts are generally dominated by

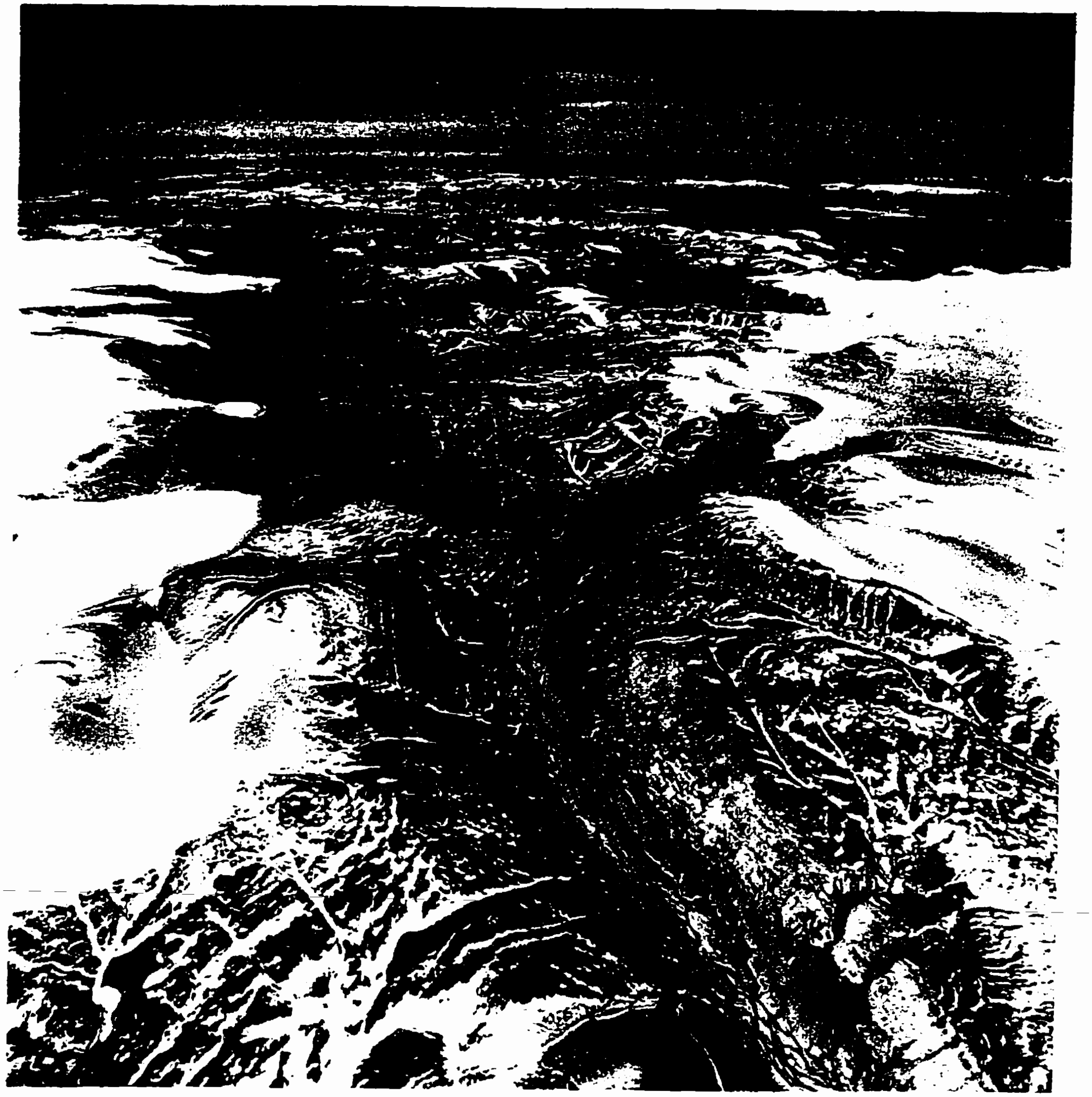


Plate 3.1: Aerial photograph of the central and western portion of Sverdrup Pass, 79°15'N, Ellesmere Island showing characteristic mountainous landscape with Irene Bay in the upper left corner. The east-west oriented valley is bordered to the north by the Benedict icefield (right) and to the south by the Beitstad icefield (left). Notice the darker coloured granitic substrate on the south side (left of the picture) and the lighter carbonate bedrock on the north side of the valley. Photograph # T508R-41, Energy, Mines and Resources Canada, July 1959.

Plate 3.2: Granitic upland and mountain slopes showing extensive light coloured 'lichen-kill' zones (a result of Little Ice Age ice/snow cover), contrasting with the darker pre-LIA lichen-covered landscape at Sverdrup Pass, Ellesmere Island.

small rosette forbs, cushion plants and few grasses (especially *Puccinellia* spp and *Phippsia algida*). Bryophytes and lichens are more important in polar semi-deserts and may bring the total cover > 50% (Bliss *et al.*, 1973). Both habitats have low to very low plant diversity and productivity (Wielgolaski, 1975; Svoboda, 1977;.Bliss and Svoboda, 1984; Bliss *et al.*, 1984). Globally these barren lands represent 33% of the Arctic landmasses (*i.e.* approx. 1 850 000 km^2; about 46% for polar deserts and 54% for polar semi-deserts; Bliss and Matveyeva, 1992). The biomass of the standing crop represents < 4% of the total carbon reserve present in arctic vegetation (Bliss and Matveyeva,1992).

Russian 'polar deserts' are often more diverse than North-American polar deserts (Bliss and Matveyeva, 1992; Matveyeva, 1994). They would fall into a category of polar semi-deserts according to North-American criteria (Bliss *et al.*, 1973). Despite cold summer temperatures (mean July temperature 2°C), the northern tip of the Taymyr Peninsula supports 50 vascular taxa, and a high moss and lichen diversity and cover (Matveyeva, 1994). Higher precipitation in the Eurasian Arctic partially explains these differences (Bliss and Matveyeva, 1992). The fact that Taymyr is connected to a large continent (Matveyeva, 1994) and that no record exists of severe impact of the last glaciation or of permanent snow cover during the most recent climatic cooling (the Little Ice Age, 1550-1850 AD; Bray, 1968), probably also favoured the development of more complex communities (Aleksandrova, 1960).

Low temperatures and short growing seasons limit all biological productivity at high latitudes (Bliss, 1977). In addition, moisture availability, nutrient limitations and disturbance due to freeze thaw cycles may hinder plant development (Billings, 1987). Across broad environmental gradients, a number of studies have classified high arctic vegetation in Canada (*e.g.* Sheard and Geale, 1983a, Bliss *et al.* 1984, Bergeron and Svoboda 1989), Greenland (Bay, 1992), Svalbard (Elvebakk, 1985) and Russia (Matveyeva, 1994). They have recognized plant communities which included snow flush, meadows, semi-desert and polar desert habitats. Batten (1987) identified seven plant communities in the uplands near Alexandra Fiord Lowland, most of which would belong to the general polar semi-desert group (*sensu* Bliss *et al.*, 1973). Within the sparsely vegetated polar deserts, most authors do not attempt to distinguish community types (*e.g.* Bliss *et al.*, 1984). Low diversity of vascular species and the almost ubiquitous nature of most species present at such barren localities limit these analyses. The diversity of bryophytes and lichens is much higher, but their cover is also low (Maycock and Fahselt, 1992) and their distribution is largely restricted to areas with relatively high moisture availability (Gold and Bliss, 1995). In such areas, a thin crust layer of lichens, cyanobacteria and fungi forms on the soil surface and this slows down evaporation and favours plant growth (Gold and Bliss, 1995).

The importance of moisture availability in terms of arctic and alpine plant distribution and on distinctions among community types is generally recognized (Chapin and Shaver, 1985; Bergeron and Svoboda, 1989; Bay, 1992; Walker *et al.*, 1994). Polar deserts receive very little precipitation (100 - 150 mm/year on Ellesmere Island; Maxwell, 1981) and surface droughts occur frequently. Lack of moisture may prevent germination or limit seedling establishment (Stöcklin and Bäumler, 1996) but has little effect on plant growth. In a study of water limitations in polar deserts, Gold and Bliss (1995) found that soil water potentials remained, in effect, saturated throughout the growing season and adult plants showed no indication of water stress, even at midday.

In a recent study of 19 polar desert stands along two altitudinal gradients on Devon and Ellesmere Islands, the major controlling factors of plant distribution were temperature, duration of moist soil surfaces, soil nutrients and the degree of soil churning (Bliss *et al.*, 1994). These authors also mentioned that some species showed substrate specificity. This is in agreement with Elvebakk's studies in Svalbard (1983 and 1985) and with the classification and zonation of vegetation based on type of geological substrate as developed in Canada by Edlund (1983).

Bliss *et al.* (1994) found a major difference between the two locations investigated. Alexandra Fiord sites at Ellesmere Island showed less diversity than the sites near Truelove Lowland at Devon Island. This suggested a possible influence of seed source availability or of other spatial constraints.

Finally, sites which have been more recently released from snow or ice have poor recruitment, which results in a very low plant cover (Bell and Bliss, 1980; Sohlberg and Bliss, 1984; Bliss *et al.*, 1994). These sites may be considered to be still in an early phase of succession. Due to the ecological marginality of these habitats, Svoboda and Henry (1987) proposed a succession/retrogression model where few species establish and maintain themselves on a site while others occur sporadically but die off before establishing viable populations.

How do factors such as environmental characteristics, geographical location and time since release from snow/ice affect the distribution of plants in polar deserts? Do these marginal landscapes support a simple, depauperate, yet homogenous plant community? Or are they mosaics of diverse communities as are found in other ecosystems? And, in the context of global change, are they in a state of expanding development or of steady state survival, and will this state change? To understand the constraints on plant community development in polar deserts, a thorough knowledge of plant distribution and diversity is imperative. For instance: 1) are the detectable variations among sites due to species diversity, plant cover or density; 2) are any environmental variations such as substrate, moisture or geographical barriers (remoteness of a seed source) influencing the species composition; 3) is the time elapsed since the onset of the development of these communities the most decisive factor in explaining the variations in plant diversity and abundance? In other words, is the diversity only a reflection of site age?

A suitable large scale survey of polar desert habitats facilitates description of the diversity or homogeneity of the plant communities and enables them to be related to environmental characteristics. Such an extensive survey leads to hypothesis formulation regarding the mechanisms of vegetation dynamics these can be addressed by further intensive studies, including experimental approaches (Carleton and MacLellan, 1994).

This paper presents the results of the survey of a total of 82 polar desert sites. Presence/absence and abundances of vascular plants are compared to variations in environmental variables. The study was conducted in the central portion of Ellesmere Island, from 75°N to 81°N, Canada.

The first descriptions of the flora of Ellesmere Island were made during successive expeditions in the late 1800's (Hart, 1880; Simmons, 1907; 1913). Since then, investigations of the flora and vegetation have continued (Polunin, 1948; Bruggemann and Calder, 1953; Brassard, 1968; Brassard and Longton, 1970) and detailed studies of polar oases were carried out at Alexandra Fiord, 78°53'N, (Henry, 1987; Freedman *et al.*, 1994; Muc *et al.*, 1994a), Sverdrup Pass, 79°08'N (Bergeron and Svoboda, 1989; Raillard, 1992; Murray, 1991), Hot Weather Creek, 79°58'N (Edlund *et al.*, 1990) and further north around Lake Hazen 81°49'N (Powell, 1961; Savile, 1964; Kevan, 1972; Gould, 1985). Some studies have described plant establishment as the glaciers retreated (Fahselt *et al.*, 1988; Jones, 1997), while others described the polar desert and semi-desert plant communities near Alexandra Fiord (Batten, 1987; Batten and Svoboda, 1994, Bliss *et al.*, 1994); at Princess Marie Bay 79°27'N (Desrosiers, 1991) and at Sverdrup Pass (Maycock and Fahselt, 1992). These preliminary studies provided much background information for the more extensive survey described here.

The specific objectives of the study were: 1) to describe the vegetation of a wide range of polar deserts, mostly on uplands sites; 2) to determine if there are major environmental limitations to plant growth on 'barren' sites; 3) to attempt a classification of the vegetation into distinct communities; 4) to test if the differences between any communities are primarily due to differences in substrate as suggested by Elvebakk (1985); and 5) to evaluate how much of the variance in the vegetation data set can be attributed to the geographical location, elevation and/or to specific environmental variables.

The presented study is largely descriptive. However, it is ground breaking, as it presents novel information on the nature, structure and distribution of plant communities in polar landscapes not covered in depth by any other previous work. This information could be useful in interpreting past climatic variation and in predicting vegetation responses to the ongoing climate change in polar regions.

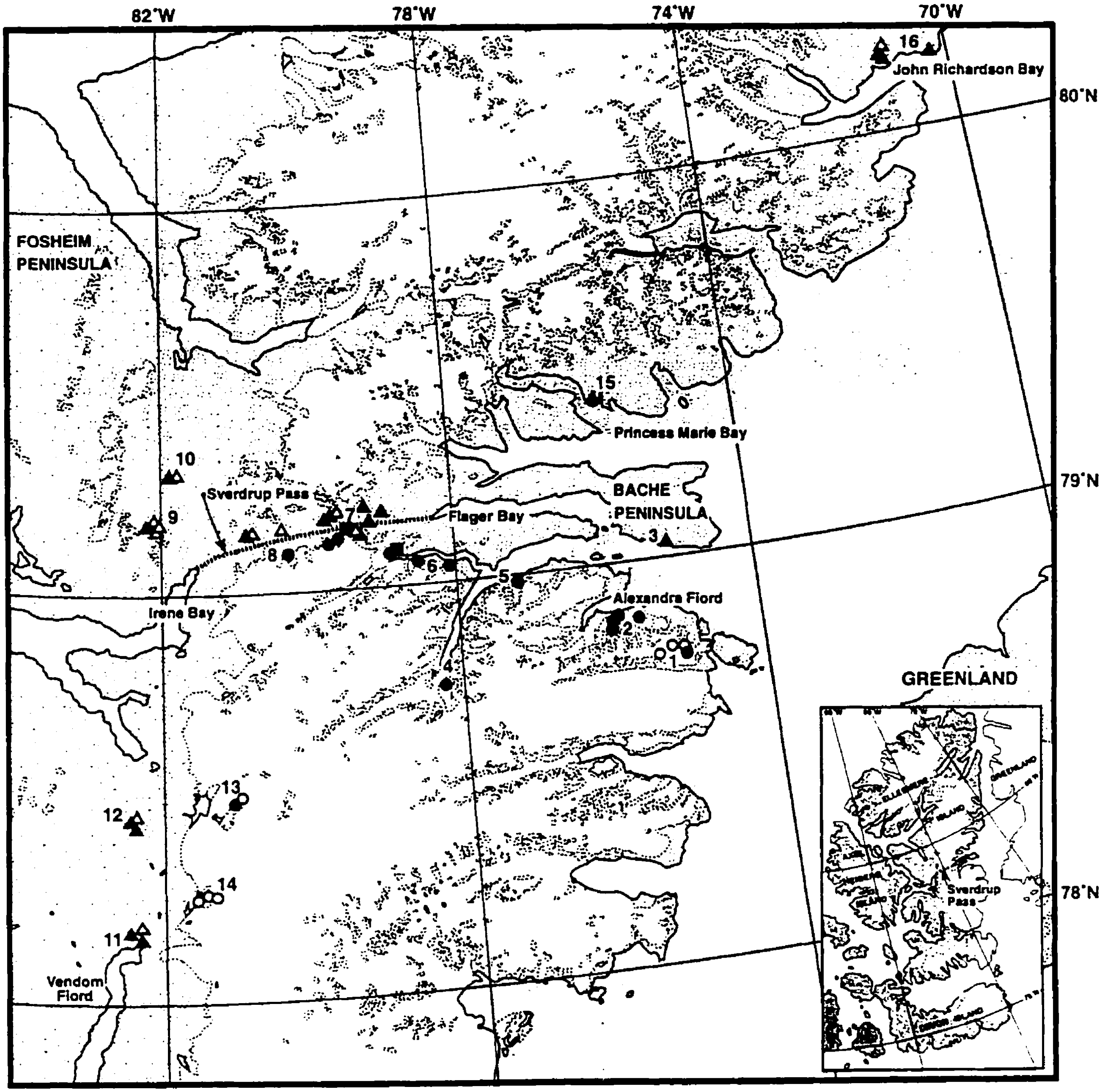
3.3 STUDY AREA

3.3.1 Geology, geomorphology and topography

Central Ellesmere Island is mountainous and partially glaciated (Figure 1). Major rock formations of varying ages have been identified and can be found sometimes in very close proximity to one another due to uplift and erosion processes (*e.g.* Plate 3.1). Sterenberg and Stone (1994) presented a summary of the stratigraphic sequences and geological provinces on Ellesmere Island. The Precambrian crystalline basement surfaces only in the south eastern portion of the Island. The Precambrian formation consists of a heterogenous group of igneous and sedimentary rocks which have been metamorphosed to granulite facies and is the northern limit of the Canadian Shield (GSC Maps 1357A, 1572A; Sterenberg and Stone, 1994). The rest of central Ellesmere Island is dominated by Palaeozoic formations which, except for relatively small outcrops of quartz sandstone, are dominated by carbonate rocks (mostly dolostone and limestone), calcareous quartz, siltstone and shales (GSC Maps 1307A 1308A, 1358A, 1359A; Sterenberg and Stone, 1994).

In this study, 82 sites on granite, sandstone and carbonate bearing rocks were surveyed in central Ellesmere Island. Granitic sites were dominated by granite, gneiss (commonly orthopyroxene-bearing and quartzofeldspathic) and

Figure 3.1: Map of central Ellesmere Island, Canada, indicating the major sampling areas (numbers 1 to 16). Stands are represented by ▲ (carbonate), ● (granite), ■ (sandstone). Filled symbols mark 'vegetated' sites, open symbols mark 'barren' sites. More than one stand may have been sampled near the points shown on the map. Sites abbreviations are as follows: In proximity to Alexandra Fiord: **1**, Nunataks (N1-N5); **2**, Eastern Plateau (E1), Skyway (S1), Granitic and Dolomitic dome (AG and AD). On the Bache Peninsula: **3**, Site B1. Near Hayes Fiord and Jokel Fiord: **4**, southern end of Jokel Fiord (H1) and **5**, opening of Jokel Fiord (J4). Along Beitstad Fiord: **6**, granitic sites (Z1 and ZL) and mixed granitic and sandstone sites (BT1-BT6). In central Sverdrup Pass, east of the divide: **7**, carbonate sites: Lockwood Mountain (LM0-LM5), VP1-VP2, Table Top (TT), Decision Peak (DP) and Dolomitic gradient (D1-D6); Eastern Mountain (EM1, sandstone site); and granitic sites: KM and Granitic gradient (G1-G7; and G8-G9). In central Sverdrup Pass, west of the divide: **8**, Witch Mountain (WM), Dolomitic Gorge (DG1-DG3) and a granitic site GB1. Western Ellesmere Island sites, North of Irene Bay: **9**, Mount Lawson (M1 and P1-P6) and **10**, Mount Moore (MM1-MM5). To the South near Vendom Fiord: carbonate sites **11**, VF1-VF3 and **12**, C1, C2 and CL; granitic sites **13**, Q1, Q2 and **14**, R2-R4. Towards the North-East of Ellesmere Island, carbonate sites: **15**, near Princess Marie Bay (PMB) and **16**, along John Richardson Bay (W1, W2, WL and X1).


82°W
78°W
74°W
70°W
80°N
79°N
78°N
16
John Richardson Bay
FOSHEIM PENINSULA
15
Princess Marie Bay
10
Sverdrup Pass
9
7
Flager Bay
BACHE PENINSULA
3
8
6
5
Alexandra Fiord
Irene Bay
2
1
4
GREENLAND
13
12
14
11
Vendom Fiord
Sverdrup Pass

related rocks from the Precambrian (Frisch, 1984). Their microtopography was ragged with many large boulders (Plate 3.3a). Most sites appeared dark due to the presence of reddish rocks (Plate 3.3b). These rocks may have been partially or totally covered by lichens and thus be even darker (Plate 3.3c). Only one site, at the southern end of Jokel Fiord, was dominated by a lighter colour granite (H1, Plate 3.3d).

A few Palaeozoic Cambrian quartz sandstone formations were also included in the survey. These formed a thin layer on the top of a granitic outcrop and supported a very low vascular plant cover, and no, or very few, bryophytes, except where the sandstone was mixed with granite. The sandstone was pale coloured and supported minimal lichen cover (Plate 3.4a). It has eroded to form a coarse sandy soil (Plate 3.4b) that provides good drainage. The granitic and sandstone sites showed the least traces of ground frost activity.

The sites with carbonate rocks (hereafter called 'carbonate sites') were located on Palaeozoic formations, mostly of Ordovician and Cambrian periods. These consisted primarily of dolostones, limestones and some shales and minor conglomerates (GSC Maps 1307A 1308A, 1358A, 1359A). Plate 3.5 presents different views of carbonate rock sites. Poorly developed sorted ground features, such as polygons and stripes, could sometimes be distinguished from the air (*e.g.* Plate 3.5a) but otherwise these sites were relatively smooth (without large boulders). From the ground, the sharp frost shattered beige or gray rocks and pebbles appear to dominate the surface (Plate 3.5b) and the fine textured soils were usually water saturated and compacted. Cracks may form whenever the surfaces dry out (Tedrow, 1977; Sohlberg and Bliss, 1984; Plate 3.5c). Marks of ground frost activity were seen at most of these sites, for example surface disturbance due to needle ice activity (Plate 3.5d). In general, moist fine textured soils are more prone to freeze-thaw activity (French, 1987) and result in the formation of non-sorted and sorted polygonal nets. The rate of such disturbance, however, is very slow (Koizumi, personal communication).

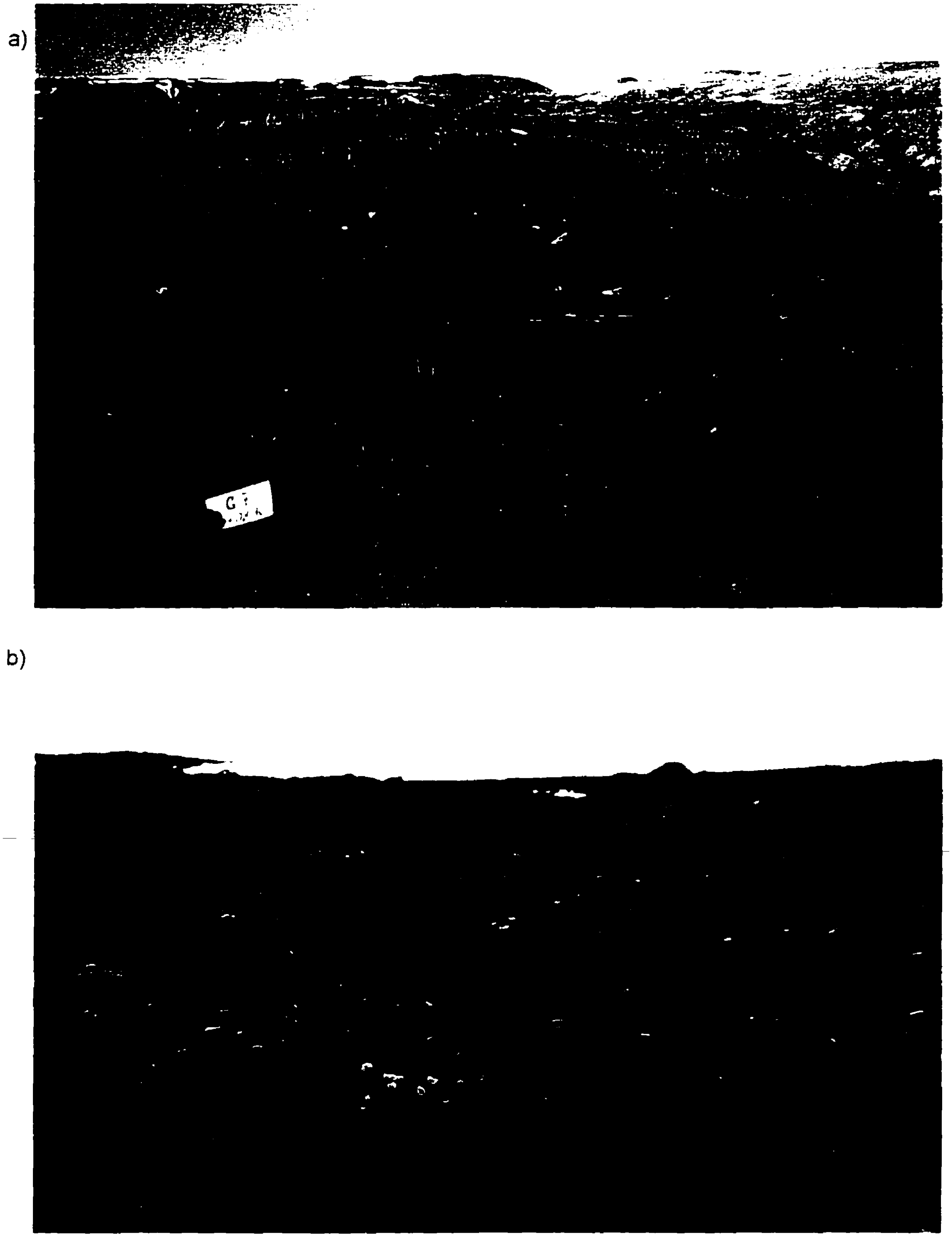


Plate 3.3: General features of granitic sites from central Ellesmere Island, Canada. a) Altitudinal gradient site G7 (727 m a.s.l.), Sverdrup Pass with large boulders. b) Eastern plateau, site E1 (818 m a.s.l.), near Alexandra Fiord. In the foreground is a flowering *Papaver radicatum*.

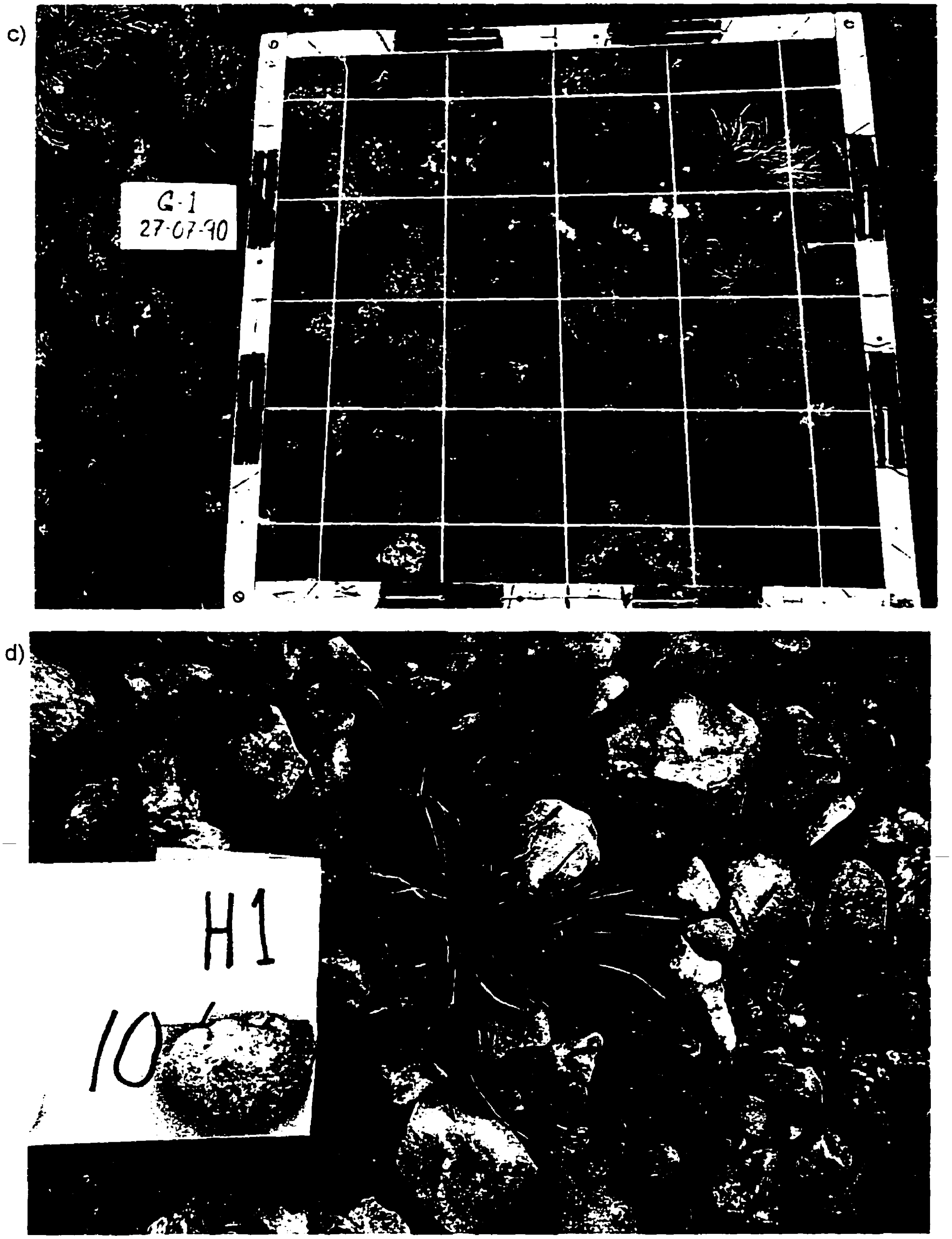


Plate 3.3: c) Lichen covered rocks at site G1 (347 m a.s.l.), lower end of altitudinal gradient, Sverdrup Pass; the quadrat is 50 cm x 50 cm. d) *Phippsia algida* in bloom among pale coloured granite on site H1 (912 m a.s.l.), Jokel Fiord.

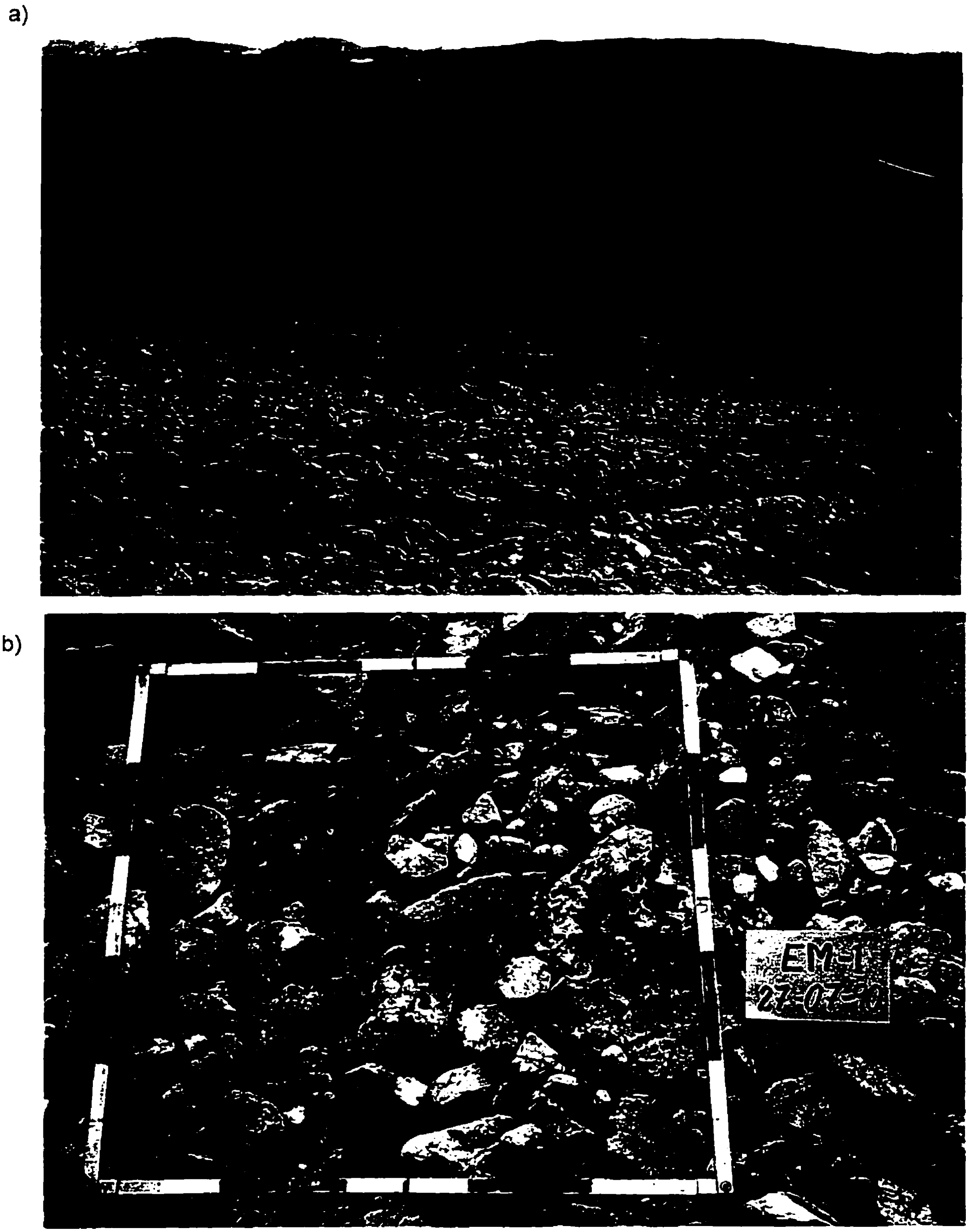


Plate 3.4: Sandstone site EM1 (636 m a.s.l.), Eastern Mountain, south side of Sverdrup Pass, Ellesmere Island. a) Pale coloured frost-weathering sandstone bedrock slope. The darker background is granitic. b) Boulder with coarse sand soil with limited lichen cover and a single plant of *Saxifraga oppositifolia* in a 50 cm x 50 cm quadrat.

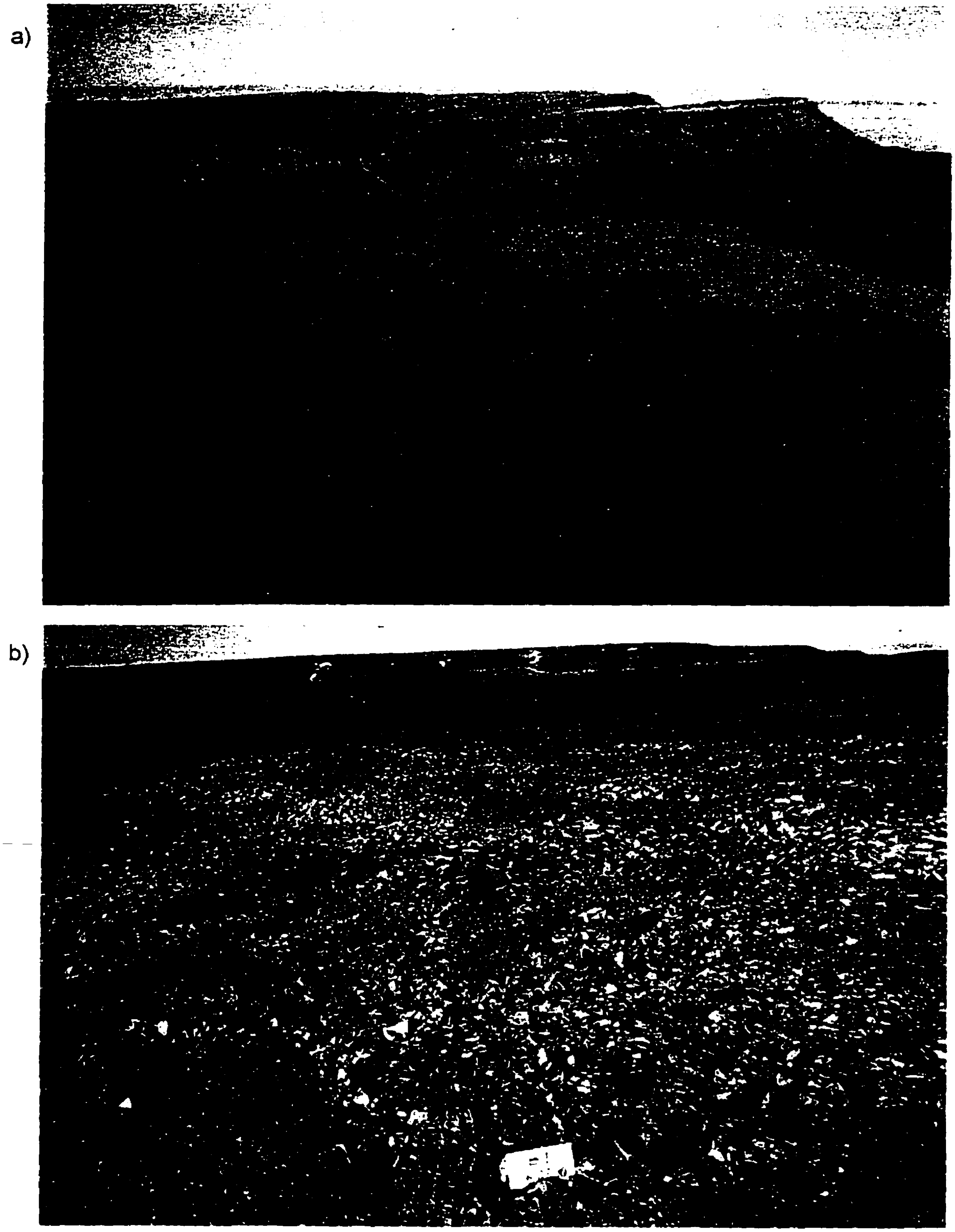


Plate 3.5: General features of carbonate rocks landscape, central Ellesmere Island, Canada. a) Aerial photograph of site B1 (608 m a.s.l.), Bache Peninsula. b) Weakly developed pattern ground of pale beige frost shattered dolomitic rocks at site B1.

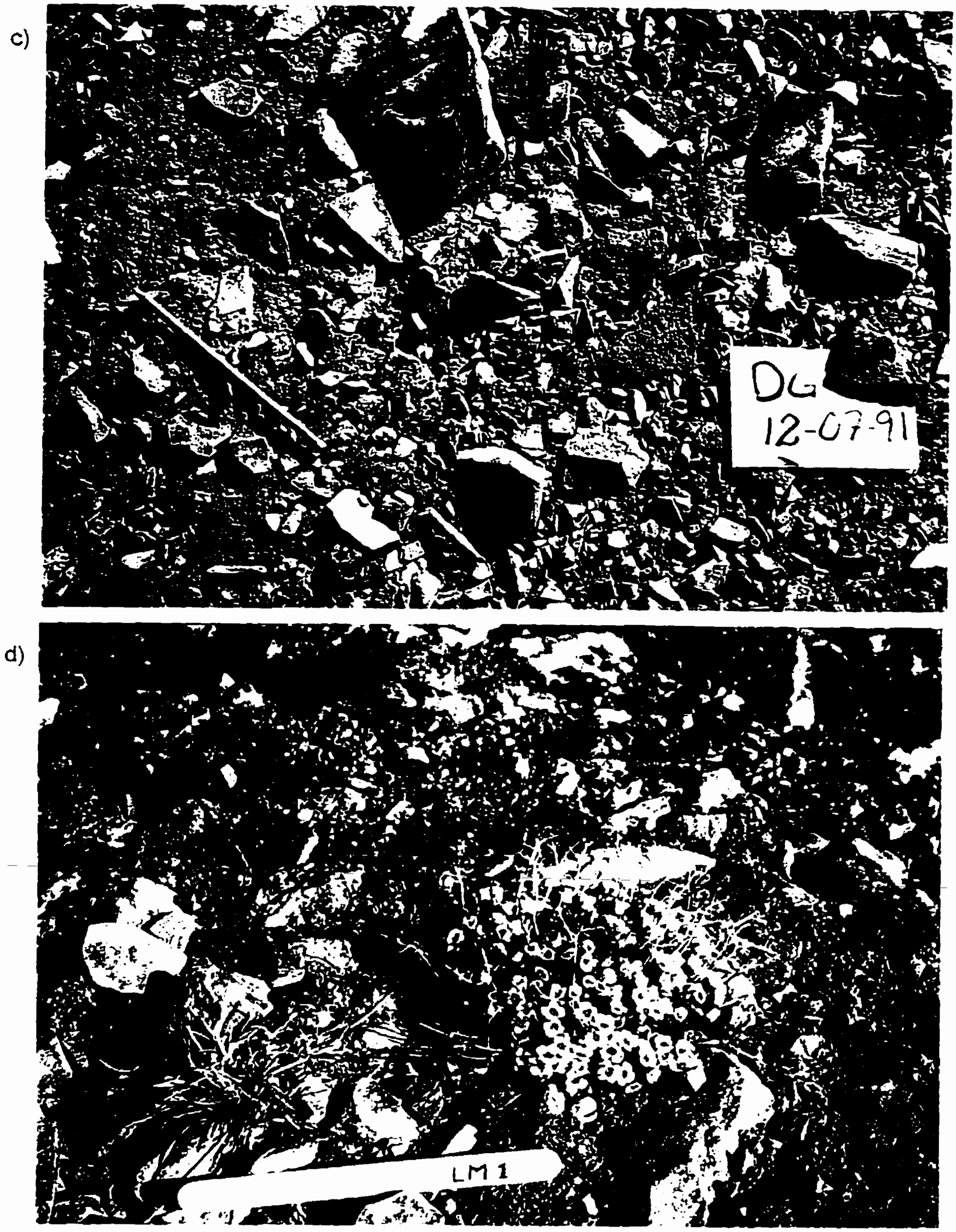


Plate 3.5: c) Close-up of compacted silty substrate with frost-heaved angular rocks on site DG1 (664 m a.s.l.); notice the clumped distribution of minute *Papaver radicatum* and *Phippsia algida* plants near the label. d) Close-up of *Phippsia algida* and *Draba corymbosa* in bloom on site LM1 (827 m a.s.l.), Sverdrup Pass; the carbonate soil surface is moist and disturbed by needle ice.

Soil development is strongly limited in the High Arctic, mostly because of low precipitation, shallow active layers and impeded leaching due to the underlying permafrost (Rieger, 1974; Pawlik and Brewer, 1975). Arctic soils are grouped in the Cryosolic order (Canada Soil Survey Committee, 1978). They show much variation due to the mineralogy of the soil parent materials (Pawlik and Brewer, 1975) and to the topographic, hydrologic and microclimatic features (Johnson, 1969; Tedrow, 1977). Polar oases have relatively well developed soils (Walker and Peters, 1977; Muc *et al.*, 1994b), whereas polar deserts and semi-deserts have minimally developed soils (Tedrow, 1977; Bliss and Svoboda, 1984; Bliss *et al.*, 1984).

3.3.2 Climate, microclimate and permafrost

According to the climatic classification of the Canadian Arctic Islands, the majority of Ellesmere Island belongs to the climatic region V (Maxwell, 1981). Most of the study sites were located in the central mountainous portion of the Island and belonged to the sub-region Vc (Axel Heiberg and Ellesmere Island Highlands). Average annual precipitation is slightly above 200 mm and the growing season is approximately 60 to 70 days (at sea level) with the first day with daily mean temperature above freezing around June 15-20 and the last day around August 20-25 (Maxwell, 1981). Mean July temperature is low (0 to +3°C) and only 20 to 30% of the precipitation falls as liquid. Sub-region Va (Nares Strait), on the eastern side of the island has a mean July temperature slightly above 3°C and receives a little more liquid precipitation (40 to 50% of 175 mm). This is mostly due to a higher frequency of fogs; whereas the lowlands on the western side of the island belong to the warmer but drier sub-region Vb. This region (Nansen Sound and adjacent lowlands) has a July mean temperature of +5°C and less than 100 mm of precipitation (Maxwell, 1981). The mean total seasonal thawing degree-days for Ellesmere Island is 250 to 350 (Edlund and

Alt, 1989). Year-to-year variation is important at these latitudes and sites at higher elevations may have an even shorter growing season (*see* Chapter 5).

3.4 METHODS

3.4.1 Field sampling and laboratory analysis

During the summers of 1990-93, 82 upland and mountain sites were visited (most by helicopter) in the central portion of Ellesmere Island, Canada, extending latitudinally from 78°N to 81°N (Figure 3.1). Fifty-four of the sites had a sporadic discontinuous vascular plant cover (the 'vegetated sites') and were usually near the altitudinal limit of vascular plant distribution (*i.e.* higher, but vascular plant-free locations were visited prior to the selection of a site). Due to time constraints only 39 of these sites were sampled in full details for vegetation and environmental characteristics and soil samples were collected in 6 additional sites (MM2, MM4P, W1, BT3, BT4 and LM2; Table 3.1). Sites without vascular plants but where some cryptogams may be found (referred here as 'barren' for brevity; n = 28) were surveyed for the basic environmental characteristics (see section on environmental variables), in addition, soil samples were collected at 13 of these sites (Table 3.1) and the lichen and bryophyte cover was measured using 20 quadrats (see section Plant frequency, cover and density) at two of them (N5 and Q2). All these sites were chosen for their habitat homogeneity and more or less level topography.

Most of the sites were reached by a helicopter and were visited only once. Thirteen sites ('gradient sites') were reached by foot and were surveyed and monitored over four seasons. These were selected along two altitudinal gradients (six on a dolostone (D1-D6) and seven on a granite slope (G1-G7)) on the valley slopes near the central portion of the deglaciated, east-west oriented Sverdrup Pass, Ellesmere Island, Canada (79°08'N, 80°30'W, Figure 3.1).

Table 3.1: Substrate and elevation of 82 polar desert sites visited at central Ellesmere Island, Canada. Analysis refers to a) sites used for complete vegetation analysis and MDA (n = 39); b) sites with soil nutrient data, used for MDA (n = 19); c) additional sites surveyed but where no soil samples were collected for nutrient analysis (n = 24). 'Vegetated' refers to sites with some vascular plants and 'barren' to sites devoid of vascular plants; substrate type abbreviations: carbonate (C), granitic (G), sandstone (S), mixture of granite and sandstone (GS).

	Vegetated (n = 54)				Barren (n = 28)		
Site	Elevation	Substrate	Analysis	Site	Elevation	Substrate	Analysis
D1	335	C	a	VF3	552	C	b
D2	336	C	a	P2	723	C	c
G1	347	G	a	P3	727	C	c
G2	357	G	a	LB	745	C	b
D3	376	C	a	LG	745	C	b
D4	420	C	a	P4	745	C	c
G3	443	G	a	R2	770	G	b
G4	461	G	a	DG2	800	C	c
AD	540	C	a	R3	803	G	c
AG	540	G	a	R4	833	G	c
VF1	550	C	a	DG3	852	C	c
VF2	550	C	c	MM1	873	C	b
B1	608	C	a	LM0	885	C	c
G5	618	G	a	P1	891	C	c
EM1	636	S	a	P5	908	C	b
G6	638	G	a	DP	909	C	c
PMB	645	C	a	CL	909	C	c
ZL	648	G	c	LM3	915	C	b
C2	661	C	a	LM4	947	C	b
DG1	664	C	a	N2	962	G	b
D5	684	C	a	WM	970	C	c
M1	703	C	a	G9	973	G	c
TT	703	C	c	Q2	977	G	b
G7	727	G	a	LM5	993	C	b
C1	758	C	a	N1	1000	G	c
D6	765	C	a	N5	1003	G	b
S1	786	G	a	P6	1025	C	b
MM2	788	C	b	WL	1121	C	c
MM3	788	C	a				
MM4	790	C	a				
MM4P	790	C	b				
KM	792	G	c				
X1	803	C	a				

Table 3.1 (con't)

G8	811	G	a
N3	812	G	a
VP1	818	C	a
VP2	818	C	a
E1	818	G	a
BT1	824	GS	c
LM1	827	C	a
BT2	833	GS	c
BT6	836	GS	c
Q1	842	G	a
W2	848	C	a
W1	852	C	b
N4	855	G	c
BT3	860	GS	b
BT4	860	GS	b
LM2	865	C	b
J4	870	G	a
BT5	900	GS	c
H1	912	G	a
GB1	939	G	a
Z1	970	G	a

Plant frequency, cover and density. Percent cover values for vascular plants, bryophytes, lichens, dead plant material (litter) and feces (mostly of arctic hare) were determined using a stratified random sampling design. The ground covering lichens were not distinguished to species and were considered equivalent to the 'cryptogamic crust cover' of Gold and Bliss (1995). To obtain the best data set on the plant communities, I used an open ended random sampling technique, in which sampling was conducted until a minimum of 30-40 quadrats with plants were obtained. The quadrats were 50 cm x 50 cm with a 5 cm x 5 cm grid. General characteristics (*e.g.* roughness, soil, pebble and boulder cover) and bryophyte, lichen, litter and feces cover were recorded only for the first 30 quadrats, afterwards, a count was kept of the empty quadrats. The total area sampled at each site was at least 10 m^2 (*i.e.* at least 40 quadrats), which was the minimum area calculated to be adequate for these plant communities (Lévesque, 1996). However, at some sites with a particularly sparse vegetation up to 50 m^2 (*i.e.* 200 quadrats) were sampled. Effort was made to gather most information about each site in the time available (the exact number of quadrats surveyed at each site is presented in Appendix 2). A complete list of the vascular flora of each study area was made, in addition to lists of vascular species found in the quadrats.

In order to facilitate the process of sampling for cover with an acceptable accuracy and speed, a Domin-Krajina abundance scale as modified by Lévesque (1996), scale-A (see Chapter 2, Table 2.3) was used. The overall site cover percentages were calculated using the class mid-point value (Lévesque, 1996) and the total number of quadrats sampled. The number of individual plants was also recorded in each quadrat to allow the determination of density. Individual forbs could be distinguished easily as each individual possessed a single tap root. Gramineae were mostly caespitose, therefore each small cluster was considered to be one individual. Quadrats with no plants were entered with a zero cover percentage.

Most of the vascular plants were identified in the field. Voucher specimens were collected for confirmation. Specimens of the various *Draba* spp. were identified following a key based on Mulligan (1976). Some samples had only vegetative parts since many plants growing in the harshest habitats did not have flowering or fruiting organs. A list of the criteria used to recognize these specimens is presented in Appendix 1. Since *Carex nardina* and *Kobresia myosuroides* rarely flowered, they could not be reliably distinguished in the field; to avoid misidentification they will be referred to as the *Carex nardina/Kobresia myosuroides* complex (Appendix 1). Nomenclature for vascular taxa generally follows Porsild and Cody (1980), see Appendix 1 for details and for the complete list of vascular taxa.

Standing crop estimates. The relationships between cover and standing crop (aboveground live and attached dead material) were established in 1994 for 16 vascular taxa collected in the vicinity of the Sverdrup Pass base-camp from carbonate and granitic substrates. Plants were randomly selected in mid- to late July. Their precise cover values were measured with a fine grid quadrat (10 cm x 10 cm with a 5 mm x 5 mm grid). The plants were then extracted with as much root as possible, sorted into above and below-ground portions, dried at 60°C and weighed to 0.01 g. The number of individuals measured and collected ranged from 10 to 69 per species (Appendix 3). Many of the species produced deep tap roots (*e.g.* Plate 3.6). Since root extraction in those rocky sites was difficult and root recovery was not consistent (reducing considerably the replication), it was impossible to establish reliable species-specific below-ground phytomass equations and so only above-ground phytomass results were calculated.

Regression equations were established and used in standing crop calculations (Appendix 3). To estimate the total standing crop at all the sites sampled for vascular plant cover, the total cover value for each species was multiplied by the appropriate equation to obtain a value in g/m^2. Whenever a

Plate 3.6: Gravelly soil profile showing the exposed root system of *Papaver radicatum* at a low elevation carbonate site (D2, 336 m a.s.l.), Sverdrup Pass, Ellesmere Island. Scale is 11 cm.

particular taxon was not collected, equation of another taxon with a similar growth form was used to estimate that taxon standing crop (*e.g.* for *Cardamine bellidifolia*, the equation of *Draba* sp. was used, see Appendix 3). A single equation established on the basis of a few specimens from various grass species (mostly from the genera *Poa* and *Puccinellia*) was used for the Gramineae and the Juncaceae. There was no collection of *Carex nardina/Kobresia myosuroides* and since these species form dense mats and have a phytomass distribution similar to cushion plants, especially *Dryas integrifolia* (Maessen *et al.* 1983), we used the equation for that species to estimate the standing crop. Comparisons of our results with those of Muc *et al.* (1994c) suggested that these equations gave a satisfactory estimate of the total standing crop. However, since the cover values obtained through the conversion of the abundance scale tended to slightly overestimate cover (Lévesque, 1996), this also resulted in a slight overestimate of the standing crop present at the sites.

Environmental variables. The following physical characteristics were noted at each site, (a summary is presented in Appendix 2): 1) The longitude and latitude; using GPS from the helicopter or read from topographic maps (1:25 000). 2) The altitude of each station; using an altimeter (Keuffel and Esser) and corrected to helicopter readings or the base camp altitude. 3) The underlying rock type and/or substrate (carbonate, granite or sandstone). Carbonate substrate samples were tested for effervescence with a weak acid solution to distinguish between dolostone and limestone. In agreement with the geological maps of the area, both rock types were frequently found together and thus the general term 'carbonate rocks' was used. 4) Slope aspect was expressed in degrees, the North being set as zero and the angles read clockwise. 5) Slope declination was measured in degrees with a clinometer (Sunnto Co.).

During the survey of the vegetated stands, ground roughness was estimated in each quadrat, using qualitative classes ranging from 1 (flat surface and fine material) to 5 (rough surface or totally covered by boulders). The percent bare ground was also recorded either as soil (< 4 mm), pebbles (between 4 mm and 10 cm) or boulders (> 10 cm in at least one dimension). Bare ground and pebbles cover were estimated in a 10 cm x 10 cm grid while the cover of boulders was evaluated over the whole 50 cm x 50 cm quadrat.

At least 5 soil samples from the top 10 cm (where roots were most abundant) were collected at each site (n = 30 at the 'gradient sites'). The soils contained a lot of rocks which made it impossible to use a soil core. To remove the larger rocks, we passed the soil through a sieve in the field (4 mm, Canadian Standard Sieve) and a known portion of firmly compacted soil (volume 156 cm^3) was collected. The moisture content (by weight and volume) was determined after samples were dried to a constant weight at 60°C. This was done only once for all sites except for the gradient sites where sampling was repeated 2-4 times a year in 1990-92. The soil samples were later passed through a 2.0 mm Canadian Standard Sieve and the fine portion was used for the following analyses: 1) Total organic matter content. This was measured by the loss-on-ignition method of Broadbent (1962). The maximum temperature was kept below 600°C to limit the risk of weight loss due to carbonate combustion. In order to ascertain that no carbonates were lost due to high temperature, pure samples of ground carbonate stones were burned following the same procedure with no significant recorded loss of weight. 2) Particle size distribution was analyzed by the hydrometric method and the percentage of each fraction, i.e sand, silt and clay calculated (Bouyoucos 1962). 3) Soil pH was measured in a water-saturated paste to 0.01 unit (Corning Scientific Instrument, Model 7). 4) Available phosphorus was extracted using a weak hydrochloric acid method (Bray and Kurtz, 1945) and measured with a spectrophotometer (Pye Unican SP6-550). 5) Exchangeable potassium and calcium were extracted by leaching from the soil with neutral N ammonium acetate and their concentrations were measured by atomic absorption spectrophotometry (Perkin Elmer 3100).

3.4.2 Data Analysis

A summary of all the sites surveyed is presented in Table 3.1, including elevation, substrate, if the site had vascular plants present ('vegetated') or not ('barren') and the analyses in which each site was used.

General data structure. To maximize the amount of information preserved in the analysis of vegetation while minimizing the effect of the few large cover occurrences, van der Maarel (1979) recommends the use of an abundance scale rather than simply presence-absence or cover values. Since a modified Domin-Krajina scale emphasizing the lower cover values (the more frequent cover classes) was employed to sample the vegetation in the field, this same scale was used in the analyses. The mean cover values for each site were transformed to the abundance scale used during sampling (0-9; Lévesque, 1996) prior to analysis (*i.e.* the cover of *Draba subcapitata* for site D6 was < 0.5%, the value entered in the analysis was 1). Species that were present on site but did not appear in sampled quadrats were given a value of 0.5. The species recorded on a single visit were used for all sites to ensure that the sampling effort was comparable. In recent studies in the Arctic, Talbot and Talbot (1994) and Forbes (1994 and 1996) have used similar scales to represent plant cover while Bliss and Gold (1994) and Bliss *et al.* (1994) have used prominence values.

In our study, analyses were performed which included and excluded species with single occurrence. Their exclusion had little influence on the overall outcome of the analyses. Since the species list represented the overall species composition of all sites, all vascular species encountered were included and given equal weighting in the analyses.

For the analysis of environmental variables, the site mean values for each variable were entered. The values were standardized (mean zero and unit variance) by the program prior to the analysis (CANOCO; ter Braak, 1991). To eliminate the risk of highly correlated variables, the variables with inflation factor > 20 were excluded (ter Braak, 1991). The final list of environmental variables included in the direct and indirect gradient analyses is given in Table 3.2. One carbonate site on the north side of Sverdrup Pass, DG1 (Figure 3.1) was the only site for which soil nutrient values were not available. As recommended by Jongman *et al.* (1987), I used mean values of the carbonate sites for those variables, at this site.

Preliminary analyses. In preliminary analyses of the vegetation data, site G8, at the end of the main granitic altitudinal gradient in Sverdrup Pass, showed an extreme response to Correspondence Analysis, CA, (sample scores for Axis 1 and 2 respectively were 2.89 and 8.41 compared to maximum scores of 1.68 and 1.02 for the other sites). Thus this site was removed from all the following vegetation classification and ordination analyses. The length of the environmental ordination gradients were longer than 2.5 standard deviation units (Table 3.3). Since the response of any species can be expected to be unimodal when the gradient length is longer than 1.5-2 standard deviation units (Jongman *et al.*, 1987), analytical methods based on Gaussian models (Detrended Correspondence Analysis, DCA and Canonical Correspondence Analysis, CCA) rather than linear models (Principal Component Analysis, PCA and Redundancy Analysis, RDA) were chosen.

The indirect ordination technique, DCA, was used to investigate compositional gradients in the vegetation data in combination with the classification analysis. The direct gradient analysis approach, CCA, where the ordination of the vegetation data is constrained by environmental predictors (Jongman *et al.* 1987) was used to analyze the relationship between the vegetation composition and the environmental variables measured. Partial Canonical Correspondence Analyses (PCCA) were used to decompose the proportion of the variance explained in order to test the importance of various

Table 3.2: The set of environmental variables used in ordination analysis. All variables were recorded in the 39 sites. For details on method see text.

Variable abbreviation	Description	Groups
Long	Longitude	A) Geographical location (relates to geological formation and climate)
Lat	Latitude	
Elev	Elevation above sea level (m)	B) Elevation (relates to climate, time since deglaciation, productivity)
Moss	Moss cover (%)	C) Biological variables (relates to productivity and to age of site)
Lichen	Lichen cover on soil and pebbles (%)	
Feces	Feces cover (%)	
Dead	Dead material or litter cover (%)	
pH	pH	D) Soil Chemical Characteristics within top 10 cm (relates to parent material, erosion and growth)
P	Concentration of available phosphorus (ppm)	
K	Concentration of extractable potassium (ppm)	
Ca	Concentration of extractable calcium (ppm)	
OM	Organic Matter content (% per dry weight)	
Rough	Roughness of soil surface scale 1 to 5	E) Soil Physical Characteristics within top 10 cm and surface microtopography (relates to parent material, erosion, glacial and periglacial history)
Sand	Percentage of sand	
Silt	Percentage of silt	
Clay	Percentage of clay	
Soil	Soil (fine materials < 4 mm) cover on site (%)	
Boulder	Boulder cover on site (%)	

Table 3.3: Results for axes 1-3 for DCA and CCA in terms of the magnitude, community- or species-environment correlations (for DCA and CCA respectively), significance and variance explained, using 18 environmental variables (see Table 3.1). Analysis$_a$: 38 sites included (G8 eliminated) and all species included with equal weight (39 species), Trace = 2.578; Analysis$_b$: same as $_a$ except that 3 species were made passive (*Draba lactea*, *Erysimum pallasii* and *Melandrium affine*), Trace = 2.471; Analysis$_c$: same as$_a$ except that 11 gradient sites were excluded (D1-D5 and G1-G6), Trace = 2.379. Level of signif. is from Monte Carlo randomization test. Subscript numbers refer to axis number (1 to 3) or to overall results (all).

	Axis eigenvalue			Community or species-environment correlation			Level of signif.		Percentage of variance explained				Gradient length		
Analysis	λ_1	λ_2	λ_3	r_1	r_2	r_3	$p(\lambda_1)$	p_{all}	$\%_1$	$\%_2$	$\%_3$	$\%_{all}$	$G.L._1$	$G.L._2$	$G.L._3$
DCA$_a$	0.414	0.269	0.175	0.925	0.942	0.849	-		16.0	10.5	6.8	-	2.65	1.96	2.02
DCA$_b$	0.406	0.279	0.178	-	-	-	-		16.4	11.3	7.2	-	2.58	1.89	1.94
CCA$_a$	0.364	0.277	0.252	0.946	0.955	0.956	0.01	0.01	14.1	10.7	9.8	67.2	-	-	-
CCA$_b$	0.354	0.272	0.245	0.942	0.951	0.956	0.01	0.01	14.3	11.0	9.9	66.8	-	-	-
CCA$_c$	0.457	0.299	0.210	0.991	0.958	0.960	0.89	0.01	19.2	12.6	8.8	84.5	-	-	-

environmental variables (Borcard *et al.* 1992; Carleton and MacLellan 1994). CANOCO version 3.12 (ter Braak, 1991) was used for all ordination analyses.

Differences between sites with and sites without plants. To test if there was a significant difference in environmental variables between the sites with or without vascular plants, I used a Multivariate Discriminant Analysis (MDA). Two groups of a set of 58 sites (45 'vegetated' and 13 'barren') were compared using 7 environmental variables (elevation, pH, P, K, organic matter content, Ca, sand). In addition, two covariables describing the geographical location of each site were used (longitude and latitude). The discriminant linear and quadratic functions were calculated and the percentage of return to the assigned group was used to test significance (Minitab, 1996).

Classification of vegetation. The vegetation of 38 sites was classified with the two-way indicator species analysis (TWINSPAN, Hill, 1979). The default options were used with the following exceptions: 1) the maximum number of indicators per division was set to 4, and 2) the pseudospecies cut levels were set at 0, 1, 2, 3, 4, 5, 6 to reflect the range of vascular species abundances after transformation of the species data to the abundance scale. The vast majority of the species occurrences (93%) had less than 1% cover and belonged in cut level 1 or 2. Cut level 6 represented > 5% cover and occurred only once, for *Salix arctica* at site AG, a low elevation granitic site at Alexandra Fiord.

To test if the substrate was the main underlying force which differentiated the vegetation, a constrained indicator species analysis (COINSPAN, Carleton *et al.* 1996) was performed using similar settings as in TWINSPAN analysis. A binary column for substrate, where sites with carbonate rocks (1) or with granite/sandstone (0) were distinguished, was used as the environmental variables constraining the classification.

Vegetation-environment gradients. Constrained ordinations (CCA, CANOCO, ter Braak, 1991) were performed to analyze the relationship between environmental variables and the plants for 38 sites. The default options were used and all species were given equal weight. To test the significance of the first axis and of the overall analysis, unrestricted Monte Carlo permutation tests were used with 99 random permutations.

Partial analyses (PCCA) were completed for each of the five main groups of environmental variables (Table 3.2). This approach facilitates quantification of the proportion of variance uniquely associated with a particular variable (or set of variables), the variable of interest is used as a predictor while all the other variables are assigned as covariables (Carleton and MacLellan, 1994). Interactions among the groups were calculated similarly by subtracting the variance explained by a single variable from the variance explained when a group of variables was used as predictor.

3.5 RESULTS

3.5.1 Vegetation diversity

Of the 82 sites surveyed, 58 were colonized by at least a few vascular species (Table 3.1). On the 39 vegetated sampled sites, 40 vascular taxa were identified. Table 3.4 presents a complete species list of vascular species and the proportion of sites by substrate in which they had been observed. The complete site-specific results are given in Appendix 4. A single Pteridophyte, *Cystopteris fragilis*, was found once (site D1). The 39 other species were Spermatophytes: 9 Monocotyledons from 3 families (5 Gramineae, 2 Cyperaceae and 2 Juncaceae) and 31 Dicotyledons from 9 families (11 Cruciferae, 6 Saxifragaceae, 5 Caryophyllaceae, 3 Rosaceae and one from each of Ericaceae, Papaveraceae, Polygonaceae, Salicaceae, Scrophulariaceae). Granitic sites were overall more diverse with 4 to 20 species per site for a total of

Table 3.4: Vascular species diversity (VSD) and occurrence (%) of individual vascular plant species found at Carbonate, Granitic or Sandstone sites in polar deserts at central Ellesmere Island. Number of sites per bedrock type visited are given in brackets; dashed line delineates the ten most frequently occurring species in all polar desert sites across substrates; *G* indicates species found only on granitic sites *C* indicates species found only on carbonate sites; * indicates species found only at Sverdrup Pass gradient sites; + indicates species found only near Alexandra Fiord.

	Species occurrence (%)			
Species	Carbonate (21)	Granitic (17)	Sandstone (1)	OVERALL (39)
Saxifraga oppositifolia	100	88	100	95
Papaver radicatum	86	94	100	90
Draba subcapitata	76	82	100	79
Draba corymbosa	71	53	100	64
Minuartia rubella	33	53	100	44
Phippsia algida	62	18		41
Poa abbreviata	29	41	100	36
Puccinellia bruggemannii	48	18		33
Cerastium arcticum	38	18	100	33
Saxifraga cernua	29	29	100	31
Cardamine bellidifolia - G		59	100	28
Luzula confusa	5	59		28
Carex nardina/Kobresia myosuroides	5	47		23
Poa arctica - G		53		23
Salix arctica	19	29		23
Saxifraga nivalis	5	47		23
Saxifraga tricuspidata	5	47		23
Dryas integrifolia	19	24		21
Stellaria longipes	10	35		21
Braya purpurascens	24	6		15
Draba alpina	5	24	100	15
Draba oblongata *	10	24		15
Draba cinerea *	5	24		13
Saxifraga caespitosa	10	18		13
Luzula arctica - G		18	100	10
Potentilla hyparctica - G		18		8
Braya thorild-wulffii - C	10			5
Carex misandra - G *		12		5

Table 3.4 (con't)

Cassiope tetragona - G		6	100	5
Draba nivalis - G		12		5
Festuca hyperborea - G		12		5
Melandrium apetalum - C *	10			5
Oxyria digyna	5	6		5
Pedicularis cf. arctica +	5	6		5
Potentilla pulchella *	5	6		5
Saxifraga rivularis	5	6		5
Cystopteris fragilis - C *	5			3
Draba lactea - G +		6		3
Erysimum pallasii - G *		6		3
Melandrium affine - G *		6		3
Range of site VSD	2 to 14	4 to 20	12	2 to 20
Total VSD	29	37	12	40

37 species whereas the carbonate sites had 2 to 14 species per site and a total of 29 vascular species. The only sandstone site had 12 species all of which were also common to granitic sites (Table 3.4).

The 10 most commonly found species may be considered the most tolerant and able to disperse to and invade isolated sites having extremely short cold growing seasons, limited fine soil and low nutrient availability (Table 3.4). Two species were present in more than 90% of the sites: *Saxifraga oppositifolia* and *Papaver radicatum* (Table 3.4). *S. oppositifolia* was ubiquitous and also frequently the dominant species either in frequency or in cover (Appendix 4). *Draba subcapitata* and *Draba corymbosa* were present at 79% and 64% of the sites respectively and were also regular components of the vegetation. All of these four species were also encountered on most of the additional sites (Appendix 4).

Of the 40 species, four were found only once and 10 twice (Table 3.4). Two species (*Braya thorild-wulffii* and *Melandrium apetalum*) were found exclusively on sites with carbonate rocks where they were sometimes frequent (Appendix 4). The fern, *Cystopteris fragilis*, was not particularly restricted to those sites; it was uncommon and was observed occasionally on granitic as well as carbonate sites. *Braya purpurascens* was also associated with carbonate sites since the only granitic site where it was found was G4, a site with granitic parent material but with a mixed glacial gravel deposit rich in dolostone. Two grasses were more frequently encountered on carbonate bearing sites: *Phippsia algida* and *Puccinellia bruggemannii.*

There were 11 species restricted to granitic (and/or sandstone) sites (Table 3.4). Of these some were associated with polar semi-desert vegetation (*e.g. Cassiope tetragona*, *Erysimum pallasii*, *Luzula arctica* and *Poa arctica*). On the other hand, *Cardamine bellidifolia*, a small crucifer was common on the granitic sites, occurring on 65% of them, particularly on those which were relatively barren or which had a recent glacial influence.

3.5.2 Vegetation abundance

Plant cover was very limited; 87% of the 39 'vegetated' sites had less than 5% vascular plant cover and 67% less than 1% (Figure 3.2). Five sites had slightly higher than 5% vascular plant cover and, in the strict sense, may be called polar semi-desert (Bliss *et al.*, 1973). These were G1, G3, G4, AD and AG (see Figure 3.1) with 7.3%, 6.4%, 7.4%, 5.2% and 11.2% respectively (Figure 3.2). Sites AG and AD had been previously described by Batten and Svoboda (1994) and Bliss *et al.* (1994) as exceptionally rich sites with a warmer microclimate.

The bryophyte cover was even lower with 92% of the sites having less than 1% cover and only one site was found with higher than 5% cover (E1, 14.4%; Figure 3.2). The only sandstone site (EM1) had no moss present. There was more variability in the lichen cover; 56% of the sites had less than 5% cover; 33% had between 5 and 25%, and 4 granitic sites (*i.e.* 10%) had larger cover; GB1, E1, J4, AG with 27.4, 33.0, 38.4 and 50.3%, respectively (Figure 3.2). On carbonate substrates, lichen cover was minimal. Site MM4 had no measurable lichen cover. All the sites with more significant total plant cover had a granitic substrate, however vascular species diversity was not directly related to cover (Figure 3.3).

The density of vascular plants was not dependent on elevation and ranged from 0.05 plants/m^2 for the high elevation carbonate site C1 to 66.4 for intermediate elevation granitic site AG (Figure 3.3). The five other sites with more than 30 plants/m^2 were granitic (G1, G3, G5, G6 and J4). Three carbonate sites (W2, AD and X1) and one granitic site (H1) had densities greater than 20 plants/m^2, three of which were above 800 m a.s.l. (Figure 3.3). Site G4 was exceptional among the sites with large cover (7.4%); it had a relatively low plant density (11.2 plants/m^2). The dominance of scattered large plants of *Salix arctica* at this site may account for this exception. A large cover was usually

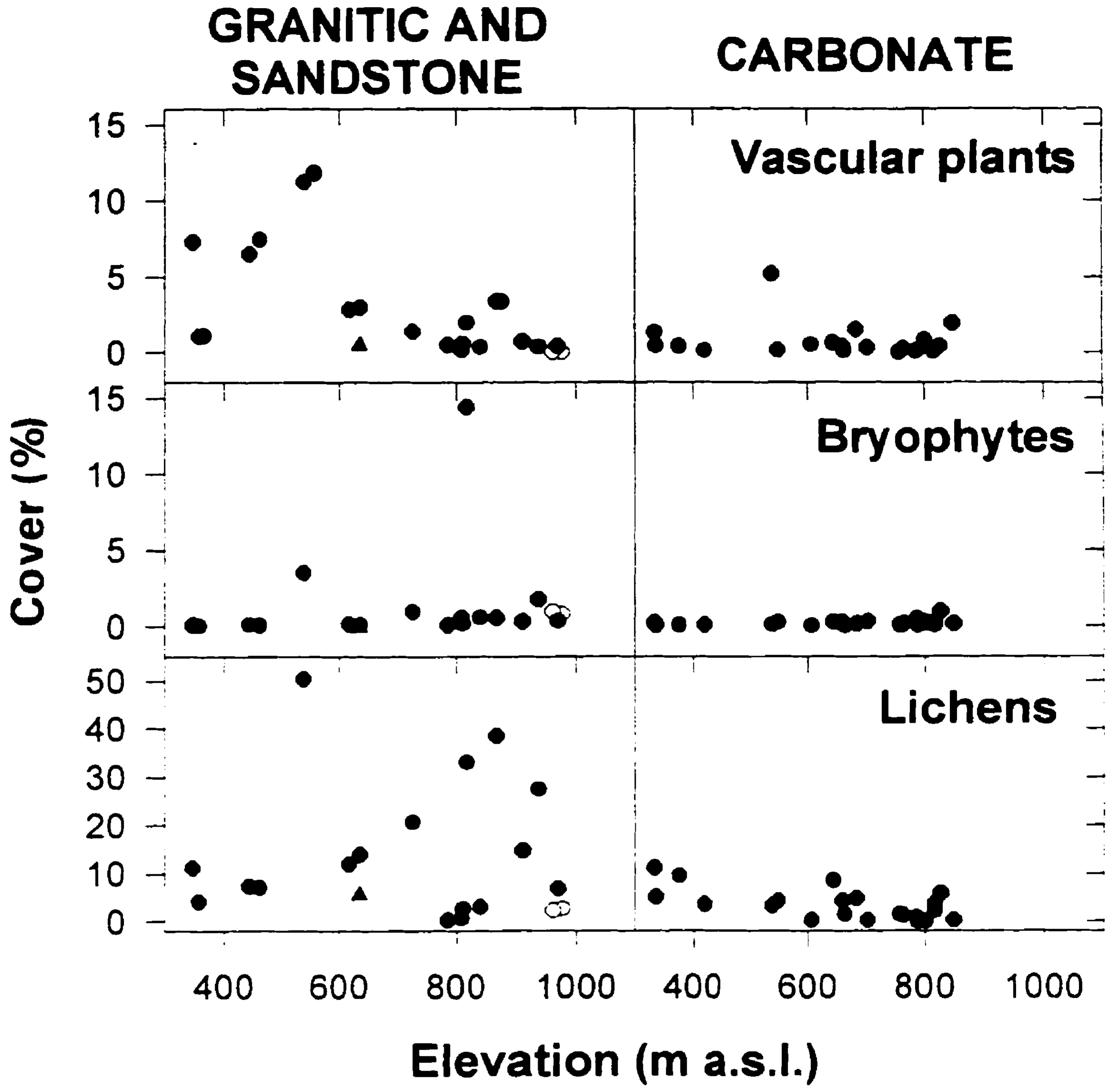


Figure 3.2: Total vascular plant, bryophyte and lichen cover (%) in relation to elevation (m a.s.l.) at 41 polar desert sites from three substrates (granitic, n = 19; sandstone, n = 1; and carbonate, n = 21) in central Ellesmere Island. The sandstone site is presented by a triangle; filled symbols represent 'vegetated' sites (*i.e.* with vascular plants, n = 39); open symbols represent 'barren' sites (*i.e.* without vascular plants, n = 2).

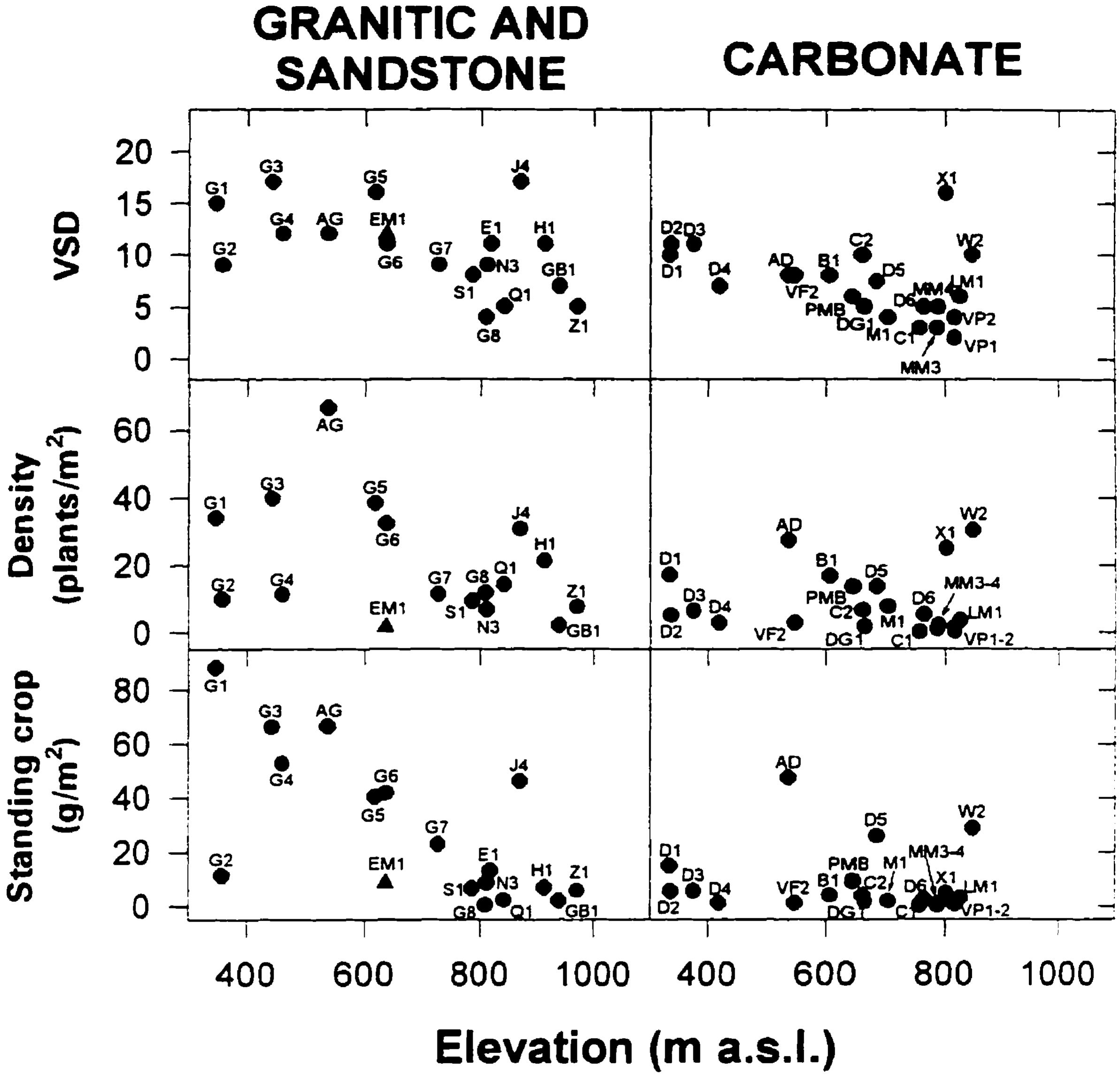


Figure 3.3: Vascular plant species diversity (VSD), density (plants/m^2) and standing crop (g/m^2) in relation to elevation (m a.s.l.) at 41 polar desert sites from three substrates (granitic, n = 19; sandstone, n = 1; and carbonate, n = 21) in central Ellesmere Island. The sandstone site is presented by a triangle; letters identify sites, see Figure 3.1.

associated with more, slightly larger, plants at most other sites. Sites with poor cover had lower densities (Figure 3.3).

3.5.3 Standing crop

According to the standing crop estimates, 64% of the sites had less than 10 g/m^2 of total above ground vascular tissue (living plus attached dead material). The median was 5.8 g/m^2 with a minimum of 0.1 g/m^2 (C1) and a maximum of 88.1 g/m^2 (G1). As mentioned in the Methods, these values were likely overestimates.

Standing crop tended to decrease with elevation on the granitic sites (Figure 3.3), though the low elevation dry ridge site G2 had only 11.1 g/m^2 and the high elevation diverse site J4 had 46.0 g/m^2. The higher standing crops were closely related to the presence of *Salix arctica*, *Carex nardina/Kobresia myosuroides*, *Dryas integrifolia*, *Saxifraga tricuspidata* and to the abundance and size of *Saxifraga oppositifolia* (*e.g.* sites D5 and W2).

The lichen, moss and cryptogamic crust biomass were not estimated, but was generally less than that of the vascular plant standing crop.

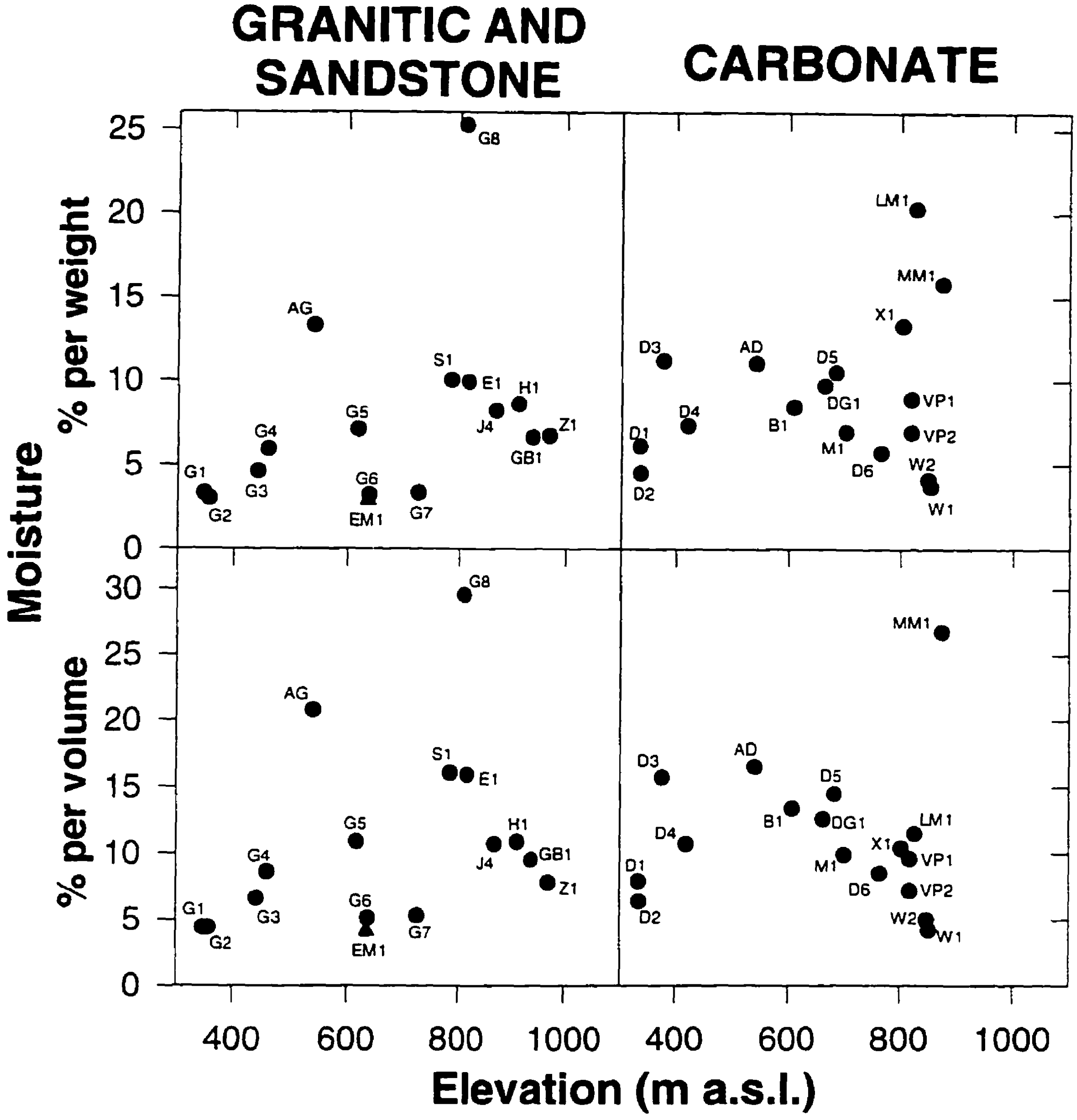
3.5.4 Soil characteristics

The soil development was minimal at all polar desert sites. Gravel, pebbles and stones were present in large proportions. The carbonate sites, in general, had higher pH, larger proportion of compacted silt and clay (Table 3.5) resembling the gleysolic static or the gleysolic turbic cryosols described by Walker and Peters (1977). In contrast, the granitic sites had sandy soils with lower pH and belonged to the regosolic static or the brunisolic static cryosol groups.

The soil moisture values measured from the top 10 cm at one barren and 32 vegetated sites showed large variations (Figure 3.4). The sandstone site had

Table 3.5: Summary of elevation and 7 soil variables (pH, P, K, Ca, OM, Sand, Silt and Clay) for 58 high arctic mountain sites grouped by substrate and according to the presence or absence of vascular plants. Soil variables represent content in the fine soil fraction (< 2 mm); Median (min-max); 45 sites with vascular plants (vegetated) and 13 sites without vascular plants (barren); except for soil moisture: [a] n = 16, [b] n = 1 and [c] n = 15.

Substrate Type	CARBONATE			GRANITE			SANDSTONE
Variables	Vegetated sites (n=26)	Barren sites (n=9)	Overall (n=35)	Vegetated sites (n=18)	Barren sites (n=4)	Overall (n=22)	Vegetated sites (n=1)
Elevation (m a.s.l.)	762 (335-912)	908 (552-1025)	788 (335-1025)	799 (347-970)	970 (770-1003)	811 (347-1003)	636
pH	7.67 (7.08-8.50)	7.75 (7.51-7.93)	7.75 (7.08-8.50)	6.50 (4.98-8.20)	5.20 (4.77-6.20)	6.25 (4.77-8.20)	5.88
P (ppm)	2.9 (0.5-8.6)	2.9 (0.5-6.0)	2.9 (0.5-8.6)	4.3 (1-19.2)	14.5 (3.7-39.0)	4.6 (1.0-39.0)	1.44
K (ppm)	19 (8-30)	16 (6-35)	18 (6-35)	16 (6-42)	10 (8-12)	12 (6-42)	4
Ca (ppm)	2165 (562-2997)	1800 (1665-2547)	1986 (562-2997)	423 (23-2690)	53 (35-84)	280 (23-2690)	45
OM (% dry weight)	4.8 (2.8-13.8)	6.0 (4.0-14.4)	4.8 (2.8-14.4)	2.8 (0.5-12.5)	1.7 (1.1-1.9)	2.2 (0.5-12.5)	0.4
Sand (%)	45.5 (26.7-68.3)	38.0 (27.5-63.9)	44.6 (26.7-68.3)	78.3 (57.6-97.9)	76.8 (62.8-85.0)	78.3 (57.6-97.9)	86.8
Silt (%)	33.3 (10.9-59.7)	32.1 (17.4-54.9)	32.7 (10.9-59.7)	19.2 (0-29.4)	17.8 (8.0-29.2)	19.2 (0-29.4)	9.3
Clay (%)	12.5 (3.7-42.3)	14.9 (5.1-29.9)	12.6 (3.7-42.3)	5.3 (0-13.0)	6.7 (4.7-8.0)	5.5 (0-13.0)	3.9
Moisture (% dry weight)	8.5[a] (3.7-20.3)	15.8[b]		8.2[c] (3.5-25.2)	n/a		2.9
Moisture (% per volume)	10.3[a] (4.2-16.5)	26.7[b]		9.5[c] (4.6-29.5)	n/a		4.1


GRANITIC AND SANDSTONE

CARBONATE

Figure 3.4: Soil moisture per weight and per volume in relation to elevation (m a.s.l.) at 31 polar desert sites from three substrates (granitic, n = 13; sandstone, n = 1; and carbonate, n = 17) in central Ellesmere Island. The sandstone site is presented by a triangle; filled symbols represent 'vegetated' sites (*i.e.* with vascular plants, n = 30); open symbol represents 'barren' site (*i.e.* without vascular plants, n = 1); letters identify sites, see Figure 3.1.

a low moisture content (2.9% dry weight). The medians of the carbonate and granitic sites were almost identical (8.5% and 8.2% respectively; Table 3.5). This was surprising since carbonate soils often appeared to hold more water, but it may be due to the year and timing in the year at which the sites were sampled. In addition, most of the carbonate sites were on isolated plateaus whereas some of the granitic sites were along slopes leading from permanent snow/ice (source of moisture; *e.g.* G8, S1, E1).

A multi-year sampling of soil moisture at a subset of 13 sites is presented in Figure 3.5. The Sverdrup Pass gradient sites were monitored 2 to 4 times per year in 1990, 1991 and 1992. In general, slightly higher moisture contents were found in carbonate soils (overall mean 9.6%), whereas granitic soils rarely had more than 10% moisture (oven dry weight) and their overall mean was 5.1%. The important variability over the course of the season requires caution on the interpretation of this variable from the multi-site, one time only sampling (Figure 3.5). Soil texture was preferred in the analyses (Figure 3.6) since soil moisture was not measured at all sites and cannot be readily interpreted from spot measurements. Soil texture was coarse (loamy sand) on all granitic sites with 70 to 80% of sand (Figure 3.6). Carbonate sites had silty soils with intermediate sand content and variable but generally low clay content (sandy loam to loam; Figure 3.6).

Soil nutrient results are presented as a proportion of the fine soil fraction (*i.e.* < 2 mm fraction), which represent only a portion (generally less than 25%) of the total soil bulk density. In general, soil nutrients were low at all sites (Table 3.5), these values were comparable with previously published information from Greenland (Bay, 1992) and from other sites in the Canadian Arctic (Tedrow, 1977; Bliss *et al.*, 1984, 1994; Muc *et al.*, 1994b) but there was an appreciable variability among the sites (Figure 3.7). At granitic sites, all chemical variables tended to decrease with altitude except for P which was highest at a high elevation barren site (Figure 3.7). Available P and pH were very consistent for the carbonate sites, but OM, K and Ca varied. These three variables were

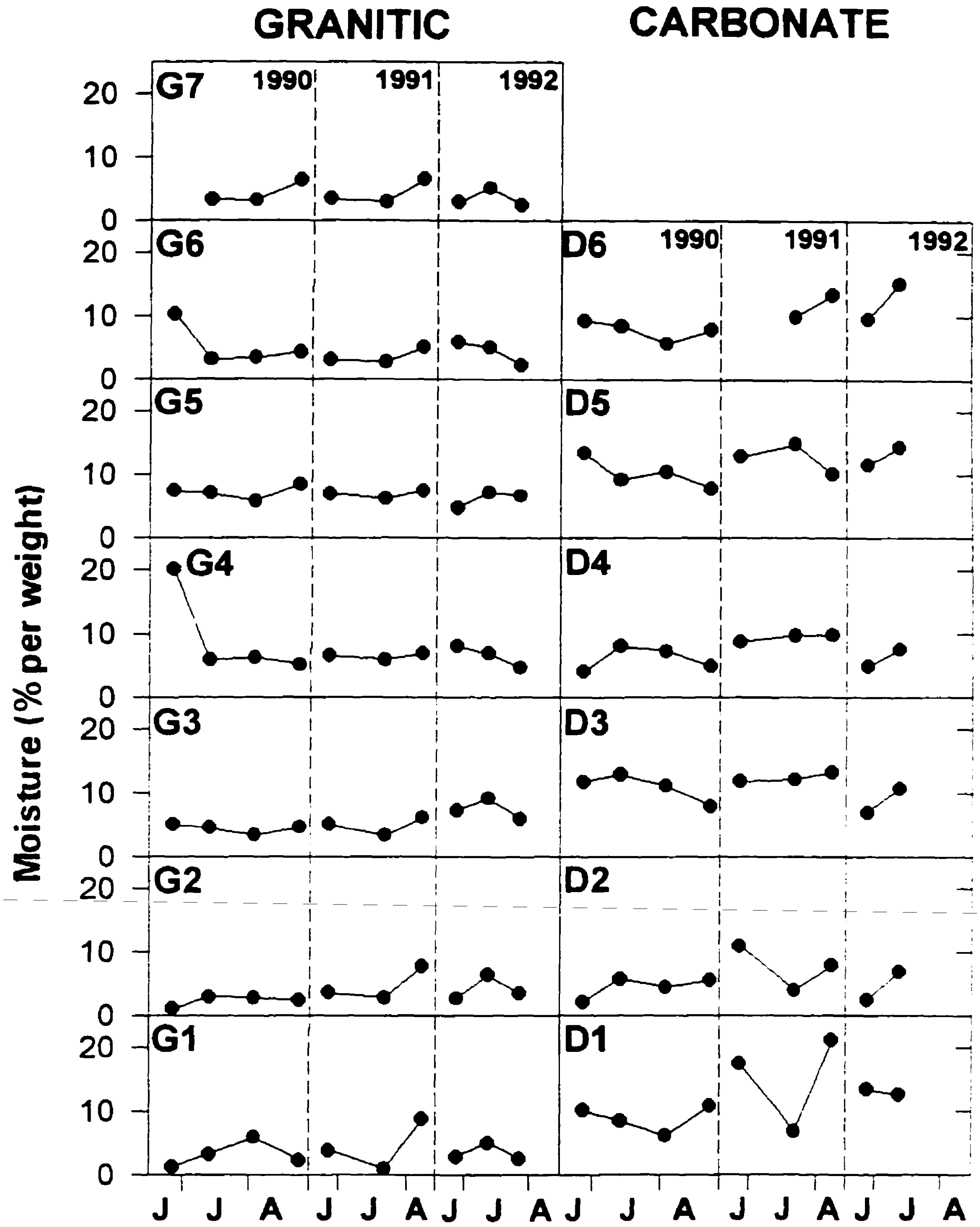


Figure 3.5: Soil moisture per weight over the course of June, July and August (J, J, A) during three summer (1990-92), at 13 polar desert sites along two altitudinal gradients at Sverdrup Pass, Ellesmere Island (*cf.* Chapter 6).

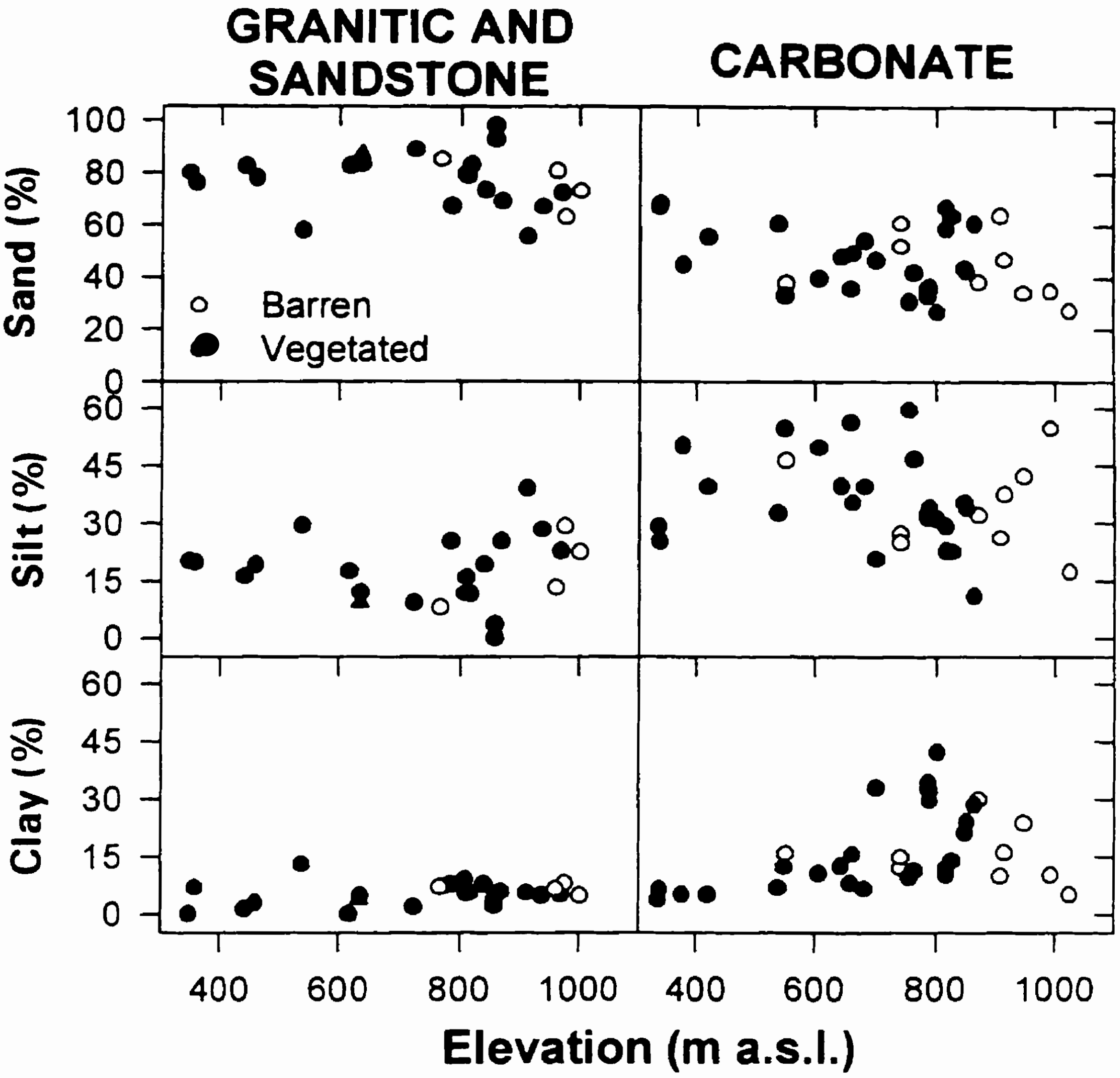
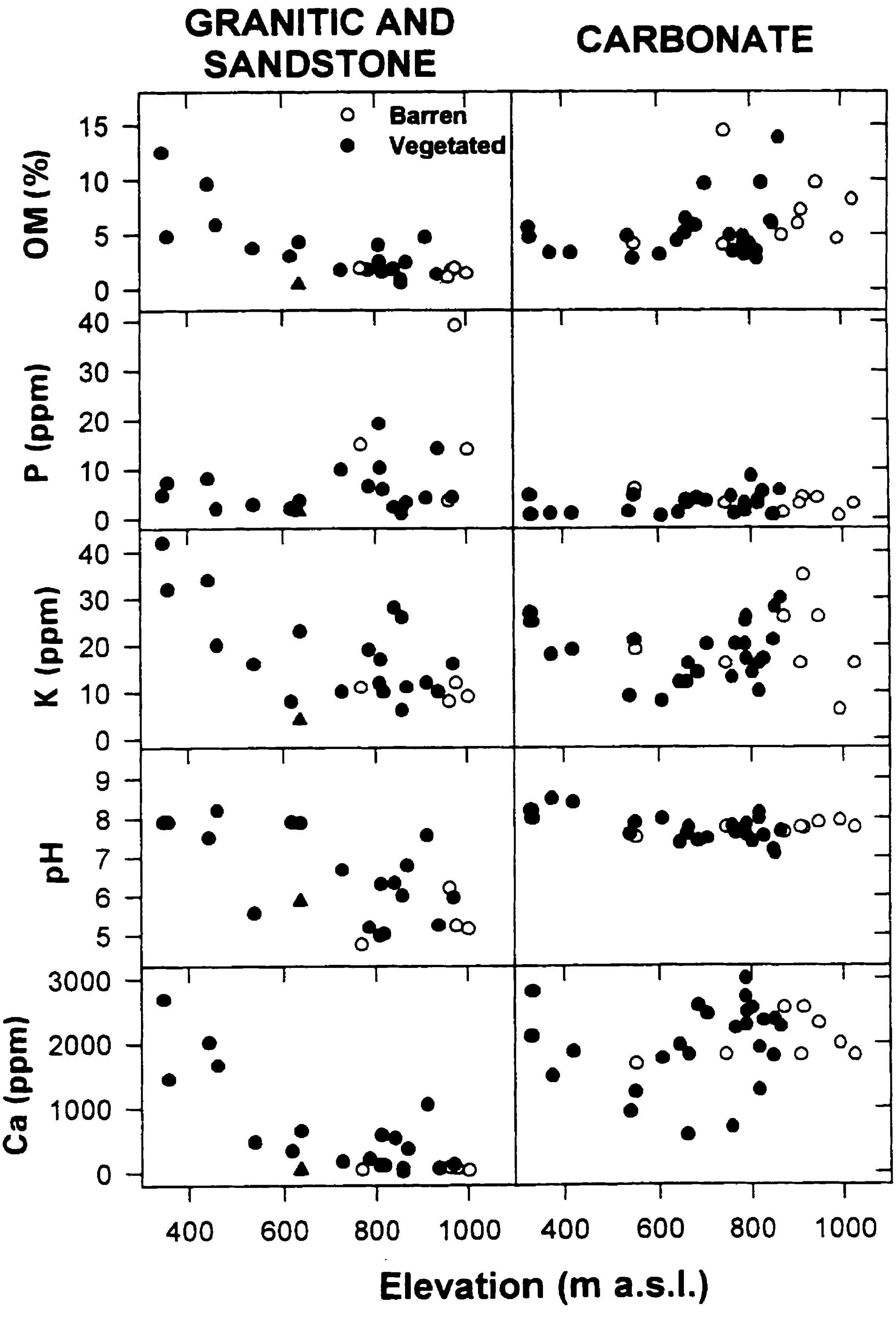


Figure 3.6: Soil texture of finer fraction of top 10 cm soils in relation to elevation (m a.s.l.) at 58 polar desert sites from three substrates (granitic, n = 22; sandstone, n = 1; and carbonate, n = 35) in central Ellesmere Island. The sandstone site is presented by a triangle; filled symbols represent 'vegetated' sites (*i.e.* with vascular plants, n = 45); open symbols represent 'barren' sites (*i.e.* without vascular plants, n = 13).

Figure 3.7: Soil chemical variables (top 10 cm) in relation to elevation (m a.s.l.) at 58 polar desert sites in central Ellesmere Island. The single sandstone site is presented by a triangle; filled symbols represent 'vegetated' sites (*i.e.* with vascular plants, n = 45); open symbols represent 'barren' sites (*i.e.* without vascular plants, n = 13); 5 to 30 replicates were analyzed for organic matter (OM), 3 replicates for the four other variables. See Table 3.1 and Methods for details.


GRANITIC AND SANDSTONE
CARBONATE
○ Barren
● Vegetated
OM (%)
0
5
10
15
P (ppm)
0
10
20
30
40
K (ppm)
0
10
20
30
40
pH
5
6
7
8
9
Ca (ppm)
0
1000
2000
3000
400
600
800
1000
400
600
800
1000
Elevation (m a.s.l.)

highly correlated. Total N was not measured at any site. Previously published results from the Sverdrup Pass gradient sites showed, on average, 0.14 ± 0.07%N (from 0.080 to 0.337%) for the carbonate sites and 0.21 ± 0.04%N (from 0.033 to 0.447%) on the granitic sites (Lévesque *et al.*, 1997; Chapter 7) which were comparable to values obtained at upland sites near Alexandra Fiord (Batten and Svoboda, 1994) but higher than values from more extreme sites (Bliss *et al.*, 1994).

3.5.5 Differences between sites with and without vascular plants

The Multivariate Discriminant Analysis (MDA; Table 3.6), was not able to distinguish reliably between 'vegetated' and 'barren' (no vascular plants) sites, based on elevation, pH, organic matter content, soil chemistry (P, K, Ca concentration) and soil texture (proportion of sand). Only 74.1% and 77.6% of the 58 sites were correctly grouped when the six soil variables were used by the linear and quadratic approach, respectively (Table 3.6). Elevation seemed to contribute to the differentiation between the two groups of sites (Table 3.5). When elevation was included in the analysis, 75.9% of the sites were returned to their true groups by the linear approach and 82.8% by the quadratic approach. The linear approach is more commonly used but assumes a normal distribution of the data whereas the quadratic approach requires less strict assumptions. No clear evidence was found that the vegetated sites differed from the bare sites using either approach when based on physical characteristics alone.

As one would expect, the barren sites tended to be associated with higher elevations (Table 3.5), for example, there was no vegetated carbonate site at more than 850 m a.s.l. (Figure 3.7). Nevertheless, three granitic sites at nearly 1000 m a.s.l. had vascular plants growing on them (H1, GB1 and Z1 at 912 m, 939 m and 970 m a.s.l. respectively; Table 3.1) whereas one carbonate site at 550 m a.s.l. was barren (VF3). Figure 3.7 shows the variation of 5 soil chemical variables (OM, P, K, pH and Ca). The barren sites compared well with

Table 3.6: Summary of the Multivariate Discriminant Analysis (MDA) between sites with vascular plants and sites without vascular plants, performed on 58 samples using 7 environmental variables (Elevation, pH, P, K, OM, Ca, Sand).

	Linear analysis		Quadratic analysis	
Sites:	Vegetated	Barren	Vegetated	Barren
Elevation included				
True groups	45	13	45	13
N correct	35	9	38	10
Proportion returned	0.778	0.692	0.844	0.769
Proportion correct	**75.9%**		**82.8%**	
Elevation excluded				
True groups	45	13	45	13
N correct	35	8	38	7
Proportion returned	0.778	0.615	0.844	0.538
Proportion correct	**74.1%**		**77.6%**	

vegetated sites of the same substrate, having similar values for P, pH and Ca, while OM and K seem slightly lower on the barren granitic sites (Figure 3.7). The same is true for soil texture: no marked differences were visible between the barren and vegetated sites, the differences observed lay between the substrates (Figure 3.6; section 3.5.4). These results suggest that none of the measured characteristics was responsible for the barrenness of these sites. Perhaps there were other factors which could hinder vascular plant colonization and establishment which were not or could not be measured (or estimated) at the study sites. These may have included; wind exposure, soil moisture, time since the site became free of permanent snow or ice, growing season length and distance to nearest site with plants.

The importance of elevation on the dispersion of points on the first axis was confirmed by a number of other exploratory analyses (RDA and CCA). The first axis was significant when the environmental data set was constrained by the binary criteria (presence or absence of vascular on the site) even though the eigenvalues and proportion of variance explained was low (< 5%). However the analysis became non-significant when elevation was eliminated. Twenty four sites were visited from which no soil samples had been collected. These showed similar tendencies; *i.e.* two low altitude carbonate sites had vascular plants (VF1, 550 m and TT, 703 m) whereas 11 carbonate barren sites were found above 700 m a.s.l. (Table 3.1). Although some vascular plants were found in five granitic sites above 800 m a.s.l., four granitic sites with relatively high elevation were also barren (R3, 803 m; R4, 833 m; N1, 1000 m; N5, 1003 m; Table 3.1).

3.5.6 Vegetation analysis

Classification. Classification of the 38 stands (site G8 was excluded, see Methods) using vascular taxa, provided a total of 11 noda at Level 4 (Figure 3.8) and 15 noda at Level 5 (Appendix 5). In view of the low number of available stands, the divisions of the TWINSPAN analysis at the 2nd and 3rd levels will receive special attention. It was possible to distinguish some community types within the groupings despite the low species diversity.

Table 3.7 presents the mean vascular plant cover, diversity, standing crop and density of the four main groups resulting from the second level of division. The most diverse sites were in Group A (14.3 species on average) and the least diverse in Group D (5.8 species on average). There was a marked reduction in plant abundance (cover, density and standing crop) between Groups A-B and C-D (Table 3.7). The first level of division reflected a gradient of plant abundance whereas the second one reflected the division between carbonate and granitic (and sandstone) sites while also reflecting the gradient in species richness (Table 3.7). The indicator species highlighted this difference. On the first axis, two pseudospecies which reflected a larger cover of *Saxifraga oppositifolia* and *Minuartia rubella* were opposed to *Phippsia algida*, the grass found frequently on the most sparsely vegetated sites. Species characteristic of the granitic sites were indicator species of the second divisions (Figure 3.8).

When compared with the constrained indicator species analysis (COINSPAN) constrained by substrate, the eigenvalue of the first axis was reduced significantly (Figure 3.9). Surprisingly, the separation of the sites into groupings with similar substrates happened at the 4th level of division, compared to the 3rd level of division in the previous TWINSPAN analysis. This suggested that although sites of one substrate do tend to have more similar vegetation, the majority of the variance in this data set was not explained by this variable. The first division was based on abundance and diversity in the vegetation.

The TWINSPAN classification produced 7 species noda at Level 3 (Table 3.7) and 13 at Level 6 (Appendix 5). The first nodum (Group 1) at Level 3 contained half of the species sampled. Those species were present almost exclusively in association with sites with high plant cover. These species were absent from the site group D, except for *Poa abbreviata* and *Stellaria longipes*

Table 3.7: General vegetation and substrate characteristics of the four main TWINSPAN sample groups (mean ± SE); and average vascular plant cover for each species according to the eight sample and seven species groups from the TWINSPAN analysis. The number of sites in each sample group is given in brackets; VSD represents vascular species diversity; standing crop is aboveground live and dead attached biomass; dashed boxes highlight sites where species are predominantly found.

Sample group	**A** (7)	**B** (9)	**C** (7)	**D** (15)
Cover (%)	3.6 ± 0.8	3.2 ± 1.2	0.7 ± 0.2	0.4 ± 0.1
VSD	14.3 ± 1.4	11.2 ± 0.7	8.0 ± 1.02	5.8 ± 0.7
Standing crop (g/m^2)	38.7 ± 7.3	25.1 ± .8	7.5 ± 1.3	3.9 ± 1.6
Density (plants/m^2)	28.0 ± 4.3	20.2 ± 6.2	6.9 ± 1.8	7.0 ± 1.9
Dominant substrate type	Granitic	Carbonate	Granitic	Carbonate

	A1 (3)	**A2** (4)	**B1** (7)	**B2** (2)	**C1** (1)	**C2** (6)	**D1** (11)	**D2** (4)
Species group 1								
Stellaria longipes	0.03	0.04	<0.001					<0.001
Carex misandra	0.03							
Carex nardina/Kobresia myosuroides	1.62	0.08	<0.001					
Draba cinerea	0.02	0.002	0.002					
Erysimum pallasii	0.008							
Festuca hyperborea		<0.001						
Melandrium affine	0.03							
Potentilla hyparctica		0.011						
Saxifraga tricuspidata	1.06	0.61	<0.001		0.001			
Draba oblongata	0.05	0.01						
Dryas integrifolia	0.83		0.49	0.34				
Potentilla pulchella	0.003		0.001					
Braya purpurascens			0.04					
Braya thorild-wulffii			0.03					
Melandrium apetalum			<0.001					
Oxyria digyna		0.01	0.02					
Pedicularis cf. arctica				0.006				
Salix arctica	0.003		0.52	0.58	0.01			
Poa abbreviata	0.07	0.15	0.01			0.01	<0.001	
Species group 2								
Luzula confusa		0.05		0.04		0.47		
Poa arctica	0.156	0.16	0.003	0.15	0.08			
Saxifraga caespitosa	0.008	0.004		<0.001				<0.001
Saxifraga nivalis	<0.001	0.03				<0.001		<0.001

Table 3.7 (con't)

Species group 3								
Cerastium arcticum		<0.001	0.008	0.01		<0.001	<0.001	0.005
Minuartia rubella	0.04	0.02	0.03			0.001		<0.001
Puccinellia bruggemannii			0.10				<0.001	0.01
Species group 4								
Draba subcapitata	0.04	0.09	0.05	0.06		0.05	0.06	0.02
Papaver radicatum	0.01	0.07	0.03	0.03	0.75	0.07	0.06	0.03
Draba alpina	0.003	0.003	<0.001			<0.001	0.01	0.002
Luzula arctica		0.003		0.10	0.43	<0.001		
Saxifraga oppositifolia	0.89	1.40	0.36	1.14	0.26	0.23	0.14	0.09
Species group 5								
Draba corymbosa	0.01	0.002	0.03		0.01	0.003	0.02	0.07
Species group 6								
Cardamine bellidifolia		0.01			0.075	0.006		
Draba lactea					0.001			
Draba nivalis					0.01	0.001		
Cassiope tetragona						<0.001		
Species group 7								
Phippsia algida				0.24		<0.001	0.04	0.17
Saxifraga cernua		0.004			0.31	0.006	0.005	0.02
Saxifraga rivularis								<0.001

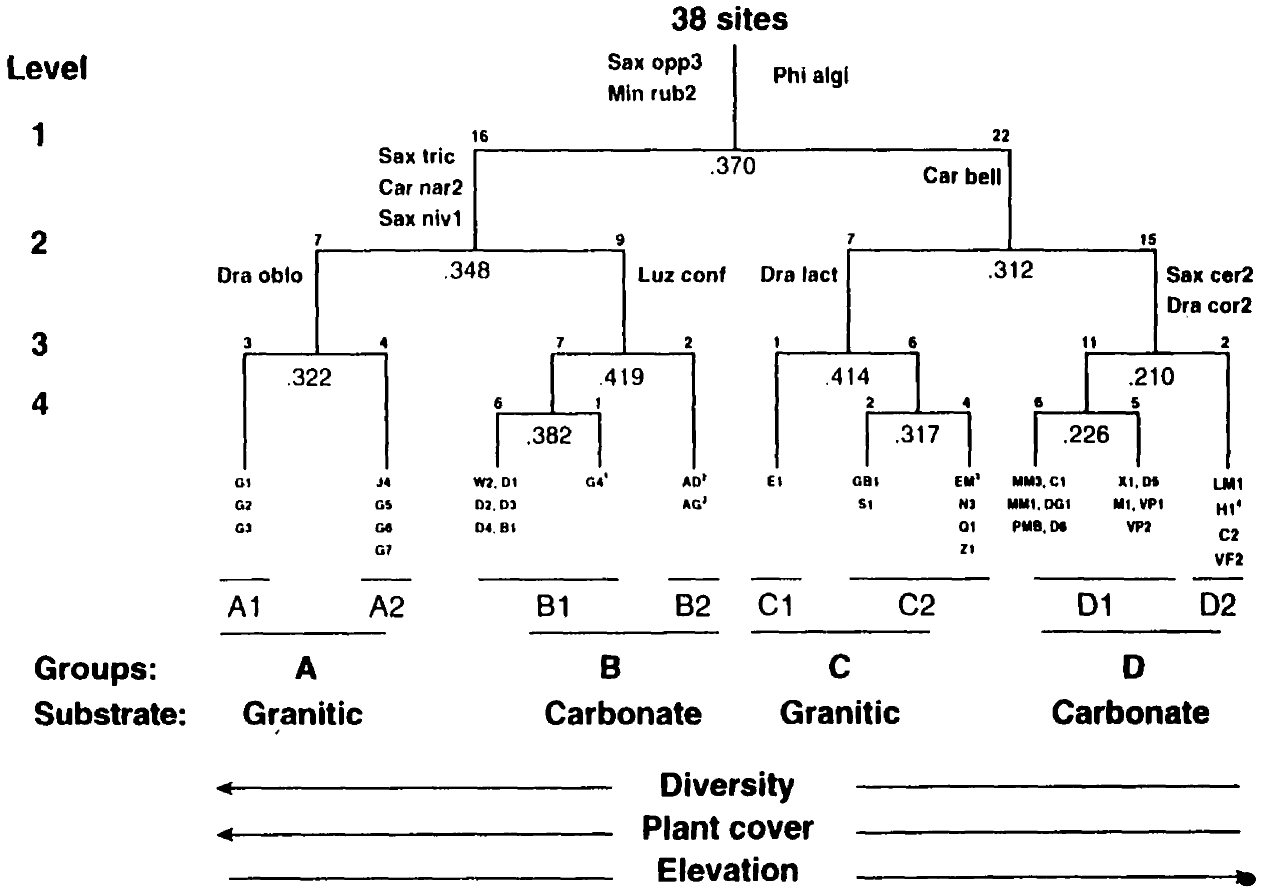


Figure 3.8: Dendrogram of 38 polar desert sites divided by the two way indicator species analysis (TWINSPAN). Eigenvalues are indicated at each division; the indicator species are given with the 3 first letters of the genus and 3-4 letters of the species, the last letter may be replaced by a number indicating the pseudospecies. Sites are represented by capital letters (see Figure 3.1). Soils were similar within each substrate group except: [1] site G4 along the granitic gradient in Sverdrup Pass had a strong admixture of a dolomitic gravel; [2] site AG (granitic) was in close proximity to site AD (calcareous); [3] site EM1 had sandstone substrate; [4] site H1 had granitic substrate.

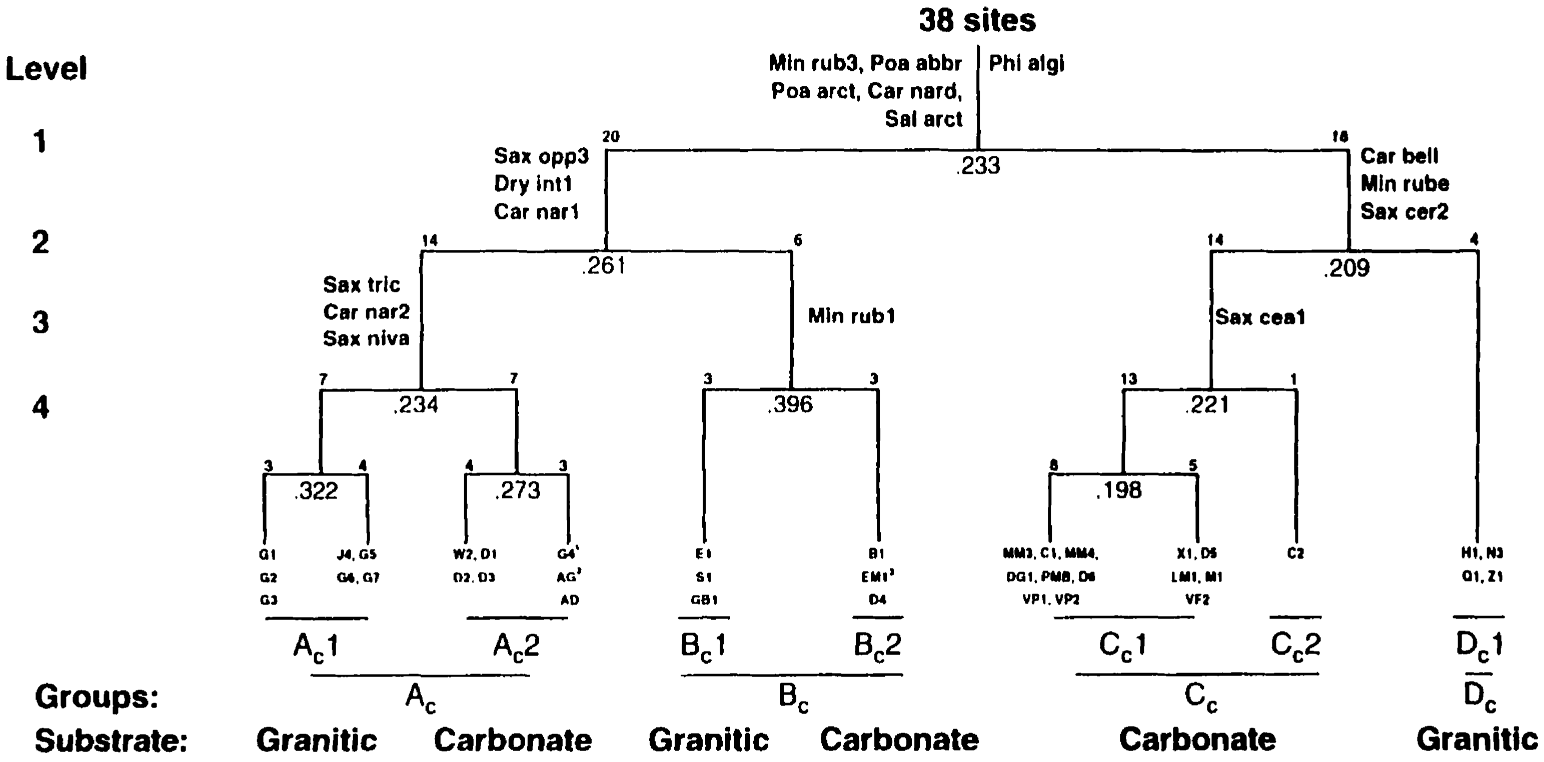


Figure 3.9: Dendrogram of 38 polar desert sites divided by the constrained two way indicator species analysis (COINSPAN). Eigenvalues are indicated at each division, the indicator species are given with the 3 first letters of the genus and 3-4 letters of the species, the last letter may be replaced by a number indicating the pseudospecies. Sites are represented by capital letters as in Figure 3.1. Soils were similar within each substrate group except: [1] site G4 along the granitic gradient in Sverdrup Pass had a strong admixture of a dolomitic gravel; [2] site AG (granitic) was in close proximity to site AD (calcareous); [3] site EM1 had sandstone substrate.

(Table 3.7). Two sub-groups of similar sizes can be distinguished after one more division. The first one dominated by *Saxifraga tricuspidata* and *Carex nardina/Kobresia myosuroides*, and the second one by *Dryas integrifolia*, *Salix arctica* and *Braya purpurascens*. This division corresponded relatively well with the division between granitic and carbonate sites (Table 3.7 and Appendix 5).

Species Group 2 has only 4 species; *Luzula confusa*, *Poa arctica*, *Saxifraga caespitosa* and *S. nivalis*. They were most frequent at granitic sites but were not restricted to the more productive sites (Table 3.7). Two species from Group 3 (*Cerastium arcticum* and *Minuartia rubella*) were similar to Group 2 except that they were also common on the richer carbonate sites. *Puccinellia bruggemannii* from group 3 was most common on carbonate substrates (exception H1).

Groups 4 and 5 contained the four most frequent species in this study (*Papaver radicatum*, *Saxifraga oppositifolia*, *Draba subcapitata*, *D. corymbosa*). Differences in abundance for *Saxifraga oppositifolia* reflected the productivity of sites (Table 3.7), and may also indicate the age of these sites since last deglaciation.

Finally Groups 6 and 7 contained species more common on the poorly vegetated sites. Group 6 had relatively infrequent species restricted to granitic sites (*Cardamine bellidifolia*, *Draba lactea*, *Draba nivalis* and *Cassiope tetragona*) whereas species from Group 7 grew on particularly barren sites of both substrates (Table 3.7) where relatively high moisture was available.

Ordination. Detrended correspondence analysis (DCA) is used as the basis for the divisions performed by TWINSPAN (Hill, 1979; Jongman *et al.*, 1987). DCA can be used to represent the result of the classification in two dimensions and passive analysis of environmental variables allows one to test the significance of the trends observed with TWINSPAN. The DCA ordination biplots presented in Figures 3.10 and 3.11 were produced using detrending by segments, of the same species and samples as for the classification. The eigenvalues declined

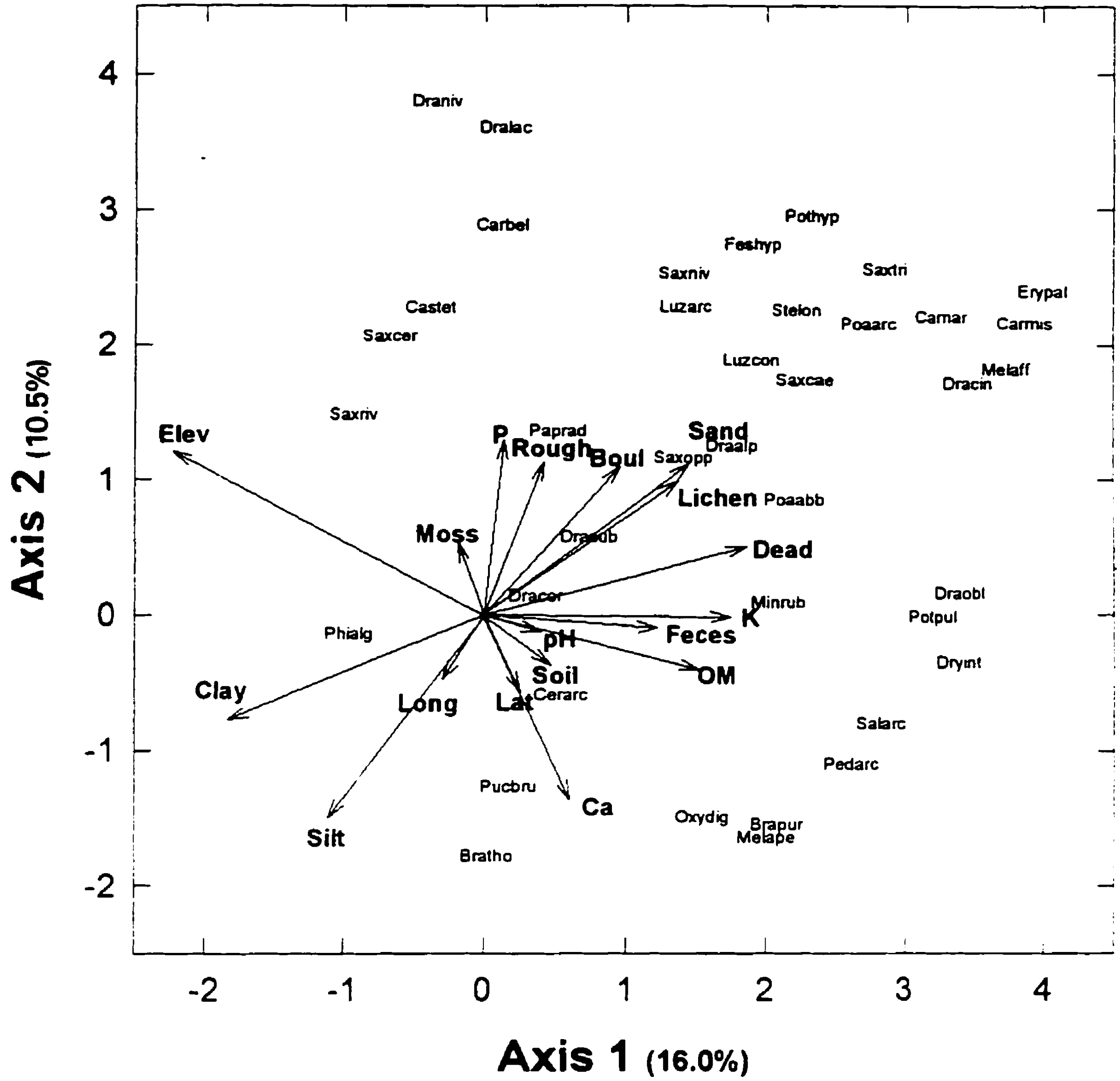


Figure 3.10: Species scores and environmental biplot of the two first axes of DCA$_a$ (Table 3.2). The abbreviations of the 14 environmental variables are given in Table 3.1; species names are combinations of the first 3 letters of the genus and first 3 of the species; see Table 3.6 for complete list of the 39 vascular taxa.

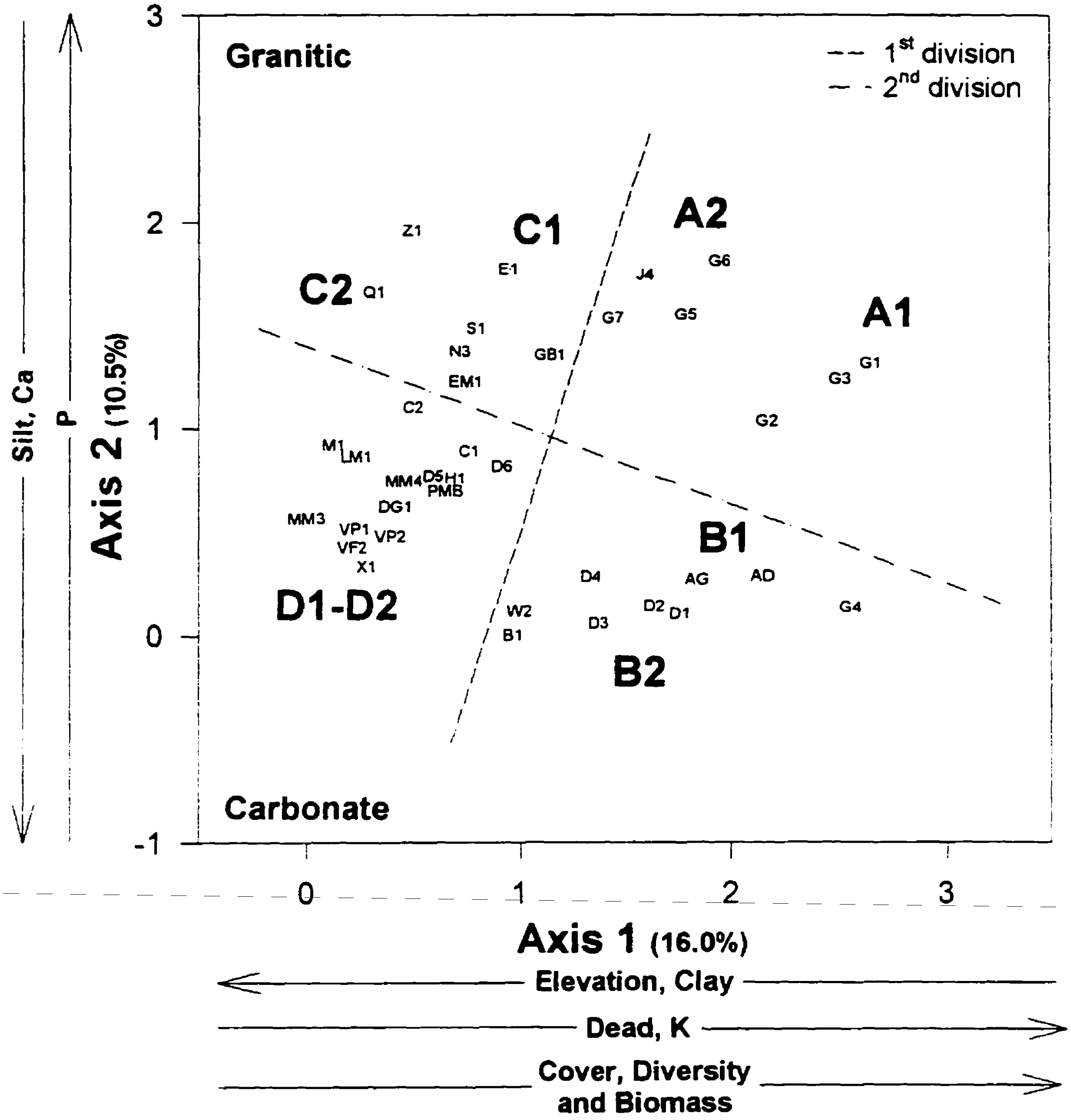


Figure 3.11: Sample scores of the two first axis of DCA_a (Table 3.2) showing the first and second divisions of the TWINSPAN analysis and the eight subsequent groups (A1, A2, B1, B2, C1, C2, D1, D2). 38 polar desert sites are included; sites are represented by capital letters as in Figure 3.1.

rapidly over the first four axes (0.414, 0.269, 0.175, 0.089). The first two axes represented 26.5% of the variance in the data (DCA_a; Table 3.3). The gradient of estimated species turnover along the first axis was relatively low (2.646 standard deviation units; Table 3.3), suggesting that there were still species in common in stands at either end of the first axis. We know that the stands studied here had a few constant species, *Saxifraga oppositifolia*, *Papaver radicatum*, *Draba subcapitata* and *Draba corymbosa*. In the case of longer gradients (s.d.u. > 4) a complete turnover of species may be expected (ter Braak, 1991). When the environmental variables were correlated passively on the DCA axes, the species-environment correlations were strong for the first two axes (0.925 and 0.942 respectively; Table 3.8).

The dispersion of species in this two dimensional space is presented in Figure 3.10. Most of the species had positive loadings on the first axis. Elevation had, by far, the strongest negative biplot score on the first axis followed by clay content (Table 3.8). Taxa from species Groups 6 and 7 were the only groups associated with the negative end of the gradient. Dead material and K had the largest positive scores on the first axis which was associated with higher species diversity and sites with larger plant abundance (Table 3.7). The second axis opposed silt and Ca at the negative end and P at the positive end (Table 3.8; Figure 3.10) and distinguished taxa more common on granitic substrate (positive loadings) from those common on carbonate substrate (negative to neutral loadings; Figure 3.10).

Figure 3.11 presents the sample plot of the first two DCA axes with the site groups from the classification analysis. More diverse noda (From Groups A and B; Figure 3.8) were easily distinguished up to Level 2, 3 and even 4 on the DCA sample score diagram while the poorer sites (Groups C and D) were not so distinct (Figure 3.11). The trends presented in the environmental biplot (Figure 3.10) are summarized by arrows beside the two axes. The first TWINSPAN division separated the low elevation sites with higher dead material, K and organic matter content from the high elevation sites with fine textured soils.

Table 3.8: Species-environment biplot scores of DCA$_a$ axes 1 and 2 on the 38 polar desert stands, Central Ellesmere Island, Canada. All correlations are passive and the largest ones are highlighted.

	Axis 1	Axis 2
R(Spec, Env)	.9253	.9418
Longitude	-.0442	-.0762
Latitude	.0401	-.0914
Elevation	**-.3566**	.1932
Moss	-.0291	.0854
Lichen	.2187	.1558
Feces	.1961	-.0155
Dead	**.2989**	.0831
pH	.0644	-.0197
P	.0242	**.2065**
K	**.2805**	-.0030
Ca	.0966	**-.2196**
OM	.2371	-.0642
Roughness	.0682	.1812
Sand	.2342	.1803
Silt	-.1830	**-.2419**
Clay	**-.2927**	-.1229
Soil	.0758	-.0605
Boulder	.1531	.1755

More diverse and abundant vascular plant assemblages are associated with the lower sites (Table 3.7). The second axis of division separates the sites by substrate, granitic sites with higher P concentrations and carbonate sites with higher silt and clay content (Figure 3.11).

Constrained ordination. The constrained ordinations had eigenvalues of the first axis only slightly smaller than that of the DCA (Table 3.3), suggesting that most of the vegetation variability was kept in the CCA analysis. This analysis was significant and explained 67% of the variance of the vegetation data set, half of which was in the first three axes (33.6%; Table 3.3). The first axis was significant and the species-environment correlations were very high (approx. 0.950; Table 3.3). This analysis has been furthered by the use of Partial Canonical Correspondence Analysis (PCCA).

The PCCA attributed 50.3% of the variance to the five main environmental components (geographical location, elevation, biological, soil chemical, soil physical; Table 3.2), 7.6% to the two-way interactions and the remainder of the explained variance, 9.3%, to the three-way interactions (Table 3.9). The soil variables measured had a very large contribution to the trace, almost 30% of the variance; 12.8% for the chemical and 16.3% for the physical components, including site roughness (Table 3.9). These two components also had notable two-way interactions among themselves and with elevation. Their interactions with geographical location and biological variables was important only in the three-way interactions (Table 3.9).

Figures 3.12 and 3.13 represent the sample scores and the environmental biplot of this analysis. The importance once again of elevation on the first axis is visible on Figure 3.13. The sample scores dispersed in three zones with most of the granitic sites in the lower portion of the diagram, the ones with smaller cover and diversity in the lower right corner and the sites in the middle left portion of the diagram were associated mostly to TWINSPAN group B, mostly sites at low elevation and with carbonate substrates (Figure 3.12). A

Table 3.9: Orthogonal decomposition of the main sources of compositional variance contribution of the five environmental variables. PCCA of abundance of 39 species from 38 polar desert sites, Ellesmere Island, Canada. Number of variables in each variable given in brackets, see Table 3.1 for abbreviations of environmental variables; ** indicates significance at 0.05 and NS no statistical significance of Monte Carlo permutation test after Bonferroni corrections; ← indicates interaction explaining more than 0.8% of the variance.

Source of variance	Contribution to trace	Percentage	P-value	
Total explained variance	**1.733**	**67.2**	**0.01**	
Unexplained	0.845	32.8		
Total compositional variance (Trace)	2.578	100		
Single factors	**1.296**	**50.3**		
A: Geographical (2)	0.139	5.39	0.02	Bonf: NS
B: Elevation (1)	0.131	5.08	0.01	Bonf: **
C: Biological (4)	0.275	10.67	0.01	Bonf: **
D: Soil chemical (5)	0.331	12.84	0.04	Bonf: NS
E: Soil physical (6)	0.420	16.29	0.01	Bonf: **
Two-way interactions	**0.196**	**7.6**		
A * B	0.006	0.23		
A * C	0.006	0.23		
A * D	0.001	0.04		
A * E	0.016	0.62		
B * C	0.004	0.16		
B * D	0.030	1.16	←	
B * E	0.042	1.63	←	
C * D	0.019	0.74		
C * E	0.007	0.27		
D * E	0.065	2.52	←	
Three-way interactions	**0.241**	**9.3**		
A * B * C	-0.004	0		
A * B * D	0.023	0.89	←	
A * B * E	-0.013	0		
A * C * D	0.016	0.62		
A * C * E	0.025	0.97	←	
A * D * E	0.029	1.12	←	
B * C * D	0.010	0.39		
B * C * E	0.021	0.81	←	
B * D * E	0.018	0.70		
C * D * E	0.099	3.84	←	

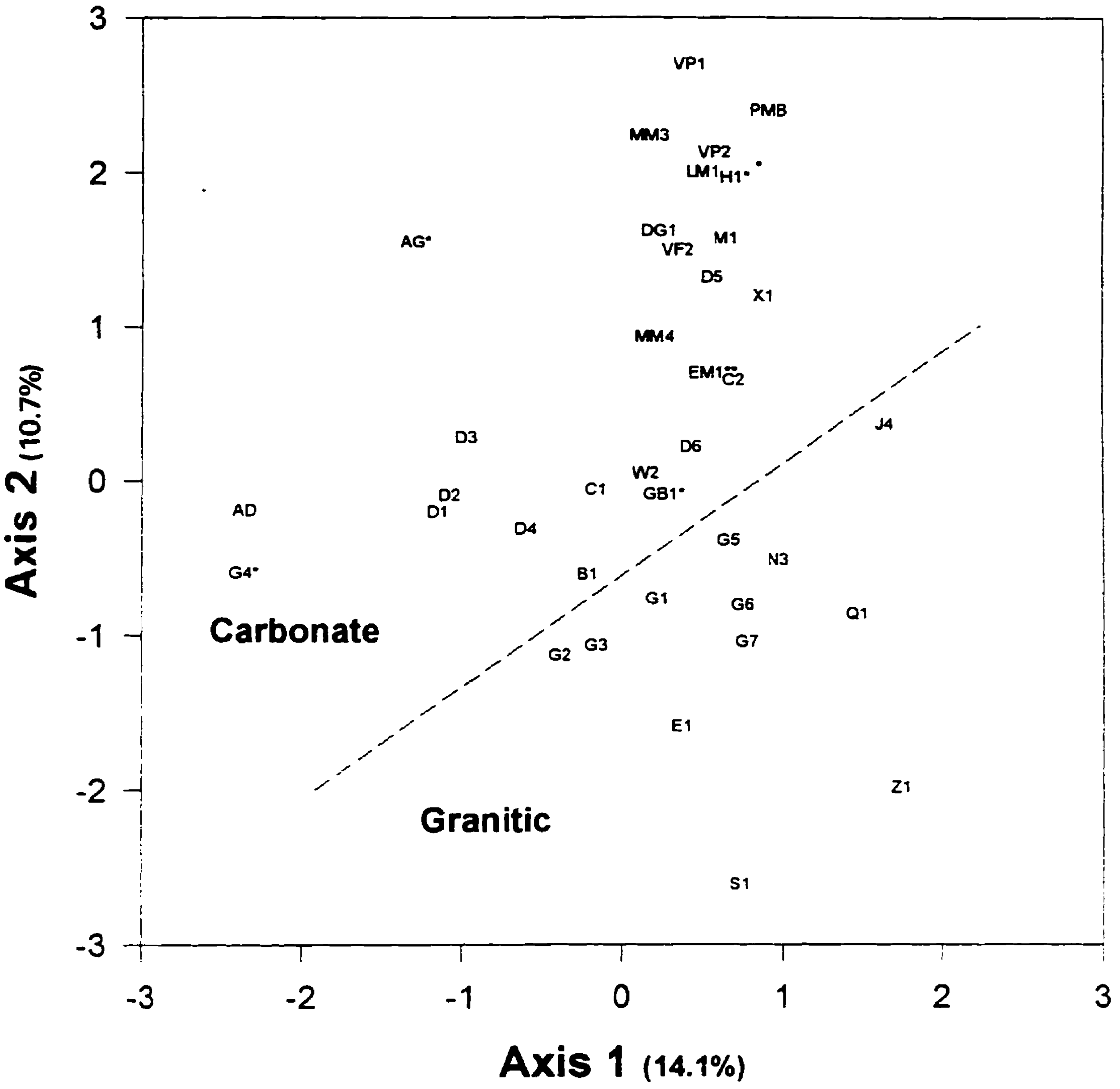


Figure 3.12: Ordination diagram of the two first axes of CCA_a (eigenvalues presented in Table 3.2. Sample scores of the 38 sites represented by capital letters as in Figure 3.1. The diagonal dashed line separates the calcareous and granitic sites; * indicates exceptions: AG and G4 had carbonate gravel on granitic parent material, H1 and GB1 had granitic substrate: ** EM1, had sandstone substrate.

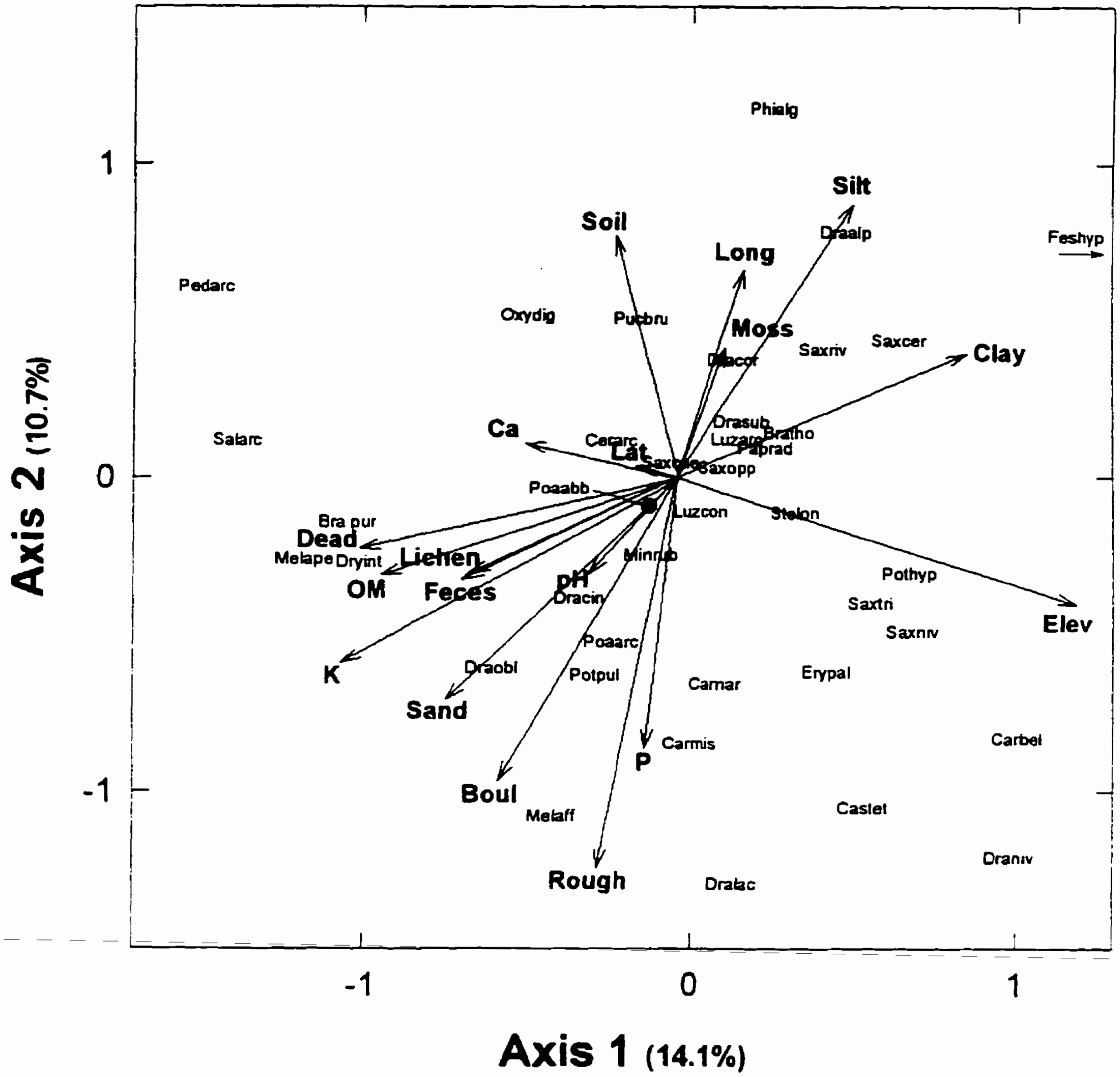


Figure 3.13: Ordination diagram of the two first axes of the CCA$_a$ of 38 polar desert sites presenting the environmental biplot over the species scores. The abbreviations of the 14 environmental variables are given in Table 3.1; species names are combinations of the first 3 letters of the genus and first 3 of the species; see Table 3.6 for complete list of the 39 vascular taxa.

third group of more depauperate and mostly carbonate sites is at the top central part of the diagram.

Elevation was the dominant variable on the first axis and geographical location, the spatial component of this analysis, was partly correlated with the soil variables. In order to test the importance of the remaining environmental variables, these three variables (elevation, longitude and latitude) were used as covariables in the analysis presented in Figure 3.14 and 3.15.

Once the influence of elevation and geographical location were partialled out, the overwhelming importance of soil variables was evident (47% of variance; Figure 3.15). The first axis separated the carbonate sites from the granitic sites (Figure 3.14) with the fine soil variables (silt, clay and Ca content) associated with the carbonate sites and the more coarse soils (sand, boulder and roughness) and higher nutrient content (P, K) associated with the granitic sites (Figure 3.15). The species preferentially found on carbonate sites (Table 3.4) have a high loading on the first axis but do not disperse much on the second axis (Figure 3.15). *Saxifraga oppositifolia* was at the centre of the diagram with the other core species, *Draba subcapitata*, *D. corymbosa* and *Papaver radicatum* slightly towards the positive end of the first axis. The more diverse flora, found mostly on granitic sites, scattered on the negative side of the first axis. On the second axis, of the five species with high loadings, only *Salix arctica* was found at more than 10% of the sites (Table 3.4). It was associated with fine soil and moss cover whereas sites with high roughness had negative loadings on this axis.

3.6 DISCUSSION

3.6.1 Vegetation at polar desert uplands

The present study found a higher number of vascular species on polar desert sites than previous studies, (*e.g.* 40 *vs* 17 and 18 at polar barrens and

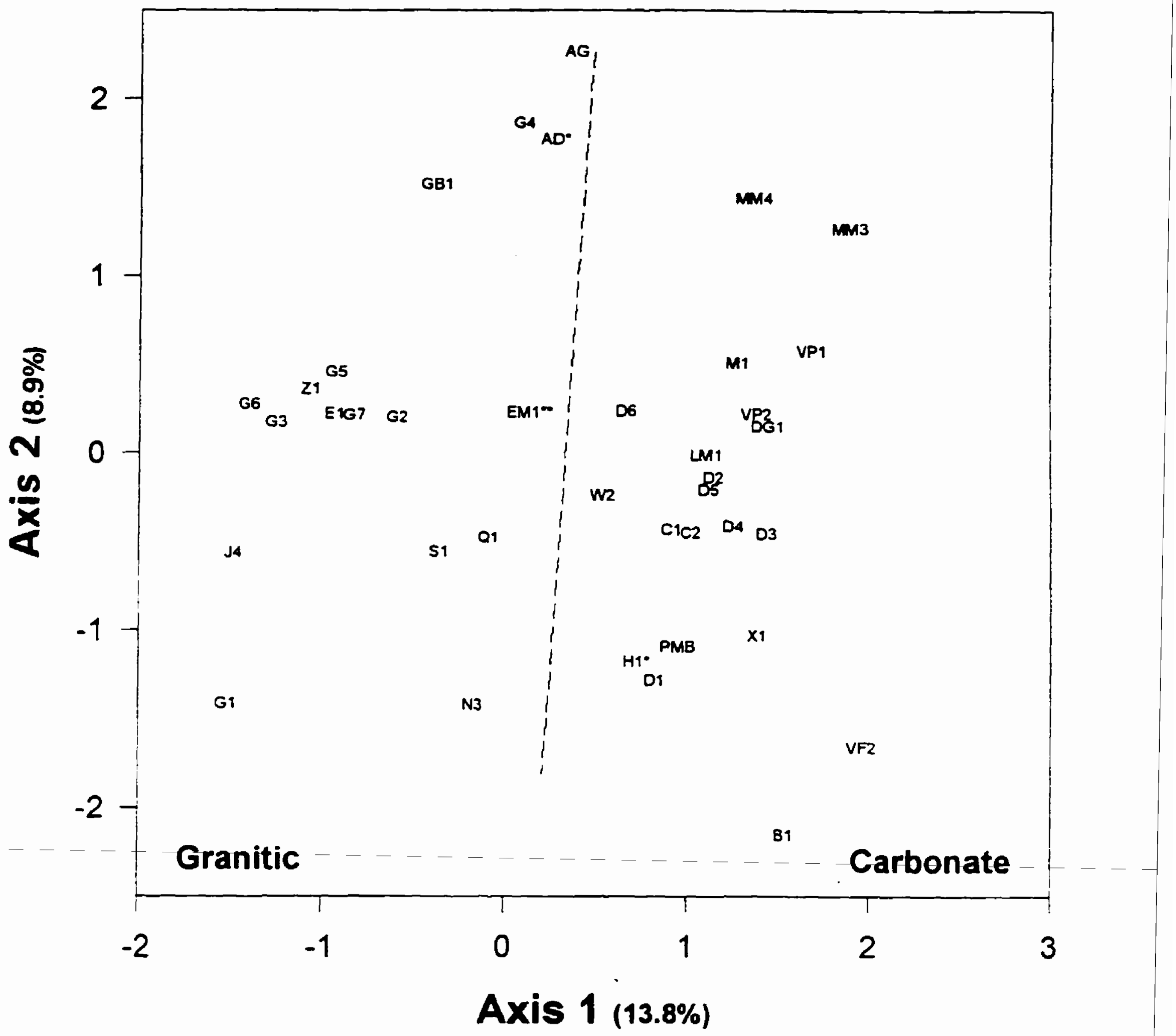


Figure 3.14: Sample scores from the two first axes of CCA_a ordination after extraction of the variance due to three covariables: longitude, latitude and altitude. Sample scores of the 38 sites are represented by capital letters (Figure 3.1). The vertical line separates the calcareous and granitic sites; * indicates exceptions: AD had a carbonate substrate and was in close proximity to AG (granitic substrate), H1 had a granitic substrate; ** EM1, had sandstone substrate.

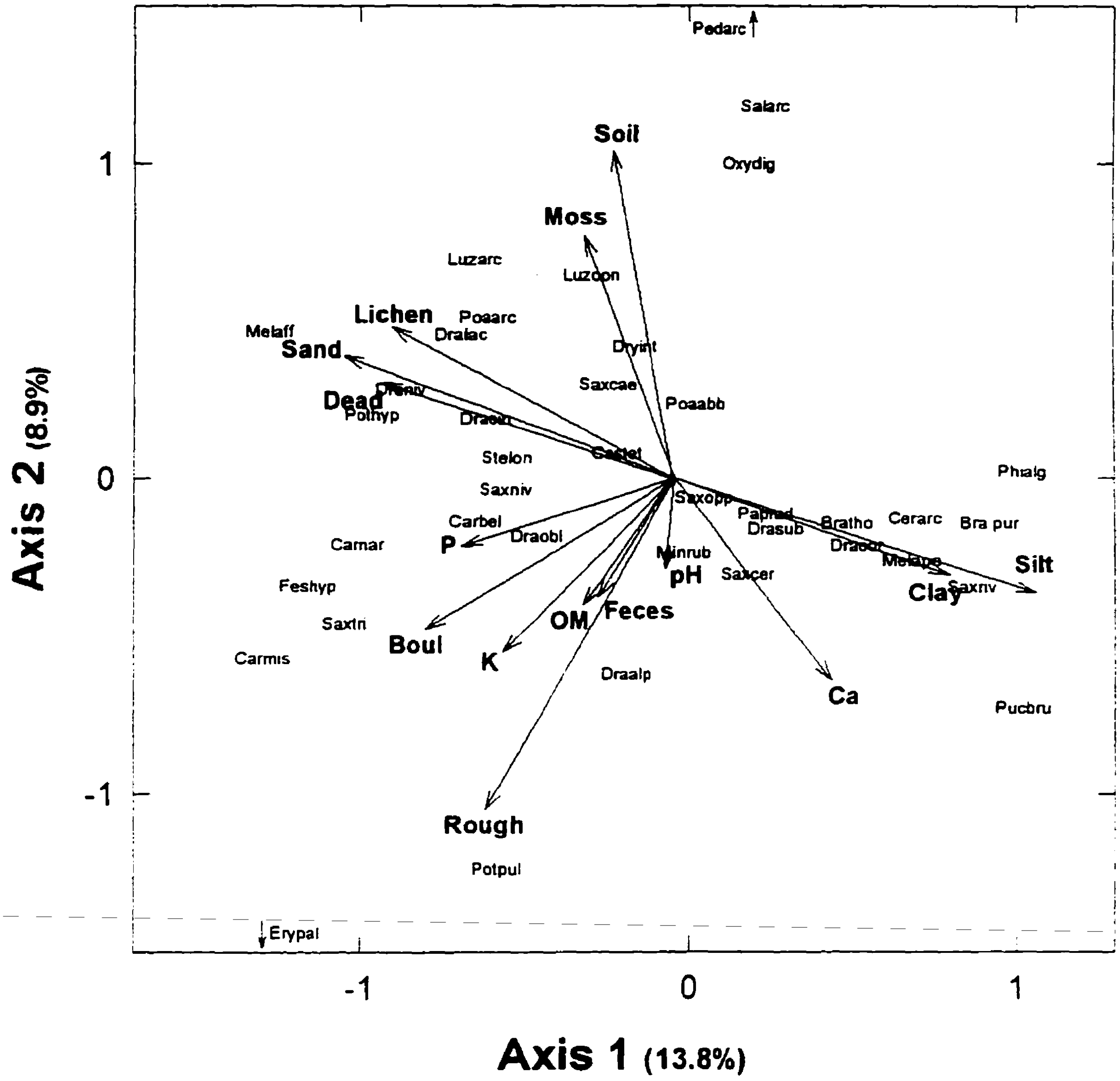


Figure 3.15: Environmental biplot and species scores of the two first axes of CCA_a ordination of 38 polar desert sites after extraction of the variance due to three covariables: longitude, latitude and altitude. The abbreviations of the 14 environmental variables are given in Table 3.1; species are abbreviated by the first 3 letters of the genus and first 3 of the species; see Table 3.6 for complete list of the 39 vascular taxa.

cushion plant community from six arctic Islands, Bliss *et al.*, 1984; or *vs* 22 along an altitudinal gradient at Devon and Alexandra Fiord, Bliss *et al.*, 1994). The broad geographical and altitudinal distribution of the sites studied here and the range of substrate types contributed to the observed species richness. The core group of species present, however, was consistent with that found by previous work (Bay, 1992; Bliss *et al.*, 1994). According to Bliss and Matveyeva (1992), the most common vascular species in polar deserts are: *Draba corymbosa*, *D. subcapitata*, *Papaver radicatum*, *Saxifraga oppositifolia*, *Puccinellia angustata* and *Minuartia rubella*. Five of these species are the five more frequently found species in the present study. We did not find *Puccinellia angustata* but rather one of its more stunted relatives, *Puccinellia bruggemannii* (Porsild and Cody, 1980). Among our 10 more frequently encountered species we also had *Phippsia algida* and *Poa abbreviata* that are reported common, in association with some of the main five species, respectively, on poorly vegetated wet solifluction soils and dry fell-fields in Northern Greenland (Bay, 1992). Finally *Cerastium arcticum* and *Saxifraga cernua* were also frequently encountered.

These species differ in growth forms, but they are all able to establish persistent populations at these marginal habitats. *Saxifraga oppositifolia* is a long-lived cushion plant (often more that 70 years old; Desrosiers, 1991), present and reproducing in most habitats at high latitudes, its seeds can be dispersed long distance (Warren-Wilson 1958; Savile, 1972) and are found in the seed banks (Lévesque and Svoboda, 1995; Chapter 5). The other forb species are shorter lived, though they may persist more than 20-30 years (Savile, 1972; Lévesque *et al.*, 1997; Chapter 6). They invest heavily into seed production, or bulbil production for *Saxifraga cernua* (Maessen *et al.*, 1983; Grulke and Bliss, 1985; Stewart and Freedman, 1994). Of the three grasses, *Phippsia algida* is known to reproduce only by seeds (Grulke, 1995) and the two others were also frequently observed in flower at these extreme sites. In habitats with high spatial unpredictability, as found in polar deserts, the variability inherent in sexual reproduction would procure a genetic potential for coping with that unpredictability (Murray, 1987). This mode of reproduction is by far the most common in polar deserts and semi-deserts.

The woody species (*Salix arctica*, *Dryas integrifolia* and *Cassiope tetragona*) were found only occasionally above 650 m a.s.l. and generally only at sites with higher vascular plant richness. They were also absent from high elevation sites in the gradient study of Bliss *et al.* (1994). Edlund and Alt (1989) suggest that the northern limit of prostrate shrubs is delineated by the 2°C mean July isotherm. They are also often found to invade sites later in succession (Fredskild, 1985; Jones, 1997).

The core group of species occurred across the range of environmental conditions. Two smaller groups of species accompanied the core group in the least vegetated sites. *Cardamine bellidifolia*, *Draba lactea* and *Draba nivalis* were restricted to granitic sites whereas *Phippsia algida*, *Saxifraga cernua* and *S. rivularis* were found on both substrate types (Species groups 6-7, Table 3.7). These species may be particularly suited to invade open landscapes (especially when high soil moisture is available) but may not maintain themselves when larger plant cover develops.

3.6.2 Limitation to plant growth at barren sites

Similarity in nutrient availability and soil physical and chemical characteristics between barren and vegetated sites as found in this study, suggests the importance of other factors at these ecologically marginal habitats. Although edaphic conditions such as poor nutrient and water supply may ultimately be limiting to plant growth, factors such as microclimate, exposure, time of snowmelt, seed import, etc, all closely associated with elevation, may be the initial primary limiting factors.

Since many barren sites were found at high elevations, extremes in low temperatures and growing season length may impede plant establishment, however, barren sites are also found at sea level and there, soil surface moisture may be more restricting (Bliss *et al.*,1994). Gold and Bliss (1995) found that sub-surface soils in polar deserts remained saturated (soil water potential > -0.1 MPa) through the growing season, even though the total moisture content decreased over the season. Adult plants appeared to tolerate drought stress, but surface soil drying was observed and may be hindering seedling establishment.

3.6.3 Classification of polar desert vegetation

In a number of previous analyses of high arctic vegetation various classification and/or ordination tools have been used to distinguish community types (*e.g.* Sheard and Geale, 1983a,b; Bliss *et al.*, 1984; Bliss and Svoboda, 1984, Bergeron and Svoboda, 1989; Forbes, 1994). In general a strong moisture gradient separates the various community types from hydric to xeric: wet meadows (*e.g.* moss-graminoid), willow-lichen and mesic grass meadows, snow beds, snow flush, polar semi-deserts (*e.g.* upland ridge communities, *Puccinellia* barrens and *Phippsia* barrens, *Dryas integrifolia* - dominated community type) and polar deserts (*e.g.* polar barrens, cryptogam-herb, herb barrens, cushion plant fields). Among the groupings recognized as polar deserts (< 5% vascular plant cover), the relative abundance of herbs (*e.g. Papaver radicatum*, Bliss *et al.*, 1984) or cushion plants (*e.g. Dryas integrifolia*, Sheard and Geale, 1983a) determined the grouping. Within each grouping, further subdivisions were not possible (Bliss *et al.*, 1984). The small number of vascular taxa found at any given site and their high constancy (*e.g. S. oppositifolia, P. radicatum, Draba sp.*) make the distinction between plant assemblages difficult to establish (Bergeron and Svoboda, 1989). Based on the large quantity of data collected from the many diverse sites in this study, distinct groupings emerged.

The groups of sites with more diverse vascular plant communities (TWINSPAN groups A1 and B1; Figure 3.8) were characterized by the presence of some shrub species which were also common to polar semi-desert plant communities (*e.g. Dryas integrifolia* and *Salix arctica*; Bliss and Svoboda, 1984). Their species composition was also similar to the dwarf-shrub heath tundra from Northern Greenland (Bay, 1992). The total plant cover, however, was still very low and these communities may be more appropriately referred to as developing versions of the cushion plant community type (sensu Bliss *et al.*, 1984). In time, some of these sites may develop a larger plant cover and thus qualify as a polar semi-desert. The bryophyte cover of these sites was also more meagre than that in polar semi-desert communities (Bliss and Svoboda, 1984; Bliss *et al.*, 1984; Matveyeva, 1994) which suggests that moisture may limit community development. The groups A2 and B2 appeared to be less developed versions of the same types as A1 and B1 above. Some species common to younger sites at higher elevation were still occasionally present (*Cardamine bellidifolia* and *Phippsia algida*). This suggests a continuum among these groupings (Maycock and Fahselt, 1992) and it may be expected that in time different community types may converge.

The poorer sites (groups C1-C2 and D1-D2) more resembled the polar barrens described by Bliss *et al.* (1984) and vegetation on fell-field and solifluction soils described by Bay (1992). They can be referred to as *Saxifraga oppositifolia* herb communities. The woody taxa were generally excluded (the only exception was site E1, in proximity of Alexandra Fiord) and there was an important overlap of species among all four groups.

The relatively clear demarcation between the species assemblages on granitic and carbonate substrates was true for both the more diverse and less diverse sites. In the first case it was mostly due to the preponderance of *Carex nardina/Kobresia myosuroides* and *Saxifraga tricuspidata* on granite and *Salix arctica*, *Braya purpurascens* and *B. thorild-wulffii* on carbonate rocks. At the more depauperate sites it was the presence of species restricted to granite (*i.e. Cardamine bellidifolia*, *Draba lactea* and *Draba nivalis*) and to carbonate substrates (*i.e. Puccinellia bruggemannii*) that separated the sites. These substrate-based community distinctions were similar to those of Elvebakk (1985) based on the phytosociological syntaxa on Svalbard.

The bryophyte and lichen flora of polar desert stands on Ellesmere Island was described in detail in a few studies (Lafarge-England, 1989; Maycock and Fahselt, 1992). Their inclusion in classification of high arctic vegetation always increased the discriminating power of the analyses (Sheard and Geale, 1983a; Bliss and Svoboda, 1984; Maycock and Fahselt, 1992; Forbes, 1996). Still, based solely on the vascular taxa, we observed some distinct plant community groupings among the sites presented here and these were not random assortments of species. Random events certainly influence the exact combination of species found on a given site, but some species certainly were not found in certain groups while others always were present.

3.6.4 Substrate preferences

Site substrate-specific characteristics were important in the distribution of plants in polar deserts. Certain species were associated with high pH, silt, clay and Ca (*Phippsia algida*, *Braya purpurascens*, *Puccinellia bruggemannii*), whereas presence of boulders seemed to be favourable for *Carex misandra*, *Saxifraga tricuspidata*, *Festuca hyperborea* and *Carex nardina*. Finally, *Pedicularis arctica*, *Salix arctica* and *Oxyria digyna* were predominant on sites with fine soil (Figure 3.15). As also observed by Batten and Svoboda (1994), the species diversity at the Alexandra Fiord polar desert plateau was less on carbonate sites. Already in 1913, Simmons noted the poverty of the vegetation of the Silurian districts as opposed to that of the Archean (Precambrian) and Carboniferous districts. He also stated that calcicolous and calciphobous plants hardly exist in the Arctic Islands (Simmons, 1913; p. 135).

Elvebakk (1982) described the vegetation of Svalbard in relation to geological preferences, grouping them as basophilous, circumneutral, indifferent and acidophilous according to their pH preferences. Of the 22 vascular taxa that he discusses the general preference of the 16 species found in our study supports his findings. *Braya purpurascens* is the only basophilous species common to both studies. *Luzula confusa* was the only preferentially acidophilous while *Cardamine bellidifolia* and *Potentilla hyparctica*, classified by Elvebakk (1982) as weakly acidophilous, were found only on granitic (or sandstone) sites. As in his study, most other species were either circumneutral or indifferent to pH. In general, polar desert soils have high pH (Tedrow, 1977) and in this study, only 13 of 58 sites had pH values below neutrality.

3.6.5 Relative importance of environmental factors

Geographical location

The diversity of vascular plants observed in this study and the range of sites visited was more important than in most previous studies of polar desert vegetation. Sites found in close proximity to oases such as Alexandra Fiord or Sverdrup Pass may benefit from a larger and more diverse seed rain and there were a few species found relatively often on nearby sites regardless of the substrate type (*e.g.* in Sverdrup Pass, *Draba oblongata*, *Draba cinerea* and *Carex misandra*). This suggests that the proximity of a seed source is more important for certain species than the substrate type. However, the plant assemblages were not different based on their geographical location. We did not find a strong large scale spatial effect on the vegetation. Longitude and latitude explained 5% of the variance in the data set but this was not concentrated on the first few axes. A large part of this spatial component may be associated to the intrinsic spatial distribution of geological material. Most species were found across a wide area suggesting that no large scale or regional restrictions occurred in the seed source. All the core species found on these polar desert sites have a circumpolar distribution pattern (Porsild, 1964; Hultén, 1971) and are considered widespread to evenly distributed in Northern Greenland (Bay, 1992).

The consistent occurrence of the core group of species suggests a non-random distribution pattern. In addition, the large proportion of the variance in the species composition explained by basic environmental variables imply that part of the differences in plant distribution is associated with environmental variation and is not totally dependent on stochastic events.

Elevation. One of the most clear cut, though not surprising, findings of this study was the negative correlation between the altitude and vascular plant distribution. Altitude was the single most important environmental variable in the various analyses, with a significant contribution to the primary axes of both DCA and of CCA ordinations. Between the vegetated and barren sites the altitude was also the most discriminating variable. This contradicts general observations made by Simmons (1913) and afterwards by Griggs (1934) that in these regions, altitude has little impact on the vegetation. Bliss *et al.* (1994), similarly to Simmons (1913) reported the presence of diverse high cover meadow communities at higher altitude, near Truelove Lowland, Devon Island. These pockets of high productivity in the otherwise almost barren landscape were associated with high moisture availability due to late lying snowbank zones (Bliss *et al.*, 1984; Bliss *et al.*, 1994).

Altitudinal boundaries to plant distribution decrease, on average, with increasing latitude to well below 1000 m at 80°N. However this boundary is not a rigid contour line but, like the altitudinal treeline, it also varies with conditions. The present study suggests that at Central Ellesmere Island, the altitudinal limit for vascular plant presence is between 1000-1100 m a.s.l.. Vascular plants were found at a site as high as 970 m a.s.l (Z1, along Beitstad Fiord) while the few sites sampled above 1000 m a.s.l. were found barren (*e.g.* N1 near Alexandra Fiord, P6 near Mount Lawson and WL near John Richardson Bay).

Elevation is a 'complex' variable since it influences the site microclimate, precipitation, growing season length (Lévesque *et al.*, 1997; Chapter 6) and availability of propagules due to low productivity and increasing remoteness from more abundant seed sources (Lévesque and Svoboda, 1995; Chapter 5). Higher elevation sites are often closer to the present permanent snow zone and may have been covered by snow or ice during the most recent cold episode (Little Ice Age, LIA, approx. 1550-1850 AD; Bray, 1968; Bradley, 1990) as shown by the presence of a 'lichen kill' zone present on certain sites (Svoboda and Freedman, 1994; Plate 3.2).

At carbonate rock sites, the increase in elevation had less effect on the total vascular plant cover. In fact, the highest such site studied (W2, 848 m a.s.l.) had a larger cover than the lowest one (D1, 335 m a.s.l.), 1.9 and 1.3%, respectively. In contrast, there was a distinct decrease in cover at the granitic sites with increasing elevation. The α-diversity, on the other hand, was not associated with elevation, J4 and X1 both at more than 800 m a.s.l., had 17 and 16 vascular species respectively. This suggests that elevation may affect growth rates, but may not be a barrier to seed dispersal and plant establishment. The above statement should, nevertheless, be qualified, since, in absolute terms, the altitude sets the ultimate boundaries for vascular plant distribution, it follows that our high elevation sites with vascular vegetation present were still below the altitudinal limit. Under present climate this limit may be even higher than is the present permanent snow line at these high latitudes.

In marginal habitats (Svoboda and Henry, 1987), as this study is dealing with, minute differences in microclimate may severely affect plant colonization, growth and survival. An increase in altitude of 100 meters may reduce by 40 the total number of thawing degree-days of one growing season (see Chapter 6). However, once established, even in severe conditions most plants seemed able to reproduce, at least during favourable years. Plants in flower and plants with flowering structures from previous years were routinely observed during the field sampling. The clumped distribution of individuals of the same species (Chapter 4, Plate 3.5c) and a direct monitoring of phenology at elevated sites (Lévesque *et al.*, 1997; Chapter 5) confirm that flowering and fruiting occur even at the edge of these plants' distribution.

The most limiting step in the development of plant communities in such locations may be the low seed availability, its low germination success and extremely low rate of seedling establishment. The relatively high plant density (approx. 30 plants/m^2) at some high elevation sites suggests that plant establishment may not be determined by elevation alone. At sites with long enough (> 100 y) history since becoming permanently snow/ice free, lack of surficial soil moisture might have been particularly critical to seed germination and establishment (Gold and Bliss, 1995).

Time and disturbance. One key element in plant colonization, is the period over which the site remains permanently snow free. Dispersal at distances > 5 m is a rare occurrence in low-stature vegetation (Ryverden, 1971; Stöcklin and Bäumler, 1996). The total seed rain was minimal (unpublished data), and the chance of a propagule reaching a safe site and successfully establishing there is low. Plant densities on these sites may depend strongly on the number of years available for plant establishment. Certain microsites offer better germination conditions while some sites have seed banks that survived from more productive times. Total vascular plant cover was not always correlated with the number of individuals. For example, G4 had one of the largest cover values (7%) but only 11 plants/m^2. Some willows were large (stem diameter near root approx. 2 cm) which would mean an approximate age of 125 years according to a growth increment measured for plants collected from northern Ellesmere, 82° N (Woodcock and Bradley, 1994). The sizes of the willows at G4 were relatively consistent and maybe establishment occurred mostly in the first few years after ice release, when the area was still moist. These plants continued to grow and expand but few new ones established in subsequent years. Seedlings were rare on most polar desert sites visited (Lévesque unpub.) suggesting that conditions for their establishment may have changed over time.

Organic matter content, feces and dead material (litter), all accumulate very slowly in the polar deserts. They also showed a negative correlation with elevation on the first CCA ordination axis. Clearly biological activity and productivity slows down with increasing altitude. Higher sites may have been released from the permanent snow or ice later than the lower lying sites. Unfortunately, no reliable measure of the time of release is available for the studied sites. Some minimum ages can be derived from the size of the largest plants (*e.g. Salix arctica* (Woodcock and Bradley, 1994) or *Saxifraga oppositifolia* (Desrosiers, 1991; Chapter 4).

Lichens often establish soon after the site's snow/ice release (Fahselt *et al.* 1988; Maycock and Fahselt 1992) and the total lichen cover may reflect the time sequence since the site was ice-free. However their rate of growth depends on many factors. The same lichen cover may be of quite a different age depending on the species found. All the carbonate rock sites sampled had a very low lichen cover (< 1%). Although Maycock and Fahselt (1992) found a very diverse lichen flora on carbonate screes, the total cover of macro-lichen was low, as found in this present study. Soil lichen cover values may therefore be of little help in estimating when the site became ice free.

Granitic sites AG, J4, E1 and H1 had more than 25% of their ground surface covered by lichens. These sites also supported more than 10 vascular plant species. It is interesting to note that although vascular plant cover at the AG site was high (> 10%), the other three relatively diverse sites above had between 0.7 to 3.3% cover. Sites with high ground surface lichen cover had relatively large vascular species diversity, but not necessarily large cover. The abundance of these soil lichens can not be associated with age, but rather with soil surface moisture (Bliss *et al.*, 1994) and stability (Bay, 1992). However, some granitic sites with a particularly low lichen cover did not seem to lack soil surface moisture (G8, Q1, S1 and N3; nunatak sites and sites in the proximity of the ice margin); the particularly young age of these sites and maybe a more intense frost activity partly may explain the low lichen cover.

The high ground surface lichen cover observed in this study corresponds with the abundance of a cryptogamic crust described by Bliss *et al.* (1994) during their sampling of sites at Alexandra Fiord. They described this crust as having large amounts of the lichen *Catillaria subnegans* and cyanobacteria. These crusts form only where surfaces remain moist in the summer (Gold and Bliss, 1995) and our results from sites with high lichen cover agree with this statement. For example, AG had very late laying snow in June (Henry personal communication) and E1 was in proximity to a permanent snowbank and at the margin of a recently released zone with abundant melt water, as suggested by the pink colour of the non weathered protruding boulders (Plate 3.3b).

Soil disturbance by freeze-thaw processes can also short-circuit plant community development (Raup, 1969; Anderson, 1996). The moist, fine-grained carbonate rock substrates are more inclined to frost activity (French, 1987). Although the rate of disturbance is relatively low (Washburn, 1989), it may be sufficient to hinder the already limited plant establishment. Frost activity may partially explain the similar plant cover on all carbonate sites. Though plant growth would be expected to be more important at lower (generally warmer) elevation sites the differences were minor among sites.

3.7 CONCLUSIONS

Despite strong environmental constraints, vegetation growing in the polar desert zone may be diverse (Bay, 1992; Maycock and Fahselt, 1992). A few consistant groupings of species were recognized: those, more diverse, where dwarf shrubs and Cyperaceae were present (cushion plant communities) and those where these species were absent and *Saxifraga oppositifolia* was dominant with *Draba subcapitata, Papaver radicatum* or *Phippsia algida* (*Saxifraga oppositifolia* herb communities). The environmentally most stressful landscapes, often described as barrens, do sustain a very low vascular species diversity and abundance, and they are dominated by a few species found circumpolarly at such sites. In the central portion of Ellesmere Island, the altitudinal limit to vascular plant distribution was estimated at 1000-1100 m a.s.l..

The bryophytes and especially lichens grow at higher elevation. In addition, their species diversity is higher than that of vascular plants, particularly if care is given to sample the full range of microsites (*e.g.* crevices, between rocks, rock surfaces; Lafarge-England, 1989), yet their cover is also low (Maycock and Fahselt, 1992).

Soil nutrient levels were very low, and most vegetated sites did not have more available nutrients than had the totally barren ones. Nutrient availability might certainly be restricting plant growth in such habitats since higher nutrients were found in the more diverse and productive habitats (Muc *et al.*, 1994b). However, shortage of nutrients may not prevent the establishment of vascular plants on polar deserts. The low nutrient availability alone cannot explain the total absence of plants, or absence of some species and their low abundance at certain sites. The relatively short period with soil surface moisture (Bliss *et al.*, 1994 and Gold and Bliss, 1995) and the presence of soil surface disturbance due to soil settling and needle ice (Anderson, 1996) have also been suggested as factors which limit successful plant establishment.

The findings of the present study support the Succession/Retrogression model at marginal habitats as developed by Svoboda and Henry (1987). The core species are those that establish and maintain a population whereas some taxa, found in extremely low numbers on sites, may not succeed in producing a 'stable' population. We thus suggest that in polar deserts 1) recruitment of new plants certainly depends first on the availability of viable seeds and 2) on favourable physical conditions (temperature and moisture). In marginal polar environments the availability of favourable (safe) microsites may be extremely scarce (Sohlberg and Bliss, 1984) even though most of the land is bare. These questions will be addressed in Chapter 4 and 5.

CHAPTER 4:

MICROSCALE DISTRIBUTION OF PLANTS AND MICROTOPOGRAPHY IN A POLAR DESERT SITE, CENTRAL ELLESMERE ISLAND, CANADA

4.1 ABSTRACT

In order to test the availability of vacant 'safe sites', the spatial distribution of plants on a sparsely vegetated dolomitic plateau (765 m a.s.l.) was studied in central Ellesmere Island, Canada (79°N). The vegetation (vascular plants and bryophytes), the boulders and the frost boils of a 10 m x 5 m plot were mapped to the closest centimetre and the microtopography of the plot was surveyed at a 10 cm x 10 cm scale. The data were processed using GIS tools. Plant spatial dispersion was tested with the variance to mean ratio and spatial autocorrelation. The distribution of plants in relation to microtopography, to distance from shelter (*e.g.* boulders) and from adult plants was tested with G-tests.

Total plant cover and density were low (0.16% and 6.9 plants/m^2). The three main species found on the site were *Draba subcapitata* (n = 300), *Saxifraga oppositifolia* (n = 8) and *Papaver radicatum* (n = 27). Plants were clustered and found preferentially in proximity to boulders and to adult plants of the same species. However, the total bare area in proximity to boulders and plants was much larger than the area covered by plants.

These results suggest that vacant 'safe sites' were abundant, at least spatially, on this dolomitic plateau. However, the rare occurrence of seedling establishment despite the presence of viable seeds suggests that the actual

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'safe site' availability may be restricted in time by extreme environmental conditions (low temperatures, short growing seasons and soil surface drought).

4.2 INTRODUCTION

Vascular plant cover and plant diversity are very restricted in polar desert landscapes (Bliss *et al.*, 1984). In the High Arctic, low temperatures, lax plant growth, a growing season of < 50 days and an arid environment are commonly suggested to explain this phenomenon on a broad scale (Edlund and Alt, 1989; Bliss and Matveyeva, 1992; Chapter 3). Plants have often been found in soil cracks and between rocks (Savile, 1972; Sohlberg and Bliss, 1984; Aleksandrova, 1988), and these microhabitats have been referred to as 'safe sites' (Savile, 1972; Sohlberg and Bliss, 1984). Thus, in addition to climatic limitations, availability of such 'safe sites' (which would protect the seedling and later the plant from temperature extremes, exposure to wind and soil perturbation) could partially explain the extremely low plant cover in inhospitable polar deserts (Walker, 1995). Moreover, the supply of viable seeds may be extremely scarce in marginal habitats (Svoboda and Henry, 1987).

Frost shattered rocks, more or less sorted by frost action, which cover a large portion of the ground, and minimal soil development are characteristic of polar deserts (Tedrow, 1977; Bliss *et al.*, 1984; Muc *et al.*, 1994b). The nutrient availability is very low. Organic matter content is also minimal, except when cryptogamic crusts are present (Gold and Bliss, 1995). Soil moisture is variable but generally not strongly limiting for the growth of adult plants (Gold and Bliss, 1995). Shortages of surface moisture, however, may be critical for seed germination and seedling establishment (Bliss *et al.*, 1994; Gold and Bliss, 1995).

Identification of factors influencing recruitment rates in different plant species is critical to the understanding of population dynamics (Harper, 1977) as well as community processes (Eriksson and Ehrlén, 1992). As pointed out by

Harper (1977), when sampling community structure, it is important to look at the system at the scale of the plant, to avoid recording the pattern of the environment itself. In the Arctic, the regional climate and the macrotopography may dictate large scale distributional patterns of the vegetation (Edlund and Alt, 1989; Bliss and Matveyeva, 1992), but for the tiny perennial arctic plants, the scale of relevance is much smaller (Sohlberg and Bliss, 1984). The importance of microsite and seed availability, as described by Eriksson and Ehrlén (1992), need to be investigated in the context of these relatively young plant communities (Svoboda, 1982).

Requirements for germination and establishment are generally recognized to be species specific (Harper, 1977; Grubb, 1977). In combination with the fine-scale spatial heterogeneity in the habitat, these requirements contribute to the diversity and spatial pattern of plant communities. Such critical elements of the plant community 'regeneration phase' have been studied mainly in grassland systems (*e.g.* Silvertown, 1981; Rabinowitz and Rapp, 1985; Rapp and Rabinowitz, 1985; Fowler, 1985; Ryser, 1993). These elements are not yet well understood (Fowler, 1985) and are difficult to determine (Fowler, 1985; 1988). Seeds have to be trapped in a site where conditions are favourable for seeds to break dormancy, germinate and establish (Chambers and MacMahon, 1994). For instance, a depression may be suitable to entrap the seeds and offer sufficient moisture, but too deep a crack may not offer sufficient light and warmth for germinating seedlings (Chapin, 1993). In addition, the conditions at a site may change over time, especially since the developing plant itself can affect these conditions (Matthews and Whittaker, 1987).

As a first attempt to determine the availability of 'safe sites' in polar deserts we set out to describe the small scale pattern of distribution of plants within the microtopography on a polar desert plateau. This allowed us to establish the characteristics of the on-site plant populations (*e.g.* total number of individuals, plant size distribution) and of the microhabitats (*e.g.* depressions, exposed surfaces, shadow of boulders) in a spatial context. To do so, we mapped the plants and the microtopography of a part of a dolomitic plateau in central Ellesmere Island. Plant community, phenology and microclimate of this upland site have been described previously (Lévesque *et al.*, 1997). The plant community of this site was a part of our other extensive polar desert study (*cf.* Chapter 3).

The specific objectives of this study were to test 1) if the distribution of plants on the studied site is random or clustered, 2) if the distribution of plants relates to the microtopography of the site, 3) if plant distribution is associated with boulders or frost boils, 4) if, in case of a clustered distribution, a positive correlation exists between smaller (younger) and larger (older) individuals which would function as propagule providers. This information will allow us to speculate on the occurrence and abundance of 'safe sites' in a polar desert and of its importance on vegetation distribution.

4.3 METHODS

4.3.1 Study site

The study site was chosen at the top of a dolomitic plateau (765 m a.s.l.), on the north side of the deglaciated east-west valley of Sverdrup Pass, Ellesmere Island, Canada (79°08'N, 80°30'W, Plate 4.1). It was part of a typical polar desert landscape characterized by frost shattered rock, a shallow active layer and sorted and non sorted polygons. This site had a gentle slope (2-3°) with a WSW aspect (Plate 4.2). It was a cold site with a short growing season and a minute plant cover for both vascular plants (0.16%) and bryophytes (0.04%; Lévesque and Svoboda, 1995).

The plant distribution was homogenous over the major portion of the upland ridge (100 m x 50 m). The local vegetation was described and microclimate of this site had been monitored over 4 years (Lévesque *et al.*,

Plate 4.1: The central area of Sverdrup Pass (79°08'N, 80°30'W). The arrow indicates the study area on a large flat dolomitic plateau (760 m a.s.l.).

Plate 4.2: Westward view from the dolomitic plateau (*cf* Plate 4.1) with abundant frost shattered rocks and poorly developed soil, Sverdrup Pass.

1997; *cf.* site D6, Chapter 6). The growing seasons were very short (40+ days) and the cumulative thawing degree-days ranged from 74 to 228 from 1989 to 1993. As in most polar deserts, soil development was insignificant (Bliss *et al.*, 1984). The texture was sandy-loam with 11.4% clay, slightly basic pH (7.6) and high Ca (2200 ppm). Organic matter content (3.4%), percentage N (0.033%) and available P and K (10 ppm and 200 ppm respectively) in the fine portion of the soil (< 2 mm) were low. These characteristics resemble those of the regosolic static cryosol described by Walter and Peters (1977).

Prevailing winds were from the west, and to a lesser degree from the east. Summer precipitation events, primarily fog condensation, mist and occasional snow, totalled less than 50 mm (Lévesque *et al.*, 1997; *cf.* Chapter 6). Soil moisture (top 10 cm) was generally around 10% of dry weight (Chapter 3, Figure 3.7). On June 27 1992 active layer development reached 27 cm.

4.3.2 Mapping of vegetation and microtopography

In July 1992, a 10 m x 5 m plot was selected within the site and marked with guiding ropes, two reference ropes were also fixed at approximately 30 cm above the surface to serve in collection of the microtopographical data (Plate 4.3a). The roped area was partitioned by string into 50 (1 m x 1 m) squares (Figure 4.1). A 50 cm x 50 cm quadrat with 5 cm x 5 cm grid was laid four times over each square meter. The position of vascular plants, bryophytes and feces pellets in each quadrat was mapped and their size measured, using additional reference 10 cm x 10 cm quadrat with a 0.5 cm x 0.5 cm grid (Plate 4.3b). Fecal pellets contribute to the organic matter on the site and they may be a source of nutrients and/or of seeds. They also reflect the activity of herbivores, mostly muskoxen and hares. Seedlings (if cotyledons were visible) were recorded independently but identification to species was not attempted here.

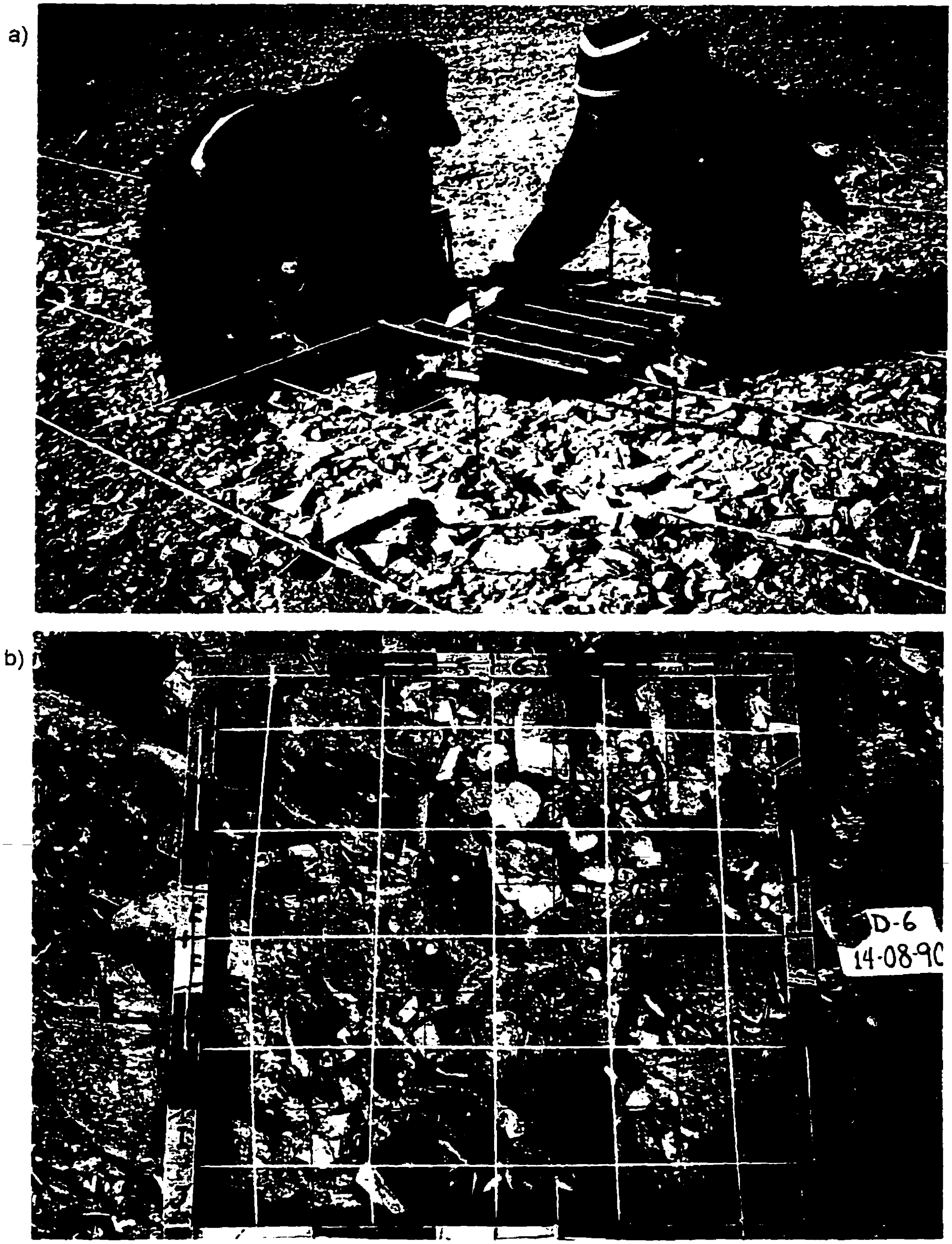


Plate 4.3: Study area on a dolomitic plateau (*cf* Plate 4.1) above Sverdrup Pass. a) Layout of the 10 m x 5 m plot and set up for the microtopographical measurements. b) Close-up of the ground surface showing a *Papaver radicatum* in bloom within the 50 cm x 50 cm quadrat and a *Saxifraga oppositifolia* above the label.

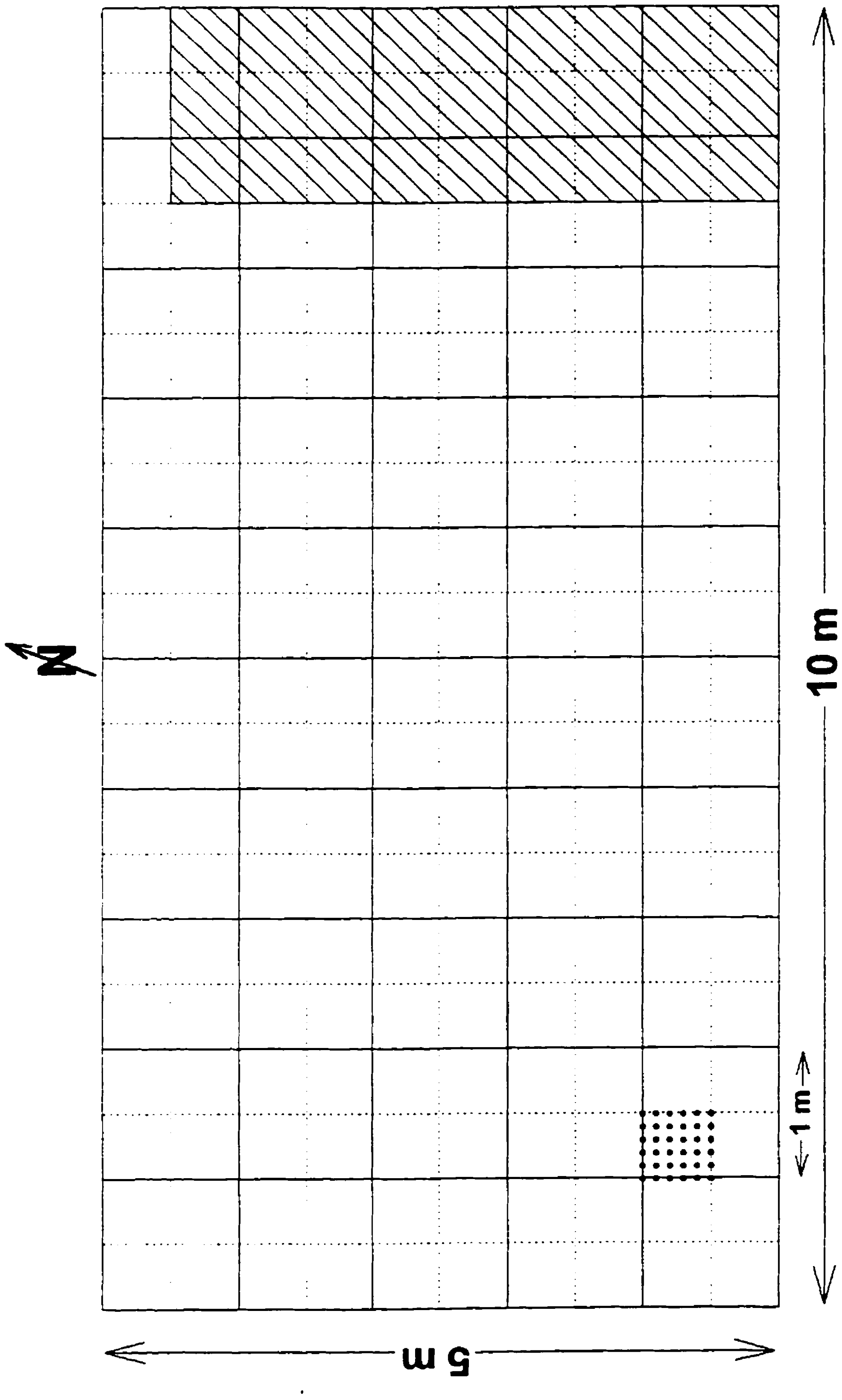


Figure 4.1: Schematic of the sampling design of the 10 m x 5 m plot used on a dolomitic plateau above Sverdrup Pass, Ellesmere Island. The shaded area was sampled for the plant position, but not for the microtopography due to icy snow fall. See Methods for details.

Specimens were collected and vouchers are kept at the Erindale College Herbarium. The nomenclature of vascular species generally follows Porsild and Cody (1980), see Appendix 1. Poor condition of the moss clusters made it impossible to recognize individual species in the field, even less to identify them. For this reason, all mosses were grouped into one bryophyte category. Macrolichens were extremely rare on the soil surface. On rock surfaces their presence was slightly more common but they were not recorded either since they represent a different habitat, unsuitable for colonization by vasculars and bryophytes. For a more detailed description of bryophytes and lichens on similar sites, see Maycock and Fahselt (1992).

The contours of boulders (at least one dimension ≥ 10 cm) and frost boils were drawn to scale onto the map. The surface roughness was assessed for each 50 cm x 50 cm quadrat, with a qualitative index from 1 (flat surface with mostly fine material) to 5 (very rough surface almost totally covered by boulders; *cf.* Chapter 3).

Following the mapping of the plants and boulders, each 50 cm x 50 cm quadrat was carefully levelled with the reference lines (30 cm above the surface). The vertical distance from the reference height to the point on the ground was measured at four corners of the 10 cm x 10 cm grid, so that 100 point measurements were obtained and recorded for 43 of 50 m^2 plots (icy snow deposition prevented completion of the microtopography measurements, Figure 4.1).

4.3.3 Data Analysis

The collected data (elevation, x and y coordinates of the centre of each plant, fecal pellets, contours of boulders and of frost boils) were transferred into the computer using a GIS software (IDRISI, 1990). This enabled us to produce a 2-D (Figure 4.2) and 3-D (Figure 4.3) image of the studied plot, and a number of vegetation maps. Some were with the same grid size as the

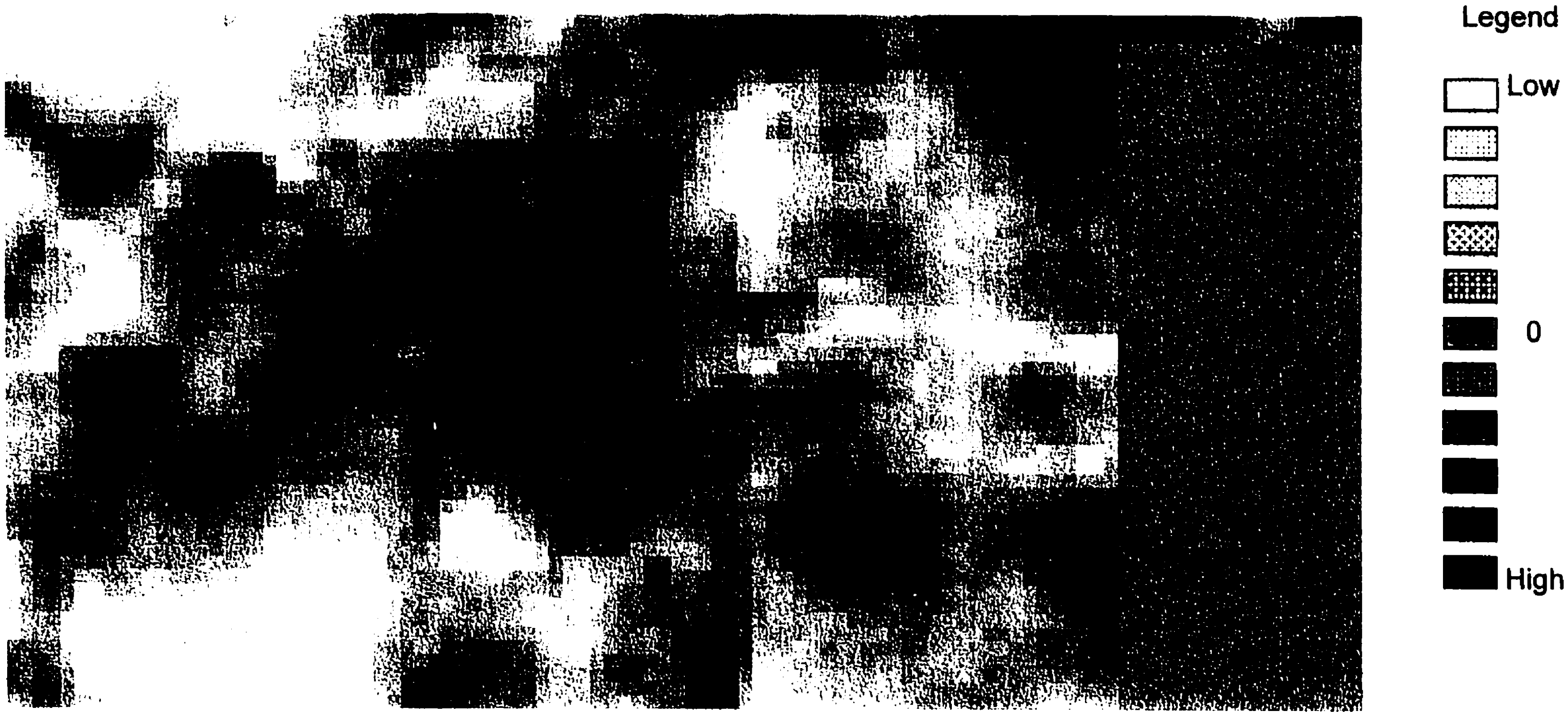
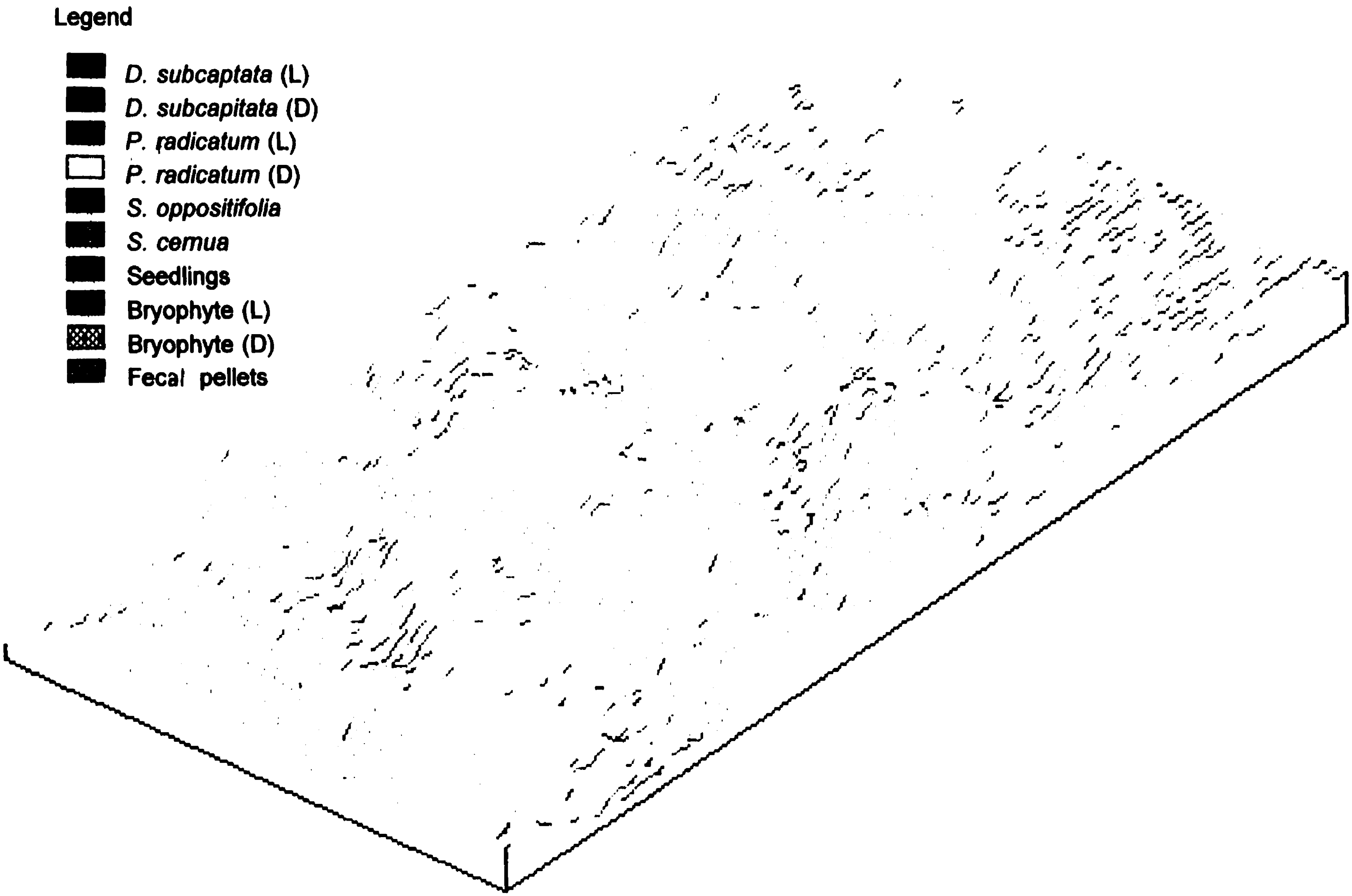


Figure 4.2: Gray shade contrast representation of microtopography model of the 10 m x 5 m plot sampled on a dolomitic plateau above Sverdrup Pass, Ellesmere Island. Each pixel represents the average of 4 measurements taken at the corner of each 10 cm x 10 cm quadrat, the South-East portion which is flat was not measured. Legend: from -15 cm (Low) to +15 cm (High) around the median (0).

Figure 4.3: Three-dimensional representation of the elevation model and of the vegetation map of the 10 m x 5 m plot sampled on a dolomitic plateau above Sverdrup Pass, Ellesmere Island. Each pixel represents the average of 4 measurements taken at the corner of each 10 cm x 10 cm quadrat. The microtopography of the South-East portion was not measured. ‘L’ represents live plants and ‘D’ dead plants.


Legend
▇ D. subcaptata (L)
▇ D. subcapitata (D)
▇ P. radicatum (L)
☐ P. radicatum (D)
▇ S. oppositifolia
▇ S. cemua
▇ Seedlings
▇ Bryophyte (L)
▨ Bryophyte (D)
▇ Fecal pellets

microtopography model (10 cm x 10 cm pixels; Figure 4.4) and some with a more precise location of each entered feature (1 cm x 1 cm pixels; Figure 4.5 and 4.6). Individual plants, boulders and frost boil boundaries were entered onto the map as points, polygons and lines respectively.

Elevation of each pixel represented the mean value calculated from the height measured at each of the four corners of the 10 cm x 10 cm quadrat. Since there was no absolute position of the 'ground surface', an arbitrary mid-point was used, the median of all heights being the theoretical 'ground surface'. The error due to the measurement, transposition of the information from the field to the grid and then to the digitized format is estimated to 0.5 to 1%. These various maps produced were analyzed in a number of ways to determine the number of plants present, their pattern of distribution and their relation with the microtopographic features.

4.3.4 Demographics

The total plant cover, species frequency, plant size and abundance were summarized from the exhaustive list of every individual plant in the plot. After normality was tested with Kolmogorov-Smirnov goodness-of-fit test, Student t-tests were performed to compare means (Zar, 1984). Size classes were established for *Draba subcapitata* plants, small (plant cover ≤ 2 cm^2), medium (2 cm^2 to 4 cm^2) and large (≥ 4 cm^2).

The cushion plant *Saxifraga oppositifolia*, was categorized according to plant age. Age was estimated by using the growth rates measured in hydric, mesic and xeric habitats at nearby Princess Marie Bay, Ellesmere Island (79°27'N, 75°35'W) by Desrosiers (1991). For age assessment of plants at our study sites, the average growth rate of plants of the xeric habitat was used, because these habitats at Princess Marie Bay and Sverdrup Pass plateau were most comparable. *S. oppositifolia* produced 2 leaves per year, the plant sets, on average, 35.5 leaves/cm of the stem length, thus the conversion factor used

Figure 4.4: Vegetation map of the 10 m x 5 m plot sampled on a dolomitic plateau above Sverdrup Pass, Ellesmere Island. Illustrating the presence of vascular plants, bryophytes and feces pellets, in 10 cm x 10 cm quadrats. Legend: *Draba subcapitata* live (1) and dead plants (2); *Papaver radicatum* live (3) and dead plants (4); *Saxifraga oppositifolia* (5); *Saxifraga cernua* (6); Seedlings (7); Bryophytes live (8) and dead clumps (9); Fecal pellets (10).

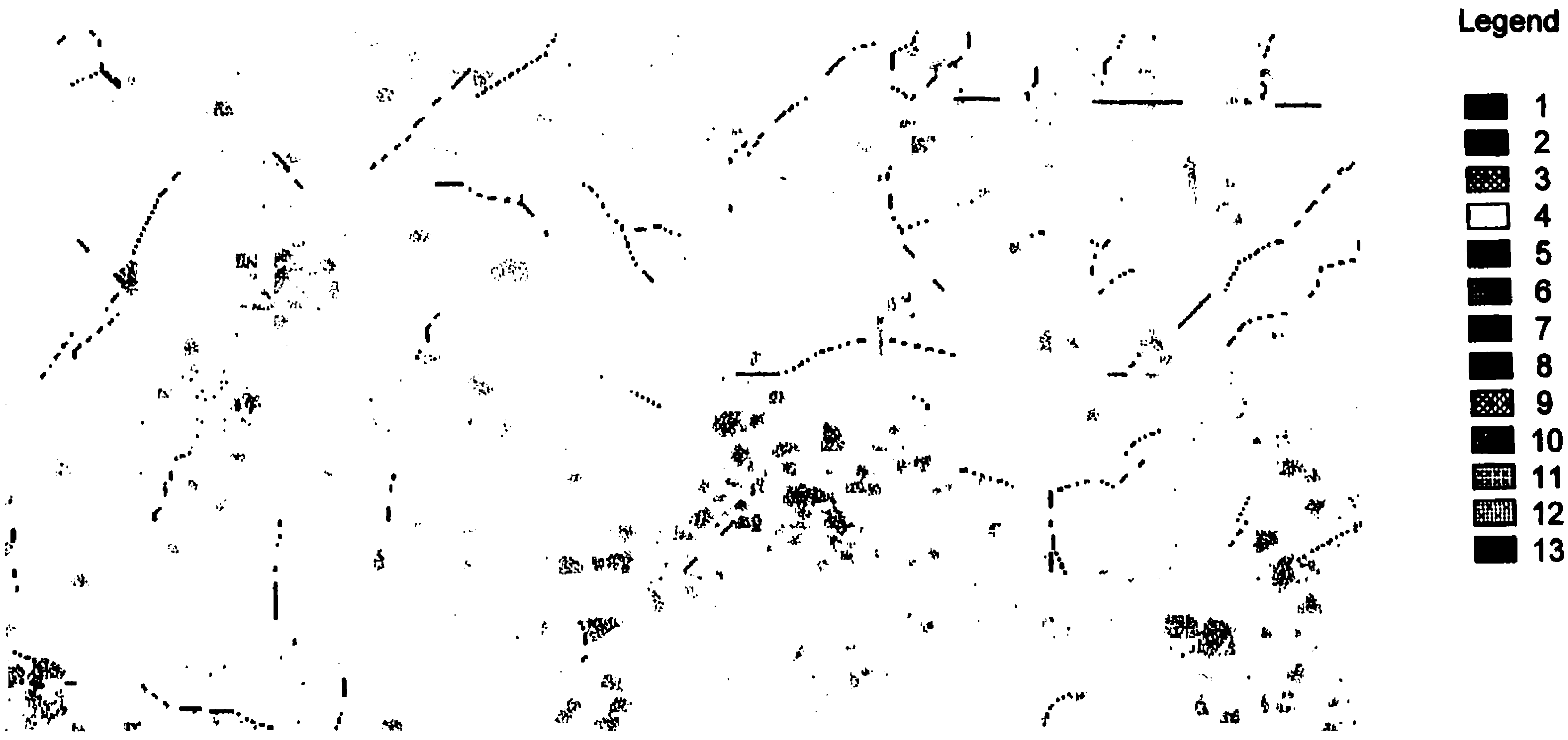


Figure 4.5: Finer scale resolution of vegetation map illustrating the distribution of plants, fecal pellets, boulders and frost boils (resolution: 1 cm x 1 cm) of the total 10 m x 5 m plot. Legend: *Draba subcapitata* live (1) and dead plants (2); *Papaver radicatum* live (3) and dead plants (4); *Saxifraga oppositifolia* (5); *Saxifraga cemua* (6); Seedlings (7); Bryophytes live (8) and dead clumps (9); Fecal pellets (10); Boulders (11); Bare ground (12); Frost boils (13).

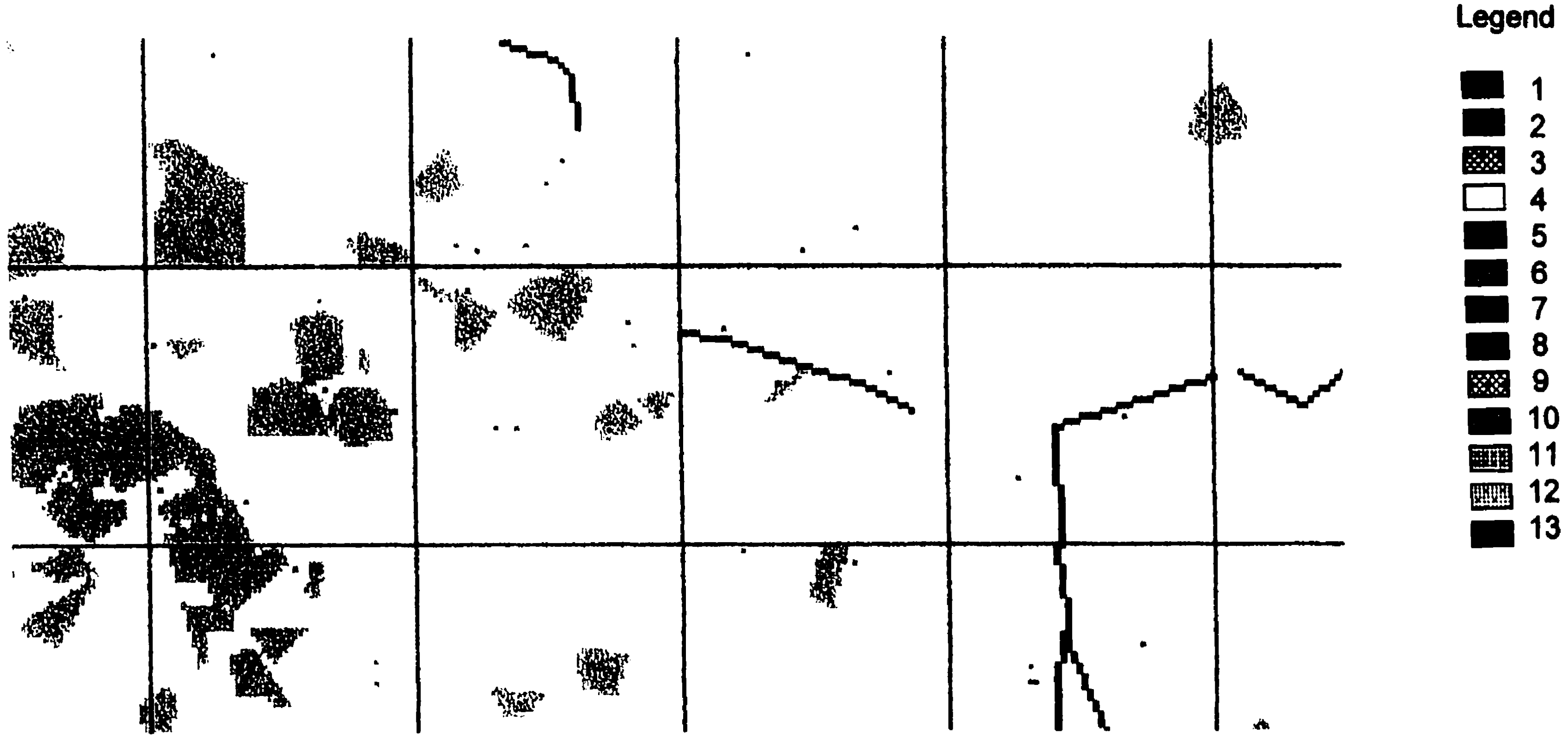


Figure 4.6: Close-up of a portion of the fine scale resolution vegetation map (*cf.* Figure 4.5) illustrating the distribution of plants, feces pellets, boulders and frost boils (resolution: 1 cm x 1 cm). The grid indicates 50 cm x 50 cm quadrats. Legend: *Draba subcapitata* live (1) and dead plants (2); *Papaver radicatum* live (3) and dead plants (4); *Saxifraga oppositifolia* (5); *Saxifraga cernua* (6); Seedlings (7); Bryophytes live (8) and dead clumps (9); Fecal pellets (10); Boulders (11); Bare ground (12); Frost boils (13).

was 17.75 years/cm stem (Desrosiers, 1991). The area of each plant measured in the 10 m x 5 m plot in Sverdrup Pass was used to calculate the radius (assuming that the plant was circular) and the radius was assumed to represent the longest shoot. This estimate was conservative since most plants did not have a circular shape but rather an elongated oval shape which would mean that on at least one axis the shoots would be longer than the radius of a circle.

4.3.5 Pattern

To characterize the horizontal pattern of the data, variance to mean ratios (v/m) were calculated for each vascular plant species, the mosses and the feces using a range of block sizes from 0.015 m^2 (block size 1) to 1 m^2 (block size 64; Greig-Smith, 1964; Pielou, 1977). The mean number and variance of plants (or fecal pellets) in quadrats of a given block size were calculated using the QUADRAT function in IDRISI (1990). This function allows the user to divide an area into any desired number of quadrats, it then calculates the number of individuals within each quadrat and computes the mean and variance. The variance to mean ratio for each block size was then compared to unity based on the equality of mean and variance of the Poisson distribution (Greig-Smith, 1964, p.62). If the ratio was significantly greater than unity the distribution was contagious, if it was less than one the distribution was regular. Significance of the differences was tested with t-tests.

The same data were analyzed for spatial autocorrelation (Odland, 1988) using King's case (AUTOCORR function in IDRISI, 1990). Moran's I statistics were used to test the spatial autocorrelation. This technique calculates the covariance in plant (or feces) abundance among quadrats that are connected adjacently and diagonally. The spatial covariance is then standardized by two terms: the variance of the data series (which is invariant with their arrangement) and by a measure of connectivity for the set of quadrats (Odland, 1988). Moran's I has an expected value of $-(1/(n-1))$. If the abundance of plants (or feces) within one quadrat is independent of the value of its neighbours, the calculated Moran's I will not be different from this expected value. A Moran's I value greater than expected indicates positive spatial autocorrelation where neighbouring quadrats tend to be similar. A value less than the expected value indicates negative spatial autocorrelation (*i.e.* neighbouring quadrats tend to be dissimilar; Odland, 1988). The significance of the Moran's I statistics was tested with z-test against the X^2-distribution (Cliff and Ord, 1981).

4.3.6 Roughness, elevation and slope

Of the 200 quadrats (50 cm x 50 cm) sampled, 185 had their roughness estimated. The frequency distribution of quadrats with at least one plant was tested against the distribution of all the quadrats in each roughness class with G-tests (see below). In addition, the same test was done on a larger data set collected on 37 polar desert sites (16 granitic and 21 carbonate) sampled in central Ellesmere Island (*cf.* Chapter 3).

At a finer scale, each pixel of the elevation model represents the average of the 4 elevation readings at the corner of every 10 cm x 10 cm quadrat (n = 4264, since 736 pixels were not measured). An estimate of the variance at each pixel was also calculated to distinguish between pixels of equal mean that are flat from those that are bordering some microtopographic feature. Variance was calculated with the following equation where **s** is the standard deviation, $\bar{x}$ is the mean elevation and **n** the number of points (in this case 4):

$$\left(\frac{s \times 100}{\bar{x}}\right) \times \left(1 + \frac{1}{4n}\right)$$

From the microtopography model, the slope angle and aspect of each pixel was calculated (using Rook's case procedure SURFACE in IDRISI). For the slope angle and aspect, the pixels that were on the edge of the map and did not have 4 neighbouring pixels were excluded (effective n = 3968) for the distribution analysis.

The data sets were classified, every 1 cm for elevation, every 5° for the slope angle, and into four classes (N, E, S, W) for the slope aspect. The distribution of each species in the various classes was compared to the distribution of the number of pixels in these same classes and H_0 (the distribution of the attribute (*e.g.* species, feces) is equal to the distribution of pixels) was tested against the alternative hypothesis H_1 (the distribution of the attribute is different from the distribution of the pixels) with G-tests (Sokal and Rohlf, 1981).

G-tests were used for all single classification goodness-of-fit tests. This statistic is recommended when occurrence is larger or equal to 5 in each class (Sokal and Rohlf, 1981). Thus, classes were pooled when necessary to ensure that all data points in every class were ≥ 5. Since type I error tends to be higher for this test, Sokal and Rohlf (1981) recommend a correction, suggested by Williams (1976). This correction was applied as follows: *'G'* was divided by the correction factor *'q'* ($q = 1 + (a^2 - 1)/6nv$; where a is the number of classes, n is the number of occurrences and $v = a - 1$). The corrected *'G'* values were compared to the X^2-distribution (Rohlf and Sokal, 1995).

4.3.7 Distance

In order to evaluate if the plants occupied microsites closer to boulders, to frost boils or to larger plants than would be expected at random, the DISTANCE feature of IDRISI was used to generate images of the distance from these objects. For example, when boulders were used as centre points, each pixel in the image was evaluated to find the shortest distance to the margin of any boulder. These distances were classified and the distribution of plants superimposed to establish the distribution of plants in relation to the position of boulders. The same procedure was utilized with frost boils and large plants as centre points. In these two cases, the pixels covered by boulders were subtracted from the total number of pixels available to plants.

The frequency distribution of plants and feces within distance classes was tested against the frequency distribution of pixels. As for elevation and slope analysis, this was done using G-tests.

4.4 RESULTS

4.4.1 Demographics

The total vascular plant cover and density were low (0.16% and 6.9 plants/m^2). These values are comparable to those obtained by the random quadrat sampling in the same area (Lévesque and Svoboda, 1995; Appendix 4). The detailed map allowed a complete enumeration of the plants and of their size (Table 4.1). *Draba subcapitata* was by far the most frequent species in the plot ($n = 300$ live and 47 dead plants) but its total cover was only marginally greater than that of the rarer but larger *Saxifraga oppositifolia* ($n = 8$, Figure 4.7), 0.09 vs 0.06% cover respectively (Table 4.1).

The average size of live *D. subcapitata* was significantly smaller than that of its dead counterparts (1.5 vs 2.5 cm^2; $p < 0.05$), living plants were also 6 times more numerous (Table 4.1; Figure 4.7). The majority (72%) of the live individuals were small ($\leq$ 2 cm^2), 20% medium size ($<$ 4 cm^2) and 8% were large ($\geq$ 4 cm^2). Analogous proportions for the dead individuals were 62%, 19% and 19% (Table 4.1). The size distribution of *D. subcapitata* is presented in Figure 4.8. It was assumed that the size of the plant in the same habitat-environment is related to its age, however, there might be exceptions. Small individuals with a stunted growth could be old (Harper, 1977). The higher

Table 4.1: Total plant cover and species specific plant size and abundance in a 10 m x 5 m plot, Ellesmere Island, Canada; where sm indicates small plants (≤ 2 cm^2); md, medium plant (2 cm^2 to 4 cm^2) and lg, large plant (≥ 4 cm^2).

Species		n	Average size (cm^2)	Cover (%)	Density (plants/m^2)
Draba subcapitata	live	300	1.5	0.09	6.0
	sm	217			
	md	60			
	lg	23			
	dead	47	2.5	0.02	0.94
	sm	29			
	md	9			
	lg	9			
Papaver radicatum	live	27	1.9	0.01	0.54
	dead	2	2.0	<0.001	0.04
Saxifraga oppositifolia	live	8	37.4	0.06	0.16
	dead	0		0	
Saxifraga cernua	live	1	0.6	0.001	0.02
	dead	0		0	
Seedlings	live	9	0.3	<0.001	0.18
Moss	live	307	0.8	0.05	6.14
	dead	6	1.8	0.002	0.12
Fecal pellets (arctic hare)		27	0.7	0.004	0.54
Total cover and density:	live vascular plants			0.16	6.9
	live vasc. plants + moss			0.21	

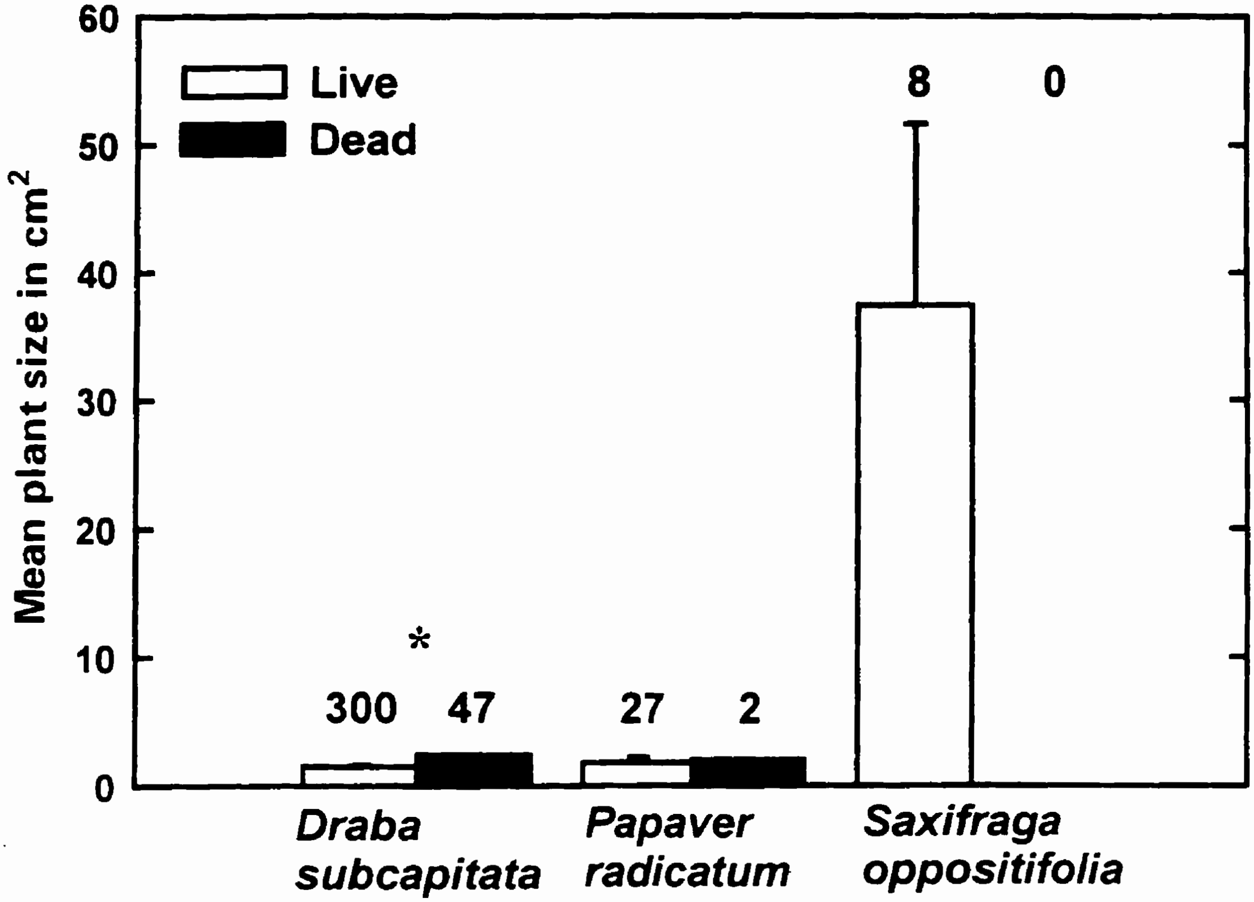


Figure 4.7: Mean size and abundance of *Draba subcapitata*, *Papaver radicatum* and *Saxifraga oppositifolia*; dominant vascular species found in 10 m x 5 m plot, on a dolomitic plateau above Sverdrup Pass, Ellesmere Island. Asterisk indicates a significant difference ($p < 0.05$).

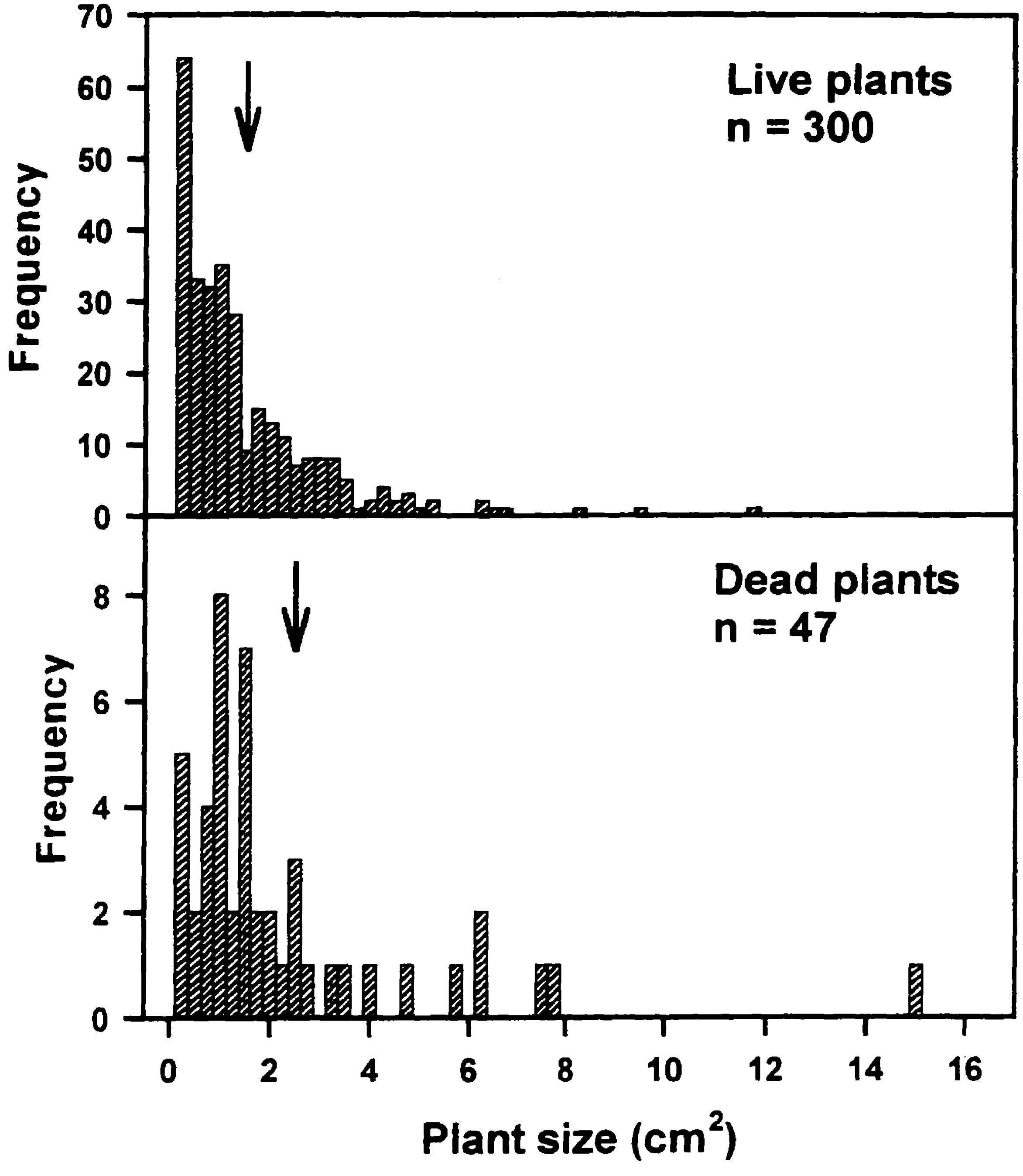


Figure 4.8: Frequency distribution by size of *Draba subcapitata* for live and dead plants in 10 m x 5 m plot, on a dolomitic plateau above Sverdrup Pass, Ellesmere Island. Arrows indicate the mean values.

proportion of large dead plants might be related to a higher rate of small plant disintegration. With a higher surface area-mass ratio, small plants would turn over faster.

The size for *S. oppositifolia* ranged from 0.1 to 95 cm^2 with an average size of 37.4 cm^2 (Table 4.2, Figure 4.7). The calculated minimum age of the largest *S. oppositifolia* was 98 years. Four plants were estimated younger than 20 years old and the other four from 76 to 98 years old. Only three plants were in flower at the time of sampling, and these were all of the older group (Table 4.2).

Papaver radicatum was the other main vascular species in the plot with 27 live and 2 dead plants representing a total cover of 0.01% (Table 4.1). There was no difference between the size of the dead and live plants (Figure 4.7). Only one small individual of *Saxifraga cernua* was found. This was a rare occurrence; this species was recorded only twice at this site over four years of intensive sampling. Five more vascular species were observed on this plateau but were not present in the 10 m x 5 m plot: *Draba corymbosa*, *Minuartia rubella*, *Phippsia algida*, *Poa abbreviata* and *Puccinellia bruggemannii* (Appendix 4).

The bryophytic cover was 0.05%; bryophyte clumps were frequent and scattered over the plot (307 clumps alive and 6 dead). Each clump was considered an individual even though it may be composed of a mixture of species, the dominant being *Ditrichum flexicaule* (Maycock and Fahselt, 1992). Finally, there were 27 fecal pellets in the plot, all from arctic hares (Table 4.1).

4.4.2 Pattern

In general, the distribution of the plants in the plot does not appear random (Figure 4.4). In order to test this, the variance to mean ratio (v/m) and autocorrelation coefficients were calculated (Table 4.3). All the species with more than 10 individuals had a v/m ratio greater than 1 ($p < 0.05$) at various

Table 4.2: Individual plant area, minimum age and number of flowers for *Saxifraga oppositifolia* in a 10 m x 5 m plot, Ellesmere Island, Canada. For minimum age estimation see methods.

Plant number	Area (cm^2)	Minimum age (years)	Number of flowers
1	0.06	2.5	0
2	0.5	7	0
3	1.5	12	0
4	3.5	19	0
5	57.5	76	6
6	60.0	78	0
7	81.3	90	30
8	95.0	98	23

Table 4.3: Variance to mean ratio (v/m) and autocorrelation analysis of the distribution pattern of two vascular species, mosses and fecal droppings sampled in the 10 m x 5 m plot, Ellesmere Island, Canada. L and D refer to live and dead plants; x is the density; p is p-value of t-test for v/m ratio and of z-test for Autocorrelation; n.s. stands for non significant; I is the Moran's I statistic; z is the z-test from randomization.

Block size	1			4			16			64		
Quadrat size	0.015 m^2			0.06 m^2			0.25 m^2			1 m^2		
n of quadrats	3200			800			200			50		
Variance to Mean ratio Analysis												
Species	x	v/m	p	x	v/m	p	x	v/m	p	x	v/m	p
Draba subcapitata (L)	0.09	2.03	<0.001	0.38	3.22	<0.001	1.5	5.35	<0.001	6.0	13.2	<0.001
Draba subcapitata (D)	0.01	1.03	n.s.	0.06	1.20	<0.001	0.24	1.54	<0.001	0.94	3.14	<0.001
Papaver radicatum	0.01	1.88	<0.001	0.03	3.04	<0.001	014	3.55	<0.001	0.54	3.64	<0.001
Moss	0.10	1.89	<0.001	0.38	2.83	<0.001	1.5	4.52	<0.001	6.14	9.00	<0.001
Fecal pellets	0.01	1.07	<0.01	0.03	1.04	n.s.	0.14	1.02	n.s.	0.54	1.30	n.s.
Autocorrelation Analysis (King case)												
Species	I	z	p	I	z	p	I	z	p	I	z	p
Expected:	-0.0003			-0.0013			-0.0050			-0.0204		
Draba subcapitata (L)	0.253	28.45	<0.001	0.335	19.06	<0.001	0.308	8.85	<0.001	-0.008	0.22	n.s.
Draba subcapitata (D)	0.058	6.48	<0.001	0.103	5.77	0.001	0.344	9.64	0.001	0.299	4.75	0.001
Papaver radicatum	0.116	14.00	<0.001	0.027	1.93	n.s.	0.018	0.84	n.s.	0.299	4.75	<0.001
Moss	0.158	17.64	<0.001	0.212	11.78	<0.001	0.311	8.65	<0.001	0.241	3.70	≈0.001
Fecal pellets	-0.007	-0.79	n.s.	0.026	1.51	n.s	0.099	2.83	<0.01	0.113	1.81	n.s.

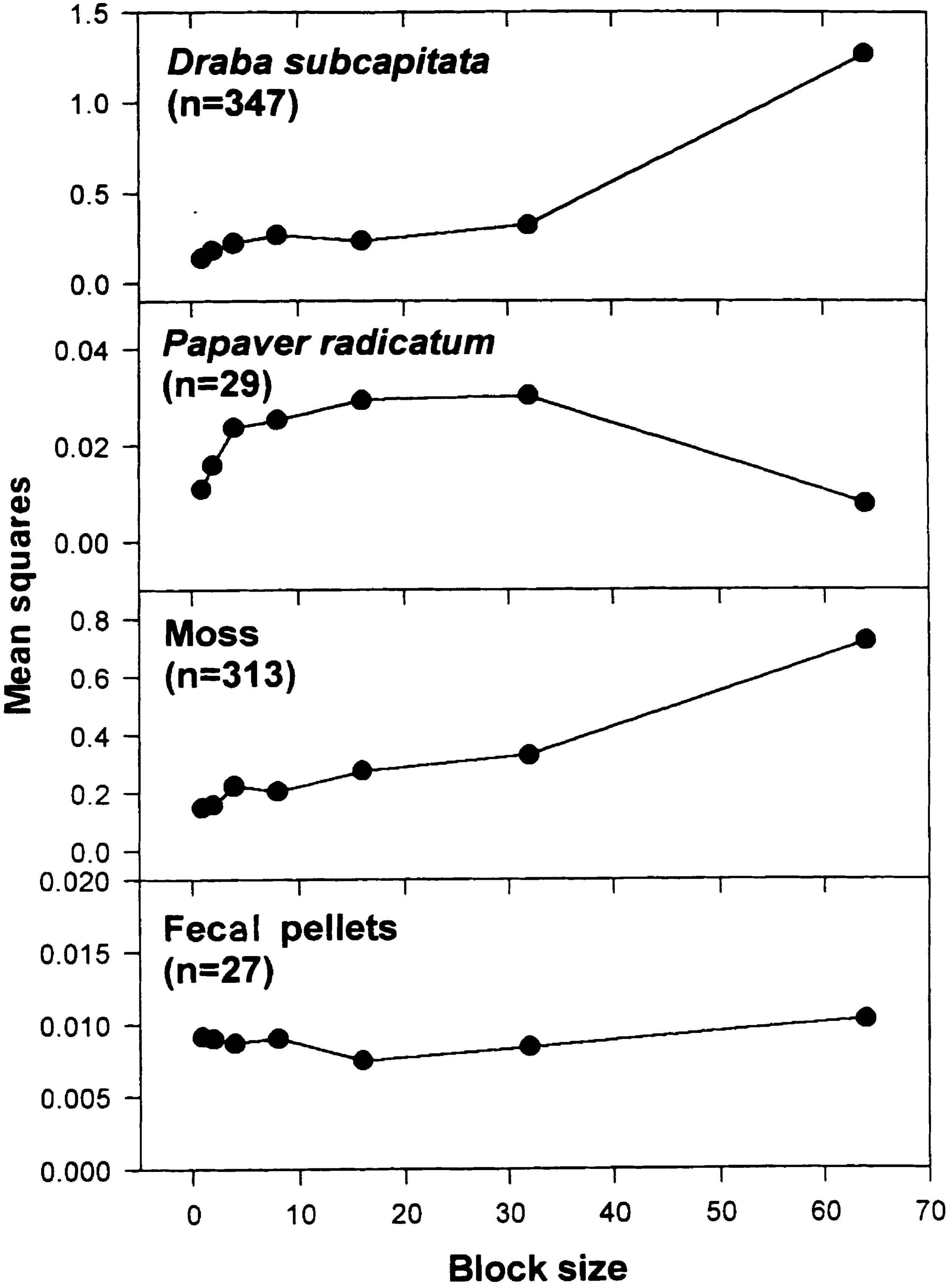
quadrat sizes indicating a clustering of the plants. The rarer species could not be tested meaningfully. There tended to be significant positive spatial autocorrelation (Odland, 1988) for the vascular species and for moss, although not at every block size. This again suggests a non-random pattern of distribution where a quadrat tends to be similar to a neighbouring one (Odland, 1988).

According to the v/m ratio, the distribution of the two most common species, live *D. subcapitata* (n = 300) and Moss (n = 307) was clustered but there was no clear block size (peak on the curve; Figure 4.9) at which the variance was maximum (Greig-Smith, 1964). From the autocorrelation analysis, the non random distribution of plants in the plot was clear, the only exception was at block size 64 for *D. subcapitata* where the v/m ratio was very large and significantly different from 1 (13.2, $p < 0.001$) but the autocorrelation was not significant. The lack of spatial autocorrelation at this larger scale suggests a random distribution at the larger scale of sampling which is consistent with the general homogeneity observed on the site. This was not the case for the rare occurrence species, nor for the moss which still had a non random pattern.

The fecal pellets v/m ratio did not differ significantly from 1, except at the smallest block size (0.015 m^2) with v/m only slightly superior to 1 (1.07) and $p < 0.01$. The absence of spatial autocorrelation at most scales suggest that their distribution does not differ from a random one.

The comparison of the values obtained for *P. radicatum* and for the fecal pellets was particularly interesting since they have the same number of occurrences (n = 27) but their v/m ratio and Moran's I statistics were drastically different (Table 4.3). The plants were not distributed at random whereas the fecal pellets, despite a small tendency to clustering at the very small scale (may be related to the 'arrival' of feces on site), were scattered at random on the plot.

Figure 4.9: Variance to mean ratio analysis for seven block sizes (1 to 64) of live and dead *Draba subcapitata*, *Papaver radicatum*, bryophytes and of fecal pellets sampled by continuous quadrats in 10 m x 5 m plot, on a dolomitic plateau above Sverdrup Pass, Ellesmere Island.


Draba subcapitata
(n=347)
1.5
1.0
0.5
0.0
Papaver radicatum
(n=29)
0.04
0.02
0.00
Moss
(n=313)
0.8
0.6
0.4
0.2
0.0
Fecal pellets
(n=27)
0.020
0.015
0.010
0.005
0.000
Mean squares
0
10
20
30
40
50
60
70
Block size

4.4.3 Microtopography

Overall, the plot was only slightly sloping towards the south-west (< 5°). There were no large erratic boulders but rather flat angular rocks laying on the surface or protruding partially from the ground. The mapped boulders (with at least one dimension ≥ 10 cm) covered 4% of the ground. Larger scale quadrat sampling of site D6 (described in Chapter 3) showed that boulders covered 32.1% of the ground surface, smaller rocks and pebbles 36.7% and fine soil 31.3% (Appendix 2). Frost boils are represented by lines on Figures 4.5 and 4.6, their pattern was irregular and did not indicate any sorting. Although soil movement has likely been happening in the fine textured substrate, the rate of movement may have been relatively low since only a few thawing and freezing cycles occur per year here and the rock content in the soil was high (Cook and Raiche, 1962; Rapp, 1970).

Roughness. The 185 quadrats (50 cm x 50 cm) that were evaluated for roughness were mostly of the intermediate class 3 (38.9%; Table 4.4). When the number of quadrats with at least one plant in each of the roughness classes was tested against the distribution of quadrats in the classes, there were no significant differences for the moss nor for *D. subcapitata* (live or dead). There was however a significant difference if all the vascular plants were used; there were more plants in the lower roughness classes. This difference seems to be due to the distribution of *P. radicatum* which tended to be preferentially found in the lower roughness classes. *P. radicatum* was recorded in 15 quadrats, six from roughness class 1 and 2 and only once from roughness class 4 (Table 4.4). Overall, 74.5% of the vascular plants were found in quadrats with roughness class 2 and 3 whereas only 62.2% of all the quadrats were from these classes (Table 4.4).

A similar analysis performed on 1321 quadrats sampled on 37 of the vegetated polar desert sites described in Chapter 3, allows a comparison on a

Table 4.4: Percentage of occurrence of plants in 50 cm x 50 cm quadrats of different roughness classes (from 1, smooth to 5, rough) sampled in a 10 m x 5 m plot in Sverdrup Pass and on 37 vegetated polar desert sites (16 granitic and 21 carbonate), Ellesmere Island, Canada. p-value of the G test, ** indicates significantly different distribution; n/a indicates not available.

	Total number of quadrats	Roughness Class					p-value
		1	2	3	4	5	
10 m x 5 m plot							
Number of quadrats	185	8	44	71	57	5	
Percentage		4.3	23.8	38.4	30.8	2.7	
Live plants:							
D. subcapitata	89	3.4	29.2	44.9	22.5	0	>0.05
P. radicatum	15	6.7	33.3	53.3	6.7	0	n/a
S. oppositifolia	7	0	28.6	42.9	28.6	0	n/a
Vascular plants	98	4.1	31.6	42.9	21.4	0	<0.05**
Moss	96	4.2	28.1	40.6	26.0	1.0	>0.05
Others:							
D. subcapitata (dead)	29	3.4	31.0	41.4	24.1	0	>0.5
Fecal pellets	22	0	36.4	45.5	13.6	4.5	>0.25
Granitic sites (16)							
Number of quadrats	569	53	162	175	124	55	
Percentage		9.3	28.5	30.8	21.8	9.7	
Vascular plants	466	9.2	28.3	31.5	22.5	8.4	>0.9
Moss	320	10.6	26.6	31.6	23.1	8.1	>0.5
Carbonate sites (21)							
Number of quadrats	752	24	261	296	145	26	
Percentage		3.2	34.7	39.4	19.3	3.5	
Vascular plants	492	3.3	30.3	42.9	20.9	2.6	>0.1
Moss	348	1.7	31.0	46.0	18.7	2.6	>0.05

broader scale. The distribution of vascular plants and of mosses, in the five roughness classes, was not different from the occurrence of these roughness classes on granitic- nor on carbonate rock sites (Table 4.4). On the carbonate rock sites (most of them similar to the site where the 10 m x 5 m plot was sampled), there was a higher proportion of the quadrats in roughness class 2 and 3 (74.1%) compared to the 50 m^2 plot (62.2%). It was the roughness class 3 that was most frequently colonized both by vascular plants (42.9%) and by moss (46.0%) but there was no difference between the proportion of quadrats in roughness class 2 and 3 and the proportion with plants (74.1% and 73.2% respectively). Although most of the plants were found in the intermediate roughness classes, there were no indication that this distribution occurred more regularly than would occur by chance since these classes were also the most abundant. This suggests that even if plants are not randomly distributed, their pattern can not be readily explained by the site roughness estimated at the 50 cm x 50 cm scale.

Elevation. The mean elevation of the pixels was centred around an arbitrary plane that was set at 0 cm, 46% of the pixels were only at 2 cm and 87% at 5 cm on either side of this mid-point plane. The distribution of plants, feces and boulders in relation to the mean elevation of the 10 cm x 10 cm pixels and to its variance were tested against the expected distribution based on the total number of pixels in each classes. Boulders in both cases had a distribution strongly different from that of all pixels (Table 4.5). As might be expected, boulders were less frequently found on low elevation pixels (Figure 4.10). Boulders were associated with the higher elevation features and with the high variance pixels.

Live *D. subcapitata* (mostly due to small individuals) and *P. radicatum* were the only plants with a significantly different distribution pattern (Table 4.5). They were distributed more often then expected on the mid- and lower elevation pixels (Figure 4.11). The distribution of variance of pixel elevation

Table 4.5: Summary of G-statistics for Elevation (average height and variance of 10 cm x 10 cm quadrats) and Slope analysis (Angle and Aspect of 10 cm x 10 cm quadrats); sampled in the 10 m x 5 m plot, Ellesmere Island, Canada. L and D indicate, respectively, live and dead; G is the value of the G-statistic after William's correction; the value in parenthesis indicates the degree of freedom; * is to indicate significantly different distribution.

		ELEVATION					SLOPE			
		Height		Variance			Angle		Aspect	
Species	n	$G_{(4)}$	p	$G_{(4)}$	p	n	$G_{(2)}$	p	$G_{(3)}$	p
Draba subcapitata										
Live	229	14.04	**<0.01***	3.34	>0.5	212	6.68	**<0.05***	4.88	>0.1
Dead	24	9.43	≈0.05	3.29	>0.5	20	2.71	>0.1	4.65	>0.1
All Draba: Small	174	9.89	**<0.05***	4.95	>0.1	161	8.49	**<0.025***	1.34	>0.5
Medium	55	3.68	>0.1	6.38	>0.1	49	1.16	>0.5	4.45	>0.1
Large	24	2.20	>0.5	4.46	>0.1	22	3.27	>0.1	2.20	>0.5
Papaver radicatum (L + D)	24	14.05	**<0.01***	8.95	>0.05	13	0.49	>0.5	n/a	
Saxifraga oppositifolia	4					4				
Saxifraga cernua	1					1				
Seedlings	3					1				
Moss										
Live	205	8.25	>0.05	6.26	>0.1	190	0.19	>0.9	1.80	>0.1
Dead	6					6				
Fecal pellets	19	8.29	>0.05	2.63	>0.5	18	3.63	>0.1	5.91	>0.1
Boulders	169	15.60	**<0.005***	38.05	**<0.001***	156	1.74	>0.1	3.30	>0.25

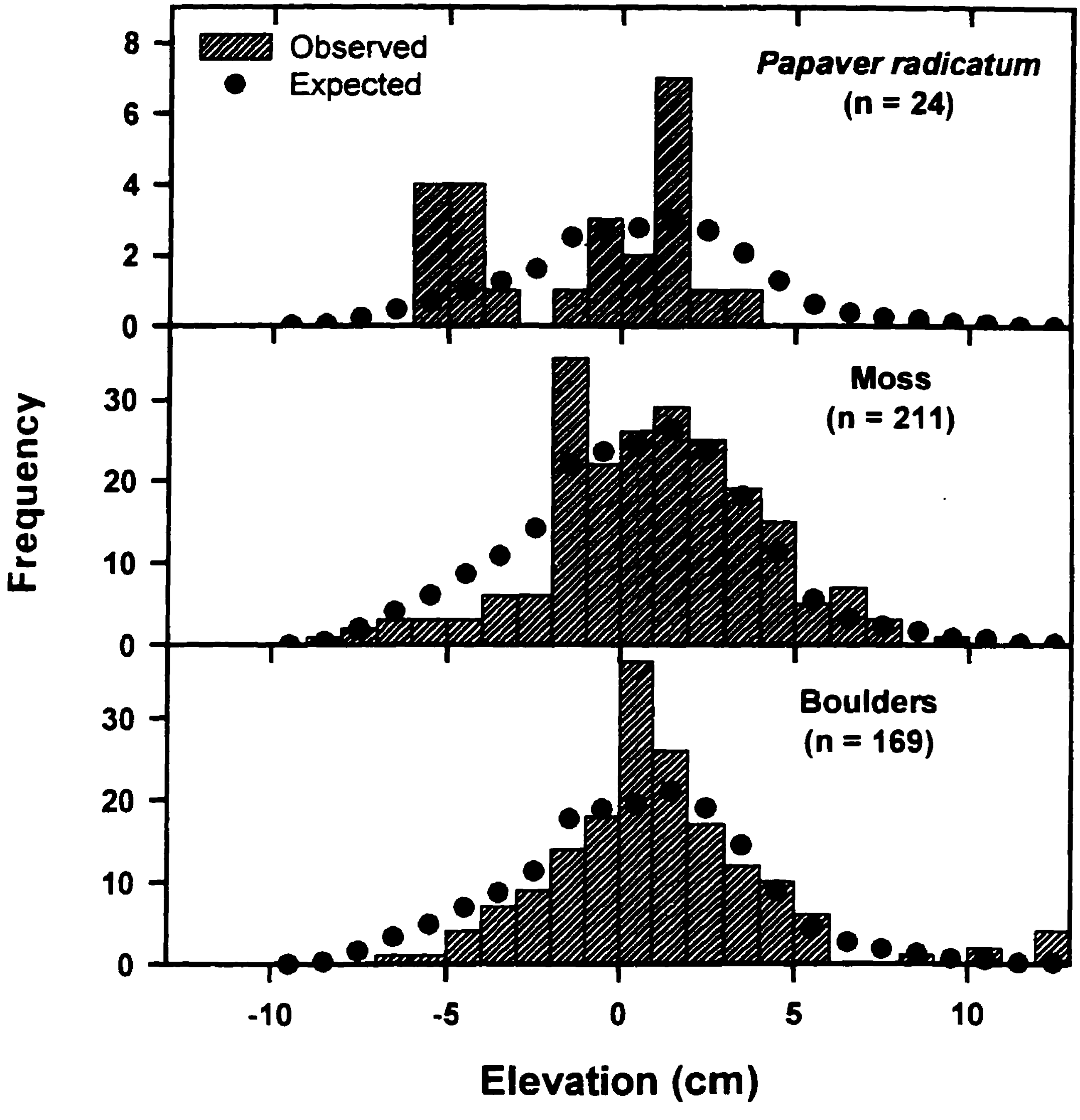


Figure 4.10: Frequency distribution of presence of live and dead *Papaver radicatum*, moss and of boulders in 10 cm x 10 cm quadrats of varying elevation in a 10 m x 5 m plot, on a dolomitic plateau above Sverdrup Pass, Ellesmere Island.

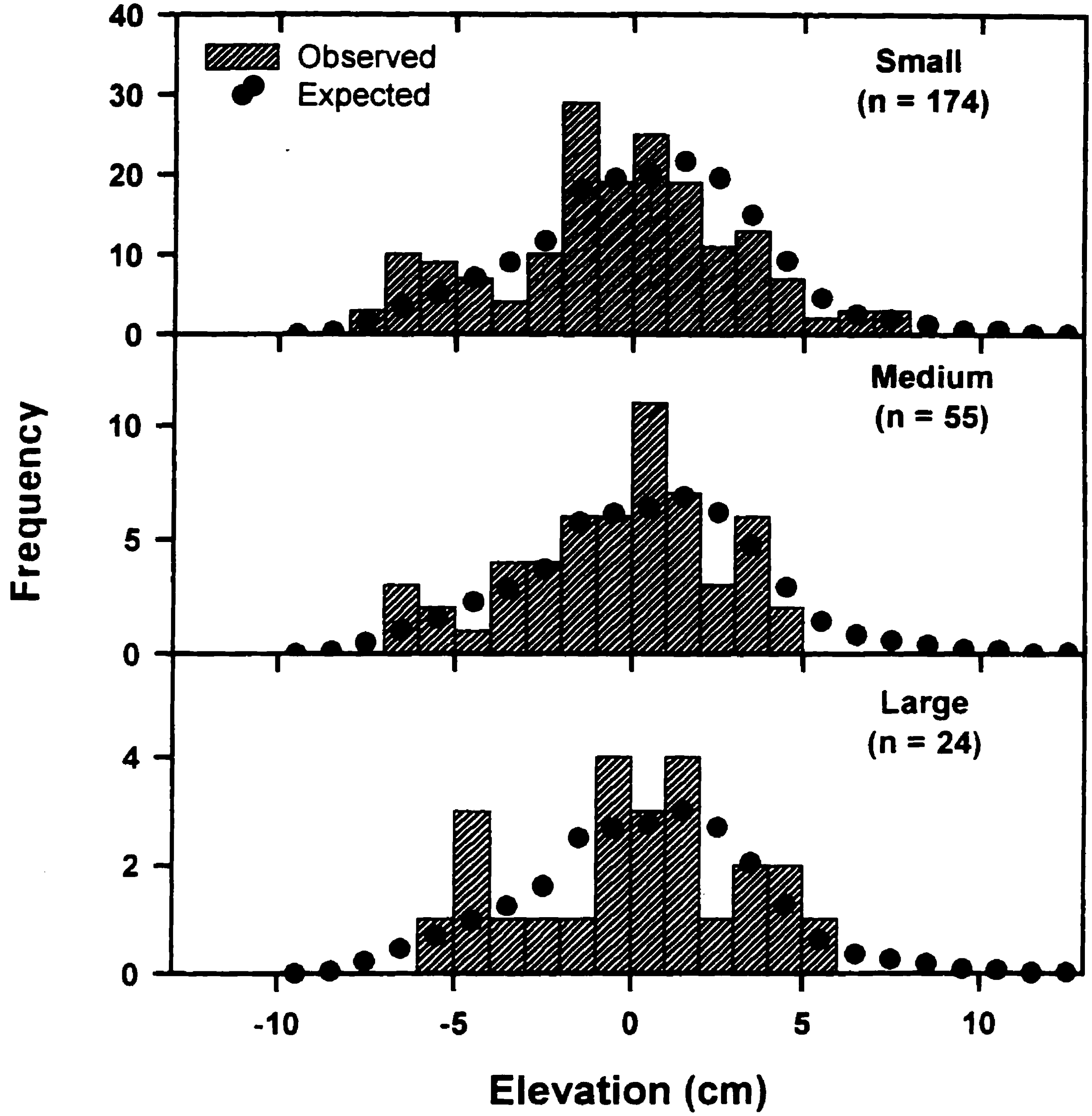


Figure 4.11: Frequency distribution of presence of three size classes of live and dead *Draba subcapitata* in 10 cm x 10 cm quadrats of varying elevation in a 10 m x 5 m plot, on a dolomitic plateau above Sverdrup Pass, Ellesmere Island.

was compared to the distribution of plants. No difference was detected (Table 4.5).

Since boulders cover space that is unavailable for plant colonization, G-tests were also performed on the distribution of pixels minus the pixels covered by boulders. This approach yielded very similar results. Since at this scale of resolution, there may be a plant in close proximity to a boulder, actually in the same pixel, the first set of analyses was kept.

Slope. Using the mean elevation, the slope and aspect of each pixel were determined in relation to the surrounding pixels. Plant distribution was not significantly affected by aspect (Table 4.5), which means that plants did not occur preferentially in the south or east facing pixels. For the slope angle, however, significant differences were found for the live *D. subcapitata* (again, mostly associated with the small individuals), which tended to occur more often then expected on flatter pixels.

4.4.4 Distance

In this section, the distribution of plants in relation to boulders, frost boils and large *Draba* plants was analyzed. This was done at a more precise scale since maps with resolution of 1 cm x 1 cm were created from the precise x and y location of plants and of the boulders and frost boils.

Distance from boulders. Boulders covered only 4% of the area mapped. They were scattered throughout the plot and only 8.9% of the pixels were at more than 50 cm from the margin of a boulder (Table 4.6).

In general, plants were found more frequently than expected in proximity (< 10 cm) to boulder margins. This was true for *D. subcapitata* (live and for all size classes), *P. radicatum*, and moss clumps (Table 4.6). Similar tendencies can be seen for *S. oppositifolia* (and the only *S. cernua*). Seedlings, however,

Table 4.6: Distribution of plants in relation to distance from boulders sampled in a 10 m x 5 m plot in Sverdrup Pass, Ellesmere Island. L and D indicate, respectively, live and dead; means p-value; n.s., non significant; *, significant: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

			Distance from boulder margin (cm)					
		n	0-10	10-25	25-50	>50	$G_{(3)}$	p
Boulders		20169						
Percentage		479831	21.7	35.6	33.9	8.89		
Draba subcapitata								
Live		300	36.0	35.7	22.0	6.3	40.3	***
Dead		47	31.9	23.4	29.8	14.9	6.0	n.s.
All *Draba*:	Small	246	33.3	34.6	24.0	8.1	21.3	***
	Medium	69	37.7	36.2	20.3	5.8	11.8	**
	Large	32	48.4	25.8	19.4	6.5	10.7	*
Papaver radicatum (L + D)		29	41.4	37.9	17.2	3.4	8.1	*
Saxifraga oppositifolia		8	50	37.5	12.5	0		
Saxifraga cernua		1	100	0	0	0		
Seedlings		9	22.2	33.3	44.4	0		
Moss (L + D)		313	45.7	30.4	21.4	2.6	101.6	***
Fecal pellets		27	25.9	29.6	37.0	7.4	0.6	n.s.

were more frequently found at more than 10, and even more than 25 cm. The dead plants of *D. subcapitata* were the exception with higher values than expected near and far from boulders (Table 4.6). Fecal pellets did not differ from the expected distribution.

Distance from frost boils. Plants tended to grow at some distance from frost boils. The pattern of distribution was different than expected for *D. subcapitata* (Live and Small $p < 0.001$; Table 4.7) with a larger proportion in the zone from 10 to 30 cm from the frost boil. A similar tendency was observed for *P. radicatum*, whereas other vascular species tended to be found even further away from the frost boils (Table 4.7).

The distribution of moss was also strongly significant ($p < 0.001$), clumps tended to be more common close to (< 10 cm) and far from (> 60 cm) the features, the same was true for fecal pellets. Finally boulders tended to be found away from frost boils (Table 4.7).

Distance from large plant. The distribution pattern of live and dead *D. subcapitata* and small individuals of that species were all strongly different from the expected distribution pattern ($p < 0.001$; Table 4.8) and the medium plants showed significance at $p < 0.05$. In all cases, plants tended to be found closer to a large plant than expected at random.

The distribution of other vascular plants and of fecal pellets were not related to the presence of large individuals of *D. subcapitata* (Table 4.8). The distribution of mosses and boulders were significantly different from random (Table 4.8). They tended to be found more often than expected within 40 cm of large *Draba* plants.

Table 4.7: Distribution of plants in relation to distance from frost boils sampled in a 10 m x 5 m plot in Sverdrup Pass, Ellesmere Island. L and D indicate, respectively, live and dead; p means p-value; n.s., non significant; *, significant: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

			Distance from frost boil margin (cm)					
		n	0-10	10-30	30-60	> 60	$G_{(3)}$	p
Total		500000	15.5	34.1	35.5	15.0		
Without boulders		480118	15.6	34.4	35.3	14.8		
Draba subcapitata								
Live		300	18.3	46.0	24.3	11.3	26.1	***
Dead		47	10.6	42.6	31.9	14.9	1.8	n.s.
All *Draba*:	Small	246	17.9	51.2	20.3	10.6	40.1	***
	Medium	69	15.9	30.4	36.2	17.4	0.6	n.s.
	Large	32	15.6	34.4	40.6	9.4	0.9	n.s.
Papaver radicatum (L + D)		29	13.8	48.3	20.7	17.2	3.6	n.s.
Saxifraga oppositifolia		8	0	0	62.5	37.5		
Saxifraga cernua		1	0	0	0	100		
Seedlings		9	0	44.4	44.4	11.1		
Moss		313	22.4	33.2	21.1	23.3	42.5	***
Fecal pellets		27	29.6	14.8	22.2	33.3	12.3	**
Boulders		19882	13.1	26.8	38.6	21.6	1047.8	***

Table 4.8: Distribution of plants in relation to distance from large *Draba subcapitata* plant sampled in a 10 m x 5 m plot in Sverdrup Pass, Ellesmere Island. L and D indicate, respectively, live and dead; G is the value of the G-statistic after William's correction; the value in parenthesis indicates the degree of freedom; p means p-value; n.s., non significant; *, significant: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

	n	Distance from large plant (cm)						$G_{(5)}$	p
		0 to 20	20 to 40	40 to 60	60 to 80	80 to 100	> 100		
Total	499968	7.2	15.7	17.7	17.8	15.9	25.6		
Without boulders	480086	7.0	15.4	17.8	17.9	16.2	25.8		
Draba subcapitata									
Live	277	21.7	30.3	20.9	11.9	5.4	9.7	156.3	***
Dead	38	13.2	13.2	31.6	31.6	2.6	7.9	20.9	***
All *Draba*: Small	246	22.8	29.3	23.6	12.2	3.7	8.5	161.1	***
Medium	69	13.0	24.6	17.4	21.7	10.1	13.0	13.6	*
Papaver radicatum (L + D)	29	17.2	6.9	13.8	14.2	13.8	31.0	5.3	n.s.
Saxifraga oppositifolia	8	0	12.5	37.5	12.5	12.5	25.0		
Saxifraga cernua	1	0	100	0	0	0	0		
Seedlings	9	0	11.1	44.4	44.4	0	0		
Moss	313	21.1	26.5	12.8	11.2	10.9	17.6	107.5	***
Fecal pellets	27	3.7	22.2	14.8	25.9	7.4	25.9	3.7	n.s.
Boulders	19882	12.8	23.0	16.7	16.3	9.6	21.6	2242.7	***

4.5 DISCUSSION

Shattered rocks and erratic boulders predominate in polar desert landscapes. After the retreat of ice, finer soil has accumulated in pockets among the boulders due to wind action and chemical and frost action (Washburn, 1973). Sparse vegetation has colonized these microsites and it is not surprising that the distribution of plants in such a patchy landscape is non-random. As noticed in previous arctic and alpine studies, plants are associated with microscale features (Worsley and Ward, 1974; Sohlberg and Bliss, 1984; Anderson, 1996). We have, however, found no indication that mosses would serve as microsites as suggested by Sohlberg and Bliss (1984) for a cryptogam-herb meadow on King Christian Island. Small button-size moss clumps were frequent and their distribution resembled that of the small *Draba subcapitata* plants, but there was no indication of direct interactions between the two. The close analysis of physical features suggests that a majority of plants were found in relatively flat pockets in close proximity to boulders. There were many locations similar to the colonized ones that were not occupied which suggested that there was no shortage, at least spatially, of suitable microsites.

Proximity to a shield may favour snow accumulation and can offer protection from desiccating winds (Carlsson and Callaghan, 1991). Boulders increase the near-surface boundary layer (Oke, 1987), they can also carry the absorbed heat into the soil and reradiate it towards the plant (Pfitsch, 1988) providing a favourable microclimate and promoting the development of a deeper active layer (Elliott and Svoboda, 1994). Boulders also affect moisture distribution (Olsvig-Whittaker *et al.*, 1983) with increased moisture early in the season associated with snow deposition (Elliott and Svoboda, 1994). Later in the season, however, the warmer microclimate may promote evaporation and reduce water availability near the surface (Pfitsch, 1988). The small scale aspect of a microsite had no significant effect on the presence of plants. This can be explained by the low variation in solar azimuth at high latitudes (Worsley and Ward, 1974; Mølgaard, 1982; Lévesque *et al.*, 1997).

Depressions in soil, because of eddies and wind shadows are particularly suitable to catch seeds (Chambers and MacMahon, 1994). At a meso-scale, this flat plateau appears smooth (Plate 4.1) and offers little resistance to the strong winds. It can be expected that during the winter after snow would have filled most depressions, relatively long distance dispersal of seeds over this 'paved' surface may occur (Warren Wilson, 1958; Bonde, 1969; Savile, 1972). However, because of the short stature of the plants present on site they may not benefit from this means of dispersal (Spence, 1990; Chambers and MacMahon, 1994). At the finer scale, the large number of small depressions between rocks would offer catchment microsites (Plate 4.3b).

Physical instability of the substrate may limit plant establishment and growth (Heilbronn and Walton, 1984; Anderson, 1996) but it may also increase nutrient availability (Jonasson and Sköld, 1983; Jonasson, 1986). Washburn (1989) measured surface displacement in the centre of sorted circles near Resolute in the Canadian High Arctic. The displacement, limited to the top 10 cm of soil, tended do go from the centre to the margins and to be maximal near the border of the circles (on average 3.85 mm/year). Somewhat divergent from these results, Anderson (1996) measured surface settling of up to 60 mm and active layer depth of 60 to 70 cm on a polar desert plateau on Devon Island. The transition microsites, intermediate between the fine grained centres and the rocky borders of non-crusted nets and stripes, were more stable and had more vascular plants. The activity was maximal in the fine sediments in the centre of the features and plant cover was minimal (Anderson, 1996). Similar to the present study, Anderson (1996) found that plants often grew in close proximity to rocks and boulders. He suggested that periodic frost heave and surface drought would contribute strongly to the limited plant cover in polar deserts. Soil moisture varied among the microsites, but no information was available for the nutrient status in these microsites in polar deserts. It appears that sites with a high cryptogamic crust cover are more stable, which certainly would contribute to the more extensive plant cover (Gold and Bliss, 1995).

Raup (1969) noticed that plants with a deep tap root were more tolerant to soil movement whereas Jonasson (1986) found that plants with more rapid root turnover were more tolerant to frost action disturbance. The three main species observed in this study had deep tap roots and an extensive network of finer roots that often extended along the edge of boulders (*e.g.* Chapter 3, Plate 3.6). Anderson (1996) noted that important plant and seedling uprooting happened on non-crusted net and stripe sites whereas sites with cryptogamic crust were not so disrupted. The negative effects were greatest in the fine textured section in the centre of stripes (32% of plants were heaved). In the present study, the frost activity was not measured directly, but the reduced number of freeze thaw cycles (Cook and Raiche, 1962), the high content of rocks in the soil and at the surface and the very gentle slope (< 5°) probably made this site less likely to suffer intense frost activity (Washburn, 1973). No strong effect of frost activity was noticed in the microsites; deeply rooted adult plants showed no indication of movement. This does not eliminate a possibility that needle ice and surface settling may be detrimental in the early stage of plant establishment and limit the availability of 'safe sites'.

In many ecosystems, the majority of seeds are dispersed near the parent (Harper, 1977; Chambers and MacMahon, 1994). In glacier forelands dispersal is frequently less than 5 m (Ryvarden, 1971; Stöckling and Bäumler, 1996). Smaller *Draba* plants tended to grow closer to larger plants, which most likely produced seeds from which the nearby smaller ones originated. Seed distribution in soil is patchy in tundra as in other plant communities (Leck, 1980; Freedman *et al.* 1982), and it is significantly higher in proximity to established plants (Lévesque and Svoboda, 1995). This suggests that the first phase of seed dispersal (from parent to ground surface, Chambers and MacMahon, 1994) prevails in polar deserts. It also implies that viable seeds are produced on such unfavourable sites. The distribution pattern observed is thus not dependent only on physical factors but also on biological forces. We suggest that the first establishment of a plant and its ability to maintain and multiply is critical in community development.

The three main vascular taxa present in our study are common to most polar deserts (Bliss *et al.*, 1984; Bliss and Matveyeva, 1992; Chapter 3). They display very different population characteristics that may in large part relate to their differences in reproductive strategy (Murray, 1987).

The genus *Draba* is a very diverse taxonomic group where polyploidy is common (Mulligan, 1972, 1976; Brochmann and Elven, 1992). From the study of populations in Spitzbergen and Northern Norway, Brochmann concluded that *D. subcapitata* is a diploid and an extreme inbreeder (Brochmann, 1993). This species is the most stress tolerant of 16 taxa studied by Brochmann; it is limited to very open habitats where environmental conditions are extreme but competition is minimal (Brochmann and Elven, 1992). In contrast, more competitive species that are able to establish in habitats where plant cover is more significant, such as *Draba alpina* and *Draba corymbosa*, are decaploid and 16-ploid respectively (Brochmann and Elven, 1992). The large number of individuals of *D. subcapitata* seems to reflect the ability of this species to spread when open space is available. The minute size of the plants keeps the species in the protective zone near the ground but also limits its dispersal ability.

Papaver radicatum is also able to self (Kevan, 1972) so, low seed production may not be due to pollen limitation. The clustered pattern observed here indicates that seeds were dispersed from a few plants, but their low number suggests that the seed supply was probably low. This species flowers later in the season compared to the two others, *D. subcapitata* and *Saxifraga oppositifolia*, and the completion of its reproductive cycle may not be possible every year (Lévesque *et al.*, 1997, Chapter 6).

Recent work on *S. oppositifolia* in Northern Sweden (Stenström and Molau, 1992) confirmed work done in the Canadian High Arctic (Kevan, 1972) and in Siberia (Tikhmenev, 1984). This species is a facultative outcrosser, it is self compatible but seed set is strongly reduced when the plant is selfing. Pollen limitation being important, the availability of pollinators is critical to the seed set of this species (Stenström and Molau, 1992). It is assumed that plants on an isolated plateau probably receive pollinator visits only infrequently and thus their seed production would be limited. In addition, *S. oppositifolia* may take many years before it produces flowers. However, this species benefits from a better dispersal mechanism than *Draba* and *Papaver*. The entire fruit capsules of *S. oppositifolia* were often seen carried by wind over very long distances (Savile, 1972). *S. oppositifolia* is relatively common in polar desert seed banks (Lévesque and Svoboda, 1995). Recruitment however was extremely limited on this polar desert site when compared with densities of this species on semi-desert sites at Spitzbergen (1 to 15 plants/m^2; Pirożnikow, 1993) or at Devon Island (28 to 50 plants/m^2; Svoboda, 1977). Although on site recruitment spaced over a long time is possible, it is also probable that seed import over longer distances took place in the beginning of the polar plateau colonization (Chapin, 1993) and continues maybe even at higher rate at present.

4.6 CONCLUSION

The analysis of the extant plant community at the Sverdrup Pass northern plateau revealed its relatively young age. There was no indication of vegetation predating the oldest *Saxifraga oppositifolia* (approx. 100 years old). This seems to support the notion that the present polar desert vegetation was established after the end of the most recent cold period (Little Ice Age, LIA, approx 350-150y BP). During this cooler period, this and other upland sites in the High Arctic were probably under permanent snow cover or the snow melted too late, resulting in the growing season being too short to allow vascular plant survival. The fact that vegetation might have been established at our study site before this cold period could not be ascertained, although remnants of lush pre-LIA vegetation were found emerging from under retreating glaciers at Alexandra

Fiord (Bergsma *et al*, 1984; Jones, 1997) and in Sverdrup Pass (Svoboda personal communication).

Plants were not distributed at random at this site; their distribution was affected by the proximity of shelters (boulders) and of seed source (adult plant). The relative importance of intrinsic (relating to properties of the plants) and extrinsic factors (environmental properties) can not be readily dissociated in the present analysis. An experiment where additional seeds would be sown and their performance recorded may make it possible to separate seed shortage from the shortage of microsites. Possibly, as pointed out by Eriksson and Ehrlén (1992) an intermediate scenario where both aspects are partially limiting plant distribution may apply best to polar desert habitats.

Although it appears that there is considerable open space available to colonization in the polar desert, the actual 'safe sites' may be limited not only to particular protected locations but also to short windows of time when conditions are favourable. Seedling establishment may occur during warmer years or after a succession of good years when seed availability may be higher (following a favourable year for production) and seed germination may be supported by a follow up good season. The relatively limited supply of propagules is also a constraint to community development, although maybe not as much as previously predicted (Lévesque and Svoboda, 1995). The relatively young age of some polar desert sites and the slow colonization processes which is hindered or even reverted by dieback or 'retrogression' (*sensu* Svoboda and Henry, 1987), certainly explain part of the meagre plant cover found in polar deserts.

CHAPTER 5:

GERMINABLE SEED BANK FROM POLAR DESERT STANDS AND SURVIVAL OF SEEDLINGS IN CONTROLLED CONDITIONS

5.1 ABSTRACT

The germinable seed bank in the surface soil was estimated in 14 polar desert sites: 13 located along two altitudinal gradients (one with a granitic, the other with a dolomitic substrate, ranging from 330 to 760 m a.s.l.), and one in the valley of Sverdrup Pass (79°N), Ellesmere Island, Canada. From each stand, 20 soil samples were collected during the summer of 1991. A known fraction of each sample was incubated for 50 days in large petri dishes at 26°C under constant light (quantum flux PAR = 15 μmolm^{-2}s^{-1}). The emerging seedlings were counted daily and transferred to a growth chamber (at 18-20°C with quantum flux PAR = 125 μmolm^{-2}s^{-1}) for later identification.

Viable seeds were found at each site. The germinable seed bank (seeds/m^2) varied within a site, and among the sites. Soil collected in the proximity of an established individual produced higher numbers of seedlings while sites with higher plant cover resulted in a larger seed bank. Dicotyledons represented 72% while Monocotyledons shared only 28% of the total emerging seedlings. Identifiable seedlings were all from species that were also present as adults on the site or in close proximity to the site.

The seedlings were maintained and allowed to grow as mature plants under controlled constant conditions for a period of up to two years. Many

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species flowered without any cues from changes in temperature or light. Some flowered more than once and a few species even produced seeds of which new seedlings established (*e.g. Draba subcapitata*, *Melandrium affine* and *Poa abbreviata*).

5.2 INTRODUCTION

Polar deserts represent approximately 49% of the Queen Elizabeth Islands, NWT, Canada (Bliss, 1977). The colonization and establishment of vascular plants in these extreme habitats following deglaciation and subsequent fluctuations of climate are still not well understood. The low density of viable seeds has been suggested as limiting to vegetation development in polar deserts (Svoboda and Henry, 1987).

In the Arctic, seed banks have been studied only a few times (McGraw and Vavrek, 1989). Some authors (Fox, 1983; Archibold, 1984) looked at low arctic xeric communities, mostly dominated by *Dryas* or *Cassiope*, while only one study (Freedman *et al.*, 1982) dealt with high arctic vegetation. Seed pools under the most depauperate polar desert vegetation have not been studied yet. It was, however, suggested that the viable seed bank decreased with increasing latitude (Johnson, 1975) and altitude (Milton, 1939). In the context of climate change, any information on the seed pool from polar desert landscape will contribute to a better understanding of present and future plant communities surviving or potentially expanding in these extreme habitats.

The main objective of the present study was to provide data on the size and diversity of the germinable seed bank in a range of polar desert sites, in order to quantify the degree to which seed abundance may be limiting plant community development. This study also provides information on the growth and phenology of the seedlings obtained from the seed bank.

5.3 METHODS

5.3.1 Study sites

Sverdrup Pass (79°N) is a deglaciated East-West oriented valley in central Ellesmere Island separating two main icefields, Agassiz to the north and Prince of Wales to the south. In its central portion, near the divide (*ca.* 330 m a.s.l.), steep dolomitic ridges (800-1200 m a.s.l.) rise on the north side. These ridges have very sparse plant cover. On the south side, granitic moraines and terraces gradually rise to an altitude of 1500 m a.s.l., and are topped with an ice cap. A slightly more diverse and abundant flora was present on these N-facing slopes. From a total of 14 sites, six were established along a dolomitic gradient, their altitudes ranged from 335 m to 765 m a.s.l. (marked D1 to D6). Seven sites were established along the granitic gradient from 347 m to 727 m a.s.l. (marked G1 to G7). One site was selected on the valley floor, in close proximity to willow field communities (Bergeron and Svoboda, 1989) at 330 m a.s.l. (V1). The general characteristics of the sites are summarized in Table 5.1. The vegetation of the 13 gradient sites, mostly cushion and rosette plants, is presented in Chapter 3. Site characteristics and species composition are presented in Appendices 2 and 5 respectively.

5.3.2 Field sampling

During the later part of July 1991, 20 soil samples were collected at each site. Ten random 50 cm x 50 cm quadrats were laid at each site and two 10 cm x 10 cm soil samples (1 cm deep) were collected within the quadrat. One sample was collected near the dominant vascular plant in the quadrat and one at least 10 cm away from a plant. If no plants were found in a quadrat, additional quadrats were thrown until 10 samples near a plant and 10 away from any plant

Table 5.1: Habitat characteristics of the fourteen sites studied along the two altitudinal gradients and in the valley, Sverdrup Pass, Ellesmere Island. Dolomitic gradient was S-facing; granitic gradient was N-facing. SD = Vascular Species Diversity.

Vegetation Sites	Altitude (m a.s.l.)	Habitat Description	SD	Dominant Species
Dolomitic gradient				
D1	335	slope, protected	10	*Puccinellia bruggemannii*, *Saxifraga oppositifolia*
D2	336	flat and exposed	9	*Puccinellia bruggemannii*, *Dryas integrifolia*
D3	376	near snow bed	9	*Saxifraga oppositifolia*
D4	420	flat ridge top	4	*Braya purpurascens*
D5	684	near snow bed	6	*Saxifraga oppositifolia*
D6	765	frost boils	4	*Draba subcapitata*, *Saxifraga oppositifolia*
Valley floor				
V1	330	fine eolian	12	*Potentilla* sp.
Granitic gradient				
G1	347	main moraine	14	*Saxifraga tricuspidata*
G2	357	small hill	8	*Carex nardina/Kobresia myosuroides*
G3	443	near snow bed, good soil	16	*Carex nardina*, *Poa arctica*
G4	461	flat plateau	9	*Salix arctica*, *Dryas integrifolia*
G5	618	boulders	14	*Saxifraga oppositifolia*
G6	638	boulders	13	*Saxifraga oppositifolia*
G7	727	boulders	8	*Saxifraga oppositifolia*

were collected. The samples were packed in paper bags and kept frozen until the start of the germination experiment in the spring of 1993.

5.3.3 In the laboratory

Each sample was passed through a standard 2 mm mesh sieve. The portions (> 2 mm and < 2 mm) were weighed (0.01 g) and a subsample of 60 ml, if available, of the finest portion was weighed and used in the germination trials. Each subsample was evenly spread in a 150 mm diameter petri dish, moistened and incubated at 26°C under continuous light (quantum flux PAR = 15 μmolm^{-2}s$^{-1\cdot}$ measured with a Licor Quantum photometer model LI-185B; Plate 5.1a).

The dishes were monitored daily for seedling emergence (appearance of cotyledons) and watered. A few days after germination, the young seedlings were transferred to a sterilized soil mixture (60% sand, 40% pot soil) and grown at 18°C under continuous light (quantum flux PAR = 125 μmolm^{-2}s^{-1}). The plants were maintained for a period of up to two years, their phenological stage being monitored periodically (Plate 5.1b). Most germination was observed within the first 12-15 days of the trials. Each germination trial was terminated after 50 days. This method was adapted from Freedman *et al.* (1982).

Seedling identification was made when the flowering stage was achieved. If flowering did not take place or if the individual died prior to flowering, identification was done on the basis of the vegetative characters and using reference material from the Erindale College herbarium collection. When identification was impossible or ambiguous, the seedling was recorded in an 'Others' category. Species nomenclature generally follows Porsild and Cody (1980; see Appendix 1); vouchers are being kept in the Erindale College herbarium.

Plate 5.1: Experimental set-up of a) seed germination in large petri dishes from collected soil and b) growth of transplanted seedlings in controlled environment.

5.3.4 Calculations and statistics

The germinable seed bank value (number of seeds per m^2) at each site, was derived from the following relationship:

$$G = g\frac{Wt_a}{Wt_b} x\, 100$$

Where G = germinable seed bank (seeds/m^2); g = number of germinated seedlings in a subsample; Wt_a = weight of < 2 mm soil portion of a 10 cm x 10 cm sample; Wt_b = weight of subsample. The multiplication factor 100 was used to convert 10 cm x 10 cm samples to 1 m^2.

Calculations of germinable seed bank in the 'bare ground' and in the 'near-the-plant' soils were done separately. It ought to be emphasized that the obtained figures represent situations of 100% bare and 100% plant cover, respectively. To obtain the real value of the germinable seed pool, both values were adjusted by using the actual percentage cover of the bare ground and that of the vascular plant cover. (The mean cover values were obtained from a minimum of 30 quadrats (50 cm x 50 cm); *cf.* Chapter 3; Appendix 2). The corrected figures were then added to represent the site's actual germinable seed bank (Table 5.2). Similar calculations were made for each seedling species.

The data were tested for normality using a Kolmogorov-Smirnov test for goodness of fit and for homogeneity of variances using Bartlett's test before parametric tests were performed (SYSTAT Version 5.02). Pearson's correlation coefficients were calculated to test the association between the number of seeds in the seed bank and the cover per site as well as with the vascular plant diversity per site. To test the significance of the near-plant and bare ground comparisons, a one-way ANOVA was used.

Table 5.2a: Germinable seed banks in the granitic gradient, in the proximity of adult vascular plants (n = 10), as if 100% cover, and in bare ground (n = 10), and total real viable seed banks when adjusted for actual plant cover (n = 20), Sverdrup Pass, Ellesmere Island. Mean (SE).

	Sites						
	G1	G2	G3	G4	G5	G6	G7
Near plant (seeds/m^2)	604 (162)	1133 (581)	1319 (434)	143 (51)	187 (59)	285 (135)	386 (129)
Bare ground (seeds/m^2)	427 (99)	107 (46)	397 (128)	13 (13)	59 (28)	49 (36)	46 (23)
Plant cover (%)	6.7	0.9	5.7	7.3	2.6	2.9	1.3
Total (seeds/m^2)	439 (104)	116 (51)	449 (145)	23 (15)	62 (29)	56 (39)	51 (24)

Table 5.2b: Germinable seed banks in the valley and the dolomitic gradient, in proximity of adult vascular plants (n = 10), as if 100% cover, and in bare ground (n = 10), and total real viable seed banks when adjusted for actual plant cover (n = 20), Sverdrup Pass, Ellesmere Island. Mean (SE).

	Sites						
	V1	D1	D2	D3	D4	D5	D6
Near plant (seeds/m^2)	448 (108)	179 (101)	293 (221)	104 (67)	0.5 (0.4)	44 (22)	116 (59)
Bare ground (seeds/m^2)	250 (165)	12 (11)	40 (29)	0	12 (11)	57 (25)	20 (19)
Plant cover (%)	2.6	1.2	0.3	0.3	0.2	1.4	0.2
Total (seeds/m^2)	256 (163)	14 (12)	41 (30)	0.3 (0.2)	12 (11)	56 (25)	20 (19)

5.4 RESULTS

5.4.1 Seed bank

Tables 5.2a and b show the mean germinable seed densities as related to the site vascular plant cover. The theoretical germinable seed densities near the plants (calculated as if full cover) were significantly larger ($p = 0.025$, $F = 5.623$, $DF = 1, 26$) than those found in bare ground. Their range was 0.5 (D4) to 1319 (G2) and 0 (D3) to 427 (G1) seeds/m^2 respectively. In 3 of the 14 sites more seeds germinated in the bare ground soil than in that collected near the plants (V1, D4 and D5).

The total adjusted germinable seed densities per site ranged from 0.3 (D3) to 449 (G3) seeds/m^2 (Table 5.2). The valley site and the three lower granitic sites had relatively large seed banks (256, 439, 116 and 449 seeds/m^2 for V1, G1, G2 and G3 respectively), in correspondence with their higher vascular plant cover. This was not the case in the dolomitic gradient. As expected, the dolomitic sites stored far fewer germinable seeds per unit area compared to the granitic sites, but, surprisingly, stored more seeds per unit of plant cover: 63 seeds vs 44 seeds per percent of cover, respectively.

The germinable seed bank was positively correlated with the vascular plant cover as well as the adult plant diversity ($p = 0.015$ and $p = 0.007$ respectively; Figure 5.1). The only exception was site G4. Although at this site, plant cover was the largest (7.3%) of all sites studied, the germinable seed bank was one of the smallest (23 seeds/m^2). This may be explained by two factors. Although this site was part of the granitic gradient, the substrate was a dolomitic gravel deposited by a retreating glacier in the past. Secondly, the plant community was dominated by large individuals of *Salix arctica* and *Dryas integrifolia*. Seedlings of these species did not emerge in our germination trials.

The large majority (72%) of the germinable seeds were Dicotyledons with 6 species of Cruciferae, 2 of Saxifragaceae, and one from each of Rosaceae,

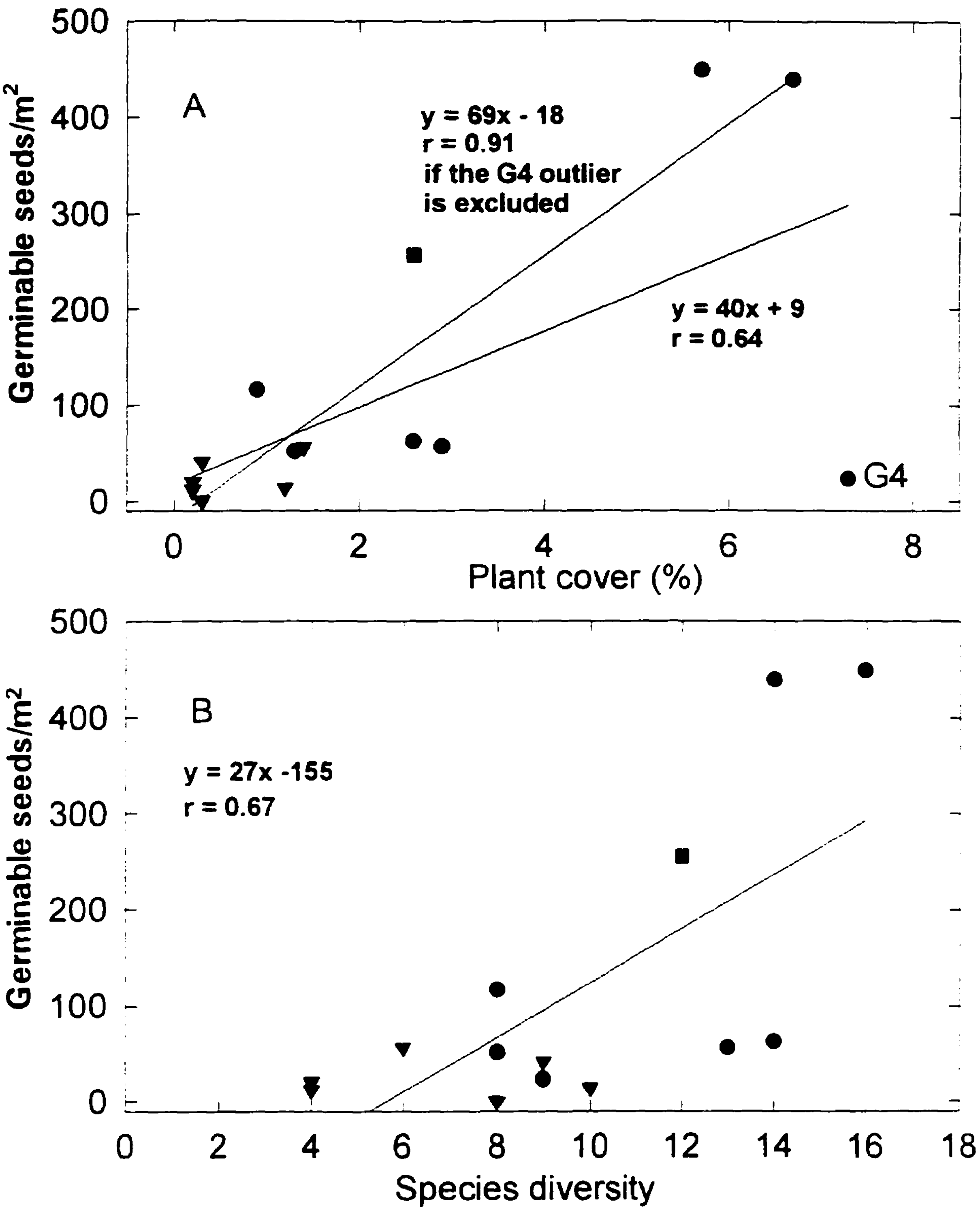

Figure 5.1: Germinable seed banks in relation to plant cover (A) and vascular species diversity (B), in 14 stands in Sverdrup Pass, Ellesmere Island. Sites from granitic gradient (●), valley (■) and dolomitic gradient (▼).

Caryophyllaceae and Papaveraceae. From the monocots, *Poa abbreviata* was the second most frequently emerging species (in 8 out of 14 sites) immediately after *Saxifraga oppositifolia* (in 10 out of 14 sites). *Draba subcapitata* was the only other species with at least 50% occurrence (7 out of 14; Table 5.3).

Only two sites, both at the bottom of the granitic gradient (G1 and G2), had a few vascular species identified among the emerging seedlings that were not represented as adults in the site. Seedlings of *Poa cf. arctica* were found, in very low numbers in the G1 samples. Also, three species (*Draba cinerea*, *P. abbreviata* and *Saxifraga tricuspidata*) emerged from the seed bank of G2 which were not present as adult on this site. In both cases, however, these species were common on neighbouring slopes and terraces.

5.4.2 Seedling growth

The controlled environment conditions were likely more favourable to plant growth than those usually encountered in the field (regular watering, approximately 20°C and constant light). Nevertheless, the seedlings here developed into small plants which were morphologically very similar to plants growing in the field (Plate 5.2). For example, *P. abbreviata* produced dense caespitose clumps, *Draba* and *Braya* grew rosettes with a small inflorescence and *Saxifraga cernua* and *Melandrium affine* produced relatively short flowering stems comparable to those observed in the field. Many individuals of the slow growing *S. oppositifolia* produced small leaves with shoots of a maximum length of 2 cm, over two years. This suggests that these plants were not very plastic morphologically. Many plants were infested by aphids, the Cruciferae and the Caryophyllaceae were particularly vulnerable.

Of the 15 species identified in this study, six were not able to produce flowers under the given conditions: *Papaver radicatum*, *Poa glauca*, *Potentilla* sp., Cyperaceae sp (*Carex cf. nardina*), *S. oppositifolia* and *S. tricuspidata*. These species, either did not grow well and died before attaining a size suitable

Table 5.3: Seedling emergence of vascular taxa in granitic and dolomitic altitudinal gradients (335-765 m a.s.l.) and the valley (330 m a.s.l.) in Sverdrup Pass, Ellesmere Island.

	Species germination					
	Granitic 7 sites		Dolomitic 6 sites		Valley 1 site	
Species	Occurrence of sites (x/7)	Range (seeds/m^2)	Occurrence of sites (x/6)	Range (seeds/m^2)	Occurrence of sites (x/1)	Range (seeds/m^2)
Braya purpurascens	1	0-14	3	0-0.1	0	0
Draba cinerea	3	0-51	0	0	0	0
Draba oblongata	1	0-22	0	0	0	0
Draba subcapitata	5	0-35	2	0-21	0	0
Cardamine bellidifolia	1	0-15	0	0	0	0
Cyperaceae sp.	2	0-28	0	0	0	0
Erysimum pallasii	1	0-2	0	0	0	0
Melandrium affine	1	0-41	0	0	0	0
Papaver radicatum	3	0-18	2	0-20	0	0
Poa abbreviata	5	0-233	2	0-12	1	0.5
Poa glauca	2	0-1	0	0	0	0
Potentilla sp	0	0	0	0	1	25
Puccinellia bruggemannii	0	0	2	0-0.1	1	1
Saxifraga oppositifolia	6	0-19	4	0-0.2	0	0
Saxifraga tricuspidata	4	0-73	0	0	0	0
Others: monocots	2	0-21	3	0-0.3	1	54
Others: dicots	7	1-210	6	0.1-25	1	175

Plate 5.2: Seedlings of *Papaver radicatum* and *Poa abbreviata* grown for 82 days under constant light at 18-20°C.

Plate 5.3: Close-up of *Draba cinerea* grown from a seed, bearing a silique and a flower after 97 days under constant light at 18-20°C.

for reproduction (*e.g. Papaver* and *Potentilla*), or they developed vegetatively but did not produce flowers over the two year period of the study (Plate 5.2). At this point it is not possible to determine if these plants needed to grow to a certain size before flowering, or if they required certain light or temperature cues.

Individuals of the remaining nine species did flower (Plate 5.3), some of them repetitively, without any special light or temperature cues (Table 5.4). Certain plants even produced viable seeds that successfully established seedlings near the parent plant (*Draba cinerea*, *P. abbreviata* and *M. affine*; Plate 5.4 and 5.5). The plants may have selfed or have been pollinated by water (during watering) or perhaps by insects (aphids and flies) occasionally present in the growth chambers.

The first flowers emerged 5 to 20 weeks after transplant (Table 5.4). All the Dicotyledon species flowered more rapidly (5 to 20 wks) than the 2 grasses species (16 to 32 wks). Many individuals of the grasses produced flowers more than once. In fact, distinct flowering events were difficult to identify in these plants, most of them maintained vegetative growth with periodical new flowering and were still alive at the end of the experiment (Plate 5.4).

For each of *Braya purpurascens*, *Cardamine bellidifolia* and *Erysimum pallasii* only one plant produced flowers. In each case, the plant died after producing seeds (like annuals). On the other hand, *M. affine* plants underwent a period of 'senescence' after flowering was complete (*i.e.* some leaf die back) before a new set of leaves was formed and new flowers were produced. All three *M. affine* plants died after the second or the third flower had been produced. The three *Draba* species had a number of plants flower and almost all of them survived after they produced a fruit. A second flowering was observed only for *D. cinerea* (Plate 5.3), but the two other *Draba* species grew well, even after the flowering event. Additional flowering may have been hindered by heavy aphid infestation.

The nine species which produced flowers under the controlled conditions are not generally considered dominant species in high arctic vegetation. Some

Table 5.4: Number of seedlings that produced flowers under controlled conditions and range of time to flowering event. Time indicated in weeks since transplant or since last flowering event.

Species	First Flowering		Second Flowering		Third Flowering		Plants Died after flowering (n)
	n	Time since transplant (weeks)	n	Time since first flowering (weeks)	n	Time since 2nd flowering (weeks)	
Braya purpurascens	1	8					1
Cardamine bellidifolia	1	approx. 5					1
Draba cinerea	4	8 - 20	3	4 - 12			
Draba oblongata	4	11 - 12					2
Draba subcapitata	8	8 - 17					1
Erysimum pallasii	1	5					1
Melandrium affine	3	10 - 12	3	5 - 24	1	12	3
Poa abbreviata	25	16 - 32	9	approx. 4			
Puccinellia bruggemannii	5	> 22	4	approx. 12			1

Plate 5.4: Flowering *Poa abbreviata* with a cluster of *Draba cinerea* seedlings established from seeds produced by a mature plant grown in the growth chamber.

Plate 5.5: Close-up of seedlings of *Draba cinerea* from Plate 5.4.

(*e.g. P. abbreviata* and *Draba subcapitata*) are common in polar deserts (*cf.* Chapter 3). Species often found as dominant in aboveground vegetation of more diverse sites either were absent from the germinable seed bank (*e.g. D. integrifolia* and *S. arctica*) or were present in the seed bank but their young plants did not produce flowers under the controlled conditions (*S. oppositifolia*, *S. tricuspidata*, *P. radicatum* and *C. cf. nardina*).

5.5 DISCUSSION

5.5.1 Seed bank

The polar desert landscape is generally covered by shattered rocks and erratic boulders while the finer material, a product of rock weathering, accumulates between them. This 'soil' is often compacted and appears as a thin crust cemented with algae, fungi and precipitated salts (Cameron, 1969). Such surface conditions may hinder seed deposition (Chambers and MacMahon, 1994). Combined with other limitations such as cold soil surface, short growing seasons and limited water supply this makes seed germination and seedling establishment an unlikely event. While some seeds get deposited, a few of those germinate, even fewer establish and reach flowering stage on these sites.

With increasing latitude and altitude, a decrease in germinable seed bank could be associated with the decreasing productivity gradient (Fox, 1983). Even in the highest latitudes, more favourable sites produce more seeds than the more limiting habitats. Polar deserts have very low standing crop and productivity (Bliss *et al.*, 1984; Chapter 3), and consequently, their seed bank may be expected to be small. This assumption has not been confirmed. In this study, we have found that these depauperate habitats may harbour seed banks comparable in size and diversity to some lusher high arctic vegetation sites such as the polar oasis, Alexandra Fiord, at 79°N. At this locality, Freedman *et al.* (1982) studied the seed banks of the raised beach ridge, the heath and the fen communities, with a relatively high plant cover of 43, 35 and 48%, and reported germinable seed banks of 131, 56 and 1 seeds/m^2, with 6, 10 and 1 vascular species, respectively. In that same study, however, the disturbed sites had much richer seed banks with 454 (gravel pad), 954 (coastal beach) and 7810 seeds/m^2 (fox den).

The fact that there are as many or even more seeds present in some meagrely vegetated polar desert compared to semi-desert sites might be explained by a proportionally higher production of seeds or by lower chances of successful germination and longer seed life-span in the cold polar desert soil. In other words, the ratio of seed deposition/seed germination is in favour of deposition at the more stressful sites. In a preliminary study, the arctic poppy was found to produce flowers on a dolomitic pinnacle and in the valley of Sverdrup Pass, even during the cold and short summer of 1989. However, only a small proportion of the seeds germinated in controlled experiments (18% from the valley plants and none from the pinnacle plants; Lévesque and Svoboda, 1992). This would suggest that in very harsh conditions, viable seeds are produced only in more favourable years, and these are added to a long lasting seed bank.

Reproduction by seed is rare in polar semi-deserts and deserts, but vegetative reproduction is even less frequent (Bell and Bliss, 1980). Our study supports the above statement and suggests that, although seedling establishment is rare in stressful polar habitats, reproduction by seeds is more important than vegetative spreading. Similarly, in a recent comparative study, Wookey *et al.* (1993) suggested that in good years a high arctic *Dryas octopetala* from polar semi-desert communities at Svalbard would benefit from a heavy investment in seed setting while a sub-arctic *Empetrum hermaphroditum* would not profit from such a strategy. This is because an abundant seed rain increases the chances of successful establishment in vacant habitats of the polar semi-desert while there is little opportunity of establishment by seeds in the closed vegetation cover of the dwarf shrub heath. The relatively large seed bank found in polar desert soils may give rise to more abundant vegetation in the context of climate change; however, the actual influence of climate warming on polar desert vegetation may also be negative if it increases evaporation or drought frequency, or delays snow melt (Maxwell, 1992).

A large proportion of the emergent seedlings were from ruderal species *sensu* Grime (1979), which are best equipped to invade vacant and disturbed sites. Despite the proximity of richer habitats supporting flowering *Dryas integrifolia*, *Salix arctica* and *Cassiope tetragona*, none of these major arctic species had germinable seed in our samples. The limited longevity of *Salix* seeds (Densmore and Zasada, 1983) and the possibly inadequate conditions for breaking dormancy and germination of the other two species might be partly responsible. Germination tests performed with seeds of *S. arctica* from a few locations in central Ellesmere Island showed more than 80% success immediately after seeds are shed, but almost no germination after a cold treatment (Jones, 1995).

In the field, the presence of adult plants increased the likelihood of finding seedlings within their proximity. These seedlings were mostly from the same species as the adult plant and were likely produced by that same plant. We also observed seedlings of other species associated with a given adult plant. The presence of an adult individual may first improve the chances of seed catchment and later seedling establishment (Chambers and MacMahon, 1994).

Poorer dolomitic sites had more germinable seeds per unit of plant cover than the granitic sites (63 vs 44%). This could be associated with the nature of the substrate or with the length of seed viability in the soil. Chambers *et al.* (1991) have shown that depending on texture of the substrate and seed morphology, the seeds may penetrate the soil and accumulate or, stay on the surface and be more subject to saltation. In our study, the porous soil of the granitic gradient might facilitate seed burial while the more compact dolomitic substrate might restrict it. Frost action could also play a role in the distribution of the seeds within the soil profile (Raup, 1969). There were, however, almost no germinable seeds at more than 1 cm depth on the studied polar desert sites (Lévesque, unpublished). At the same time, the temperature and moisture content of these substrates also tend to differ which would, most likely, influence the viability of the seeds in the soil (Murdoch and Ellis, 1992).

5.5.2 Seedling growth

The ability of some high arctic species to produce flowers under constant conditions in growth chambers is revealing. This suggests an opportunistic strategy where, if conditions are adequate, the plant can repeatedly go through all its reproductive stages as long as the conditions are favourable. If the season is too short however, the plant will stop its development and may suffer a set back. No particular light or temperature cues were necessary to stimulate flowering in the nine species presented in Table 5.4 and in four more species (*Minuartia rubella*, *Sagina intermedia*, *Saxifraga caespitosa* and *Saxifraga cernua*) observed from seed bank analysis performed on polar desert soils from additional sites (Lévesque, unpublished).

These preliminary results also suggest that the perennial status of some arctic forbs (*e.g. Braya purpurascens*, *Cardamine bellidifolia* and *Erysimum pallasii*) may be induced by the harsh conditions that prolong their vegetative development over several years before the reproductive stages can be completed. A period of five weeks under the controlled growth chamber conditions used in this study is approximately equivalent to 1400 degree-days. In the polar desert sites studied, this is equivalent to 2 to 3 full years of degree-day accumulation in the more favourable sites (*e.g.* G1, G2 and G3) and to 4 or more years for more extreme sites (*e.g.* D4, D5 and D6; *cf.* Chapter 6).

Most of the species that flowered in our experiment were found as small scattered plants, sometimes with a relatively high frequency (*e.g. Draba* sp.; Chapter 4), in the polar desert sites studied. None of the cushion plant species produced flowers in the growth chamber study. This reflects the opportunistic nature of the small herbaceous species, which depend on rapid and successful reproduction to maintain their population (Brochmann and Elven, 1992). In contrast, the slow growing cushion plants are similar to woody species in southern latitudes and generally have a few large and long lived individuals per stand (*cf.* Chapter 4). These plants are more dependant on their ability to grow well and persist under harsh conditions rather than on a rapid or high production of offspring.

CHAPTER 6:

PHENOLOGICAL AND GROWTH RESPONSES OF *PAPAVER RADICATUM* ALONG ALTITUDINAL GRADIENTS IN THE CANADIAN HIGH ARCTIC

6.1 ABSTRACT

Phenology and growth of *Papaver radicatum* Rottb. was monitored over four summers (1990-1993) at 12 sites, along a dolomitic and a granitic altitudinal gradient (330 m a.s.l. to 770 m a.s.l.) at Sverdrup Pass, central Ellesmere Island, Canada. The gradients provided substantial differences in environmental characteristics. Three of the four seasons (1990, 1991 and 1993) had more than 400 thawing degree-days (TDD) in the valley, while the 1992 season had less than 300. The granitic sites had consistently higher temperatures than the dolomitic sites, despite their northerly aspect. Increasing elevation reduced total degree-day accumulation (*ca*. 40 degree-days/100 m) and length of potential growing season.

The proportion of the population producing flower buds was similar at all sites in any given year, but there were differences among years. Production of flowers and fruits per site decreased with altitude along the dolomitic gradient in 1991 and 1992. There was no difference in the number of buds or flowers produced per plant with increasing altitude, although larger plants with multiple flowers were found only on low elevation granitic sites. Plants from the dolomitic sites were smaller and flowered, on average, after the site accumulated 150

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degree-days, while plants on the granitic sites were larger and bloomed after 200 degree-days. *Papaver* is able to grow and reproduce over a wide range of environmental conditions and moderate climate warming would likely promote its growth and establishment, unless other factors, especially snow free periods and water availability, become limiting.

6.2 INTRODUCTION

In the High Arctic, extensive areas are occupied by sparse polar desert vegetation (Aleksandrova, 1988; Bliss and Matveyeva, 1992), generally dominated by vascular plants (Bliss *et al.*, 1984). Recent work compared plant distribution (Bliss *et al.*, 1994), seed bank availability (Lévesque and Svoboda, 1995) and water limitation (Gold and Bliss, 1995) in polar deserts. However, except for the extensive and comprehensive contribution made by Sørensen (1941), there is still little information available on the biology and phenology of vascular plants in these extreme habitats. More information on polar desert plant growth and reproductive pattern is needed to improve our understanding of plant distribution, colonization and survival at present and during the past and possible near-future extreme climatic events.

Natural gradients provide an excellent opportunity to study responses of plants to a range of changing environmental conditions (Whittaker and Niering, 1975; Kudo, 1991) and for understanding the present environmental controls over their distribution (Walker *et al.*, 1994). Documentation of plant responses to climatic conditions across their distributional range may allow the determination of thresholds that would not be seen if plants were studied at only one geographical location. Studies of altitudinal gradients may, to a degree, substitute for latitudinal gradients, and consequently also for climatic gradients (Billings, 1987).

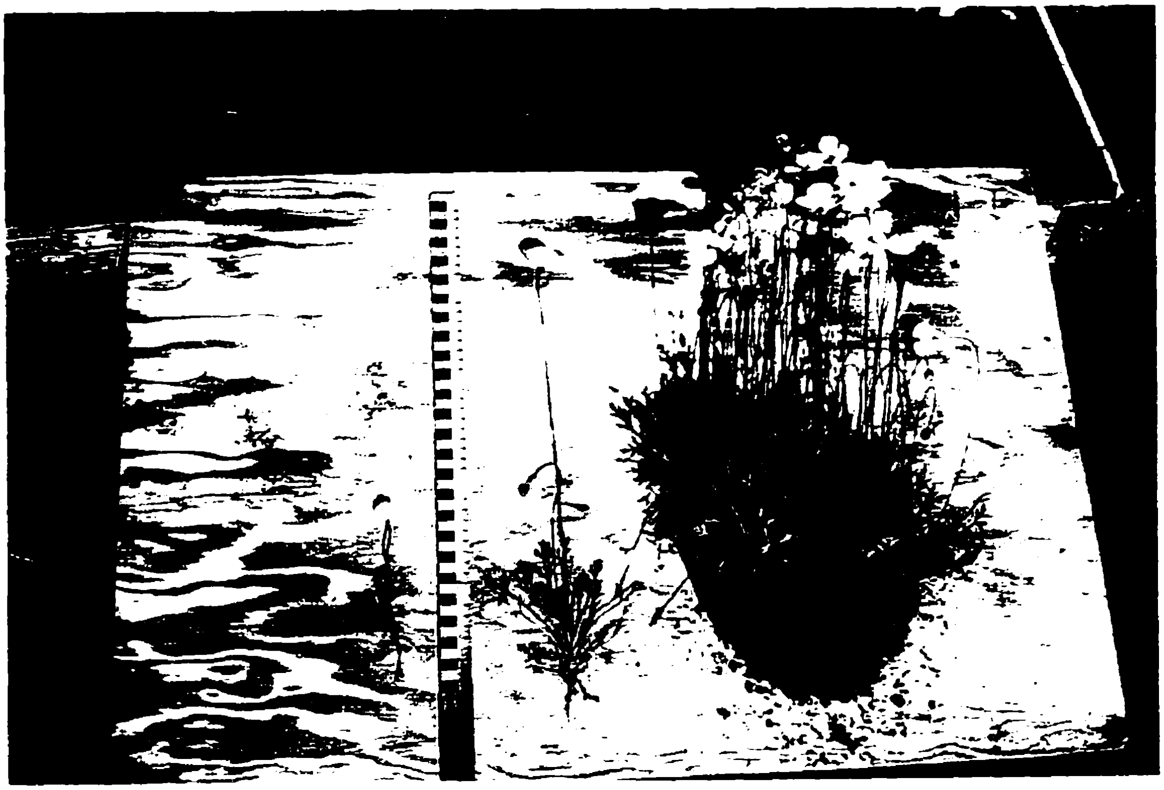
Experimental manipulation using closed chambers (*e.g.* Wookey *et al.*, 1993; Chapin *et al.*, 1995) and open top chambers (e.g. International Tundra

Experiment climate warming approach; Henry and Molau, 1997) are designed to ameliorate the microenvironment, and to induce conditions similar to those expected under climate warming predictions. In contrast, our study was concerned with plant performance along naturally occurring altitudinal gradients, where climate-controlled site conditions ranged from less than optimal to colder and more stressful; thus we approximated conditions expected under a climate cooling scenario (Svoboda, 1996).

Papaver radicatum Rottb. is one of the vascular species most frequently growing in polar deserts (Bliss and Matveyeva, 1992; Chapter 3). It was chosen in our altitudinal gradient study in order to determine the degree of climatic control on the growth and flowering of this circumpolar forb across a range of microenvironmental conditions. *P. radicatum* has been recognized for its phenotypic plasticity, as documented in several field studies and fertilizer and greenhouse experiments (Savile, 1972; Mølgaard, 1982; Henry *et al.*, 1986; Lévesque and Svoboda,1992; Woodley and Svoboda, 1994). At Alexandra Fiord 78°N, in an unheated polyethylene greenhouse with higher temperatures (mean July temperature of 15°C vs 10°C in the open tundra; Bergsma, 1986) and increased moisture availability (by reduction of the drying effect of the wind), a transplanted *Papaver* rosette grew to be more than six times larger than did plants collected from the surrounding mesic tundra during the same season. The following year, a cluster of new plants had been recruited from the dropped seeds (extreme right cluster, Svoboda, unpublished; Plate 6.1a). In contrast, the growth of a flowering *Papaver* plant on a wind-swept dolomitic upland, with the July mean around 5°C, was stunted with an almost horizontal pedicel (Plate 6.1b). When small greenhouse caps were individually installed over similarly stunted *Papaver* plants growing on an exposed ridge at Sverdrup Pass (Lévesque and Svoboda, 1992) vertical pedicels were produced (Lévesque unpublished). This suggests that even in extreme situations *Papaver* has the potential to respond to amelioration. Although there is likely some genetic variation in populations of this species, the authors believe that most of the

Plate 6.1: Blooming *Papaver radicatum* grown in three contrasting habitats: a) a single individual separated from a cluster of *Papaver* plants (right of the scale), grown in an unheated polyethylene greenhouse, is compared with a control plant (left of the scale), excavated from the surrounding dry-mesic tundra, Alexandra Fiord; b) a stunted *Papaver* plant, with a horizontally stretching pedicel on a wind-swept dolomitic upland at Bache Peninsula (79°N). All habitats at central Ellesmere Island. The photographs demonstrate the plasticity, acclimation potential and tolerance range of this hardy species.

a)



b)

variation observed in the field can be attributed to phenotypic response to varying environmental conditions.

Phenology of this species was monitored at 12 sites along two slopes (six sites on each slope) over four growing seasons (1990-1993). The slopes rising from the Sverdrup Pass Valley vary in lithology, aspect, species composition and both soil nutrient and moisture availability (*cf.* Chapter 3). Based on preliminary results (Lévesque and Svoboda, 1992) we set out to test the following assumptions: 1) a delay in phenology will be associated with altitude; 2) plant performance (*i.e.* number of flowers/plant and biomass/plant) will decrease with altitude; 3) fewer plants will flower on the dolomitic than the granitic sites, as they are colder and nutritionally poorer (Lévesque and Svoboda, 1992); and 4) plants at the highest and therefore most stressful sites may not produce flowers or complete flowering in cold years.

6.3 METHODS

6.3.1 Site characteristics

The study area was located near the drainage divide in Sverdrup Pass, Ellesmere Island, Canada (79°10'N, 79°30'W; Figure 6.1). Sverdrup Pass is a deglaciated valley running East-West across central Ellesmere Island, and is bounded by rocky slopes and ice caps to the North and South. The Pass marks the northern edge of the Canadian Shield in this region; the southern slopes are granitic and the northern slopes are composed of dolomitic limestones. Climatically, Ellesmere Island is part of the Northwestern Arctic zone, with a mean July temperature of 3-5°C and less than 150 mm of precipitation per year (Maxwell, 1981). Botanically, the island belongs to the polar desert vegetation zone (Edlund and Alt, 1989). The vegetation of the valley in Sverdrup Pass was described by Bergeron and Svoboda (1989), and that of the dolomitic scree slopes by Maycock and Fahselt (1992) and in Chapter 3. Approximately 3 km

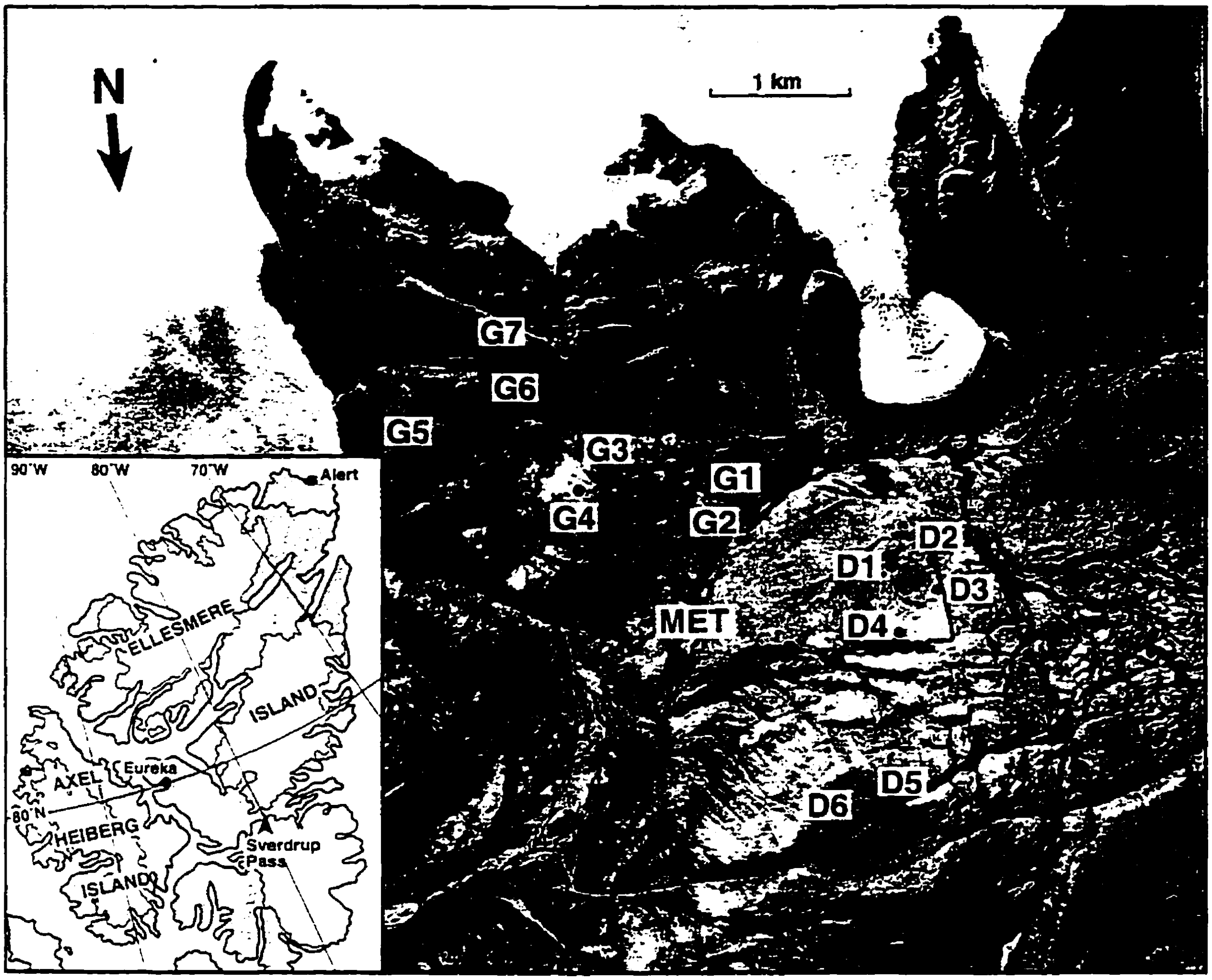


Figure 6.1: Map of Ellesmere Island and an aerial photograph of the central portion of Sverdrup Pass. The dolomitic sites marked as D1-D6, granitic sites as G1-G7 and the microclimate station as MET. Cropping of photograph # T508R-42 taken in July 1953 for the Department of Energy, Mines and Resources Canada. Note that the aerial photograph is oriented with North towards the bottom of the page.

east of the major drainage divide, a research base was established in 1986. Climatic data, including maximum and minimum temperature, relative humidity, cloud cover, wind speed and direction were collected during each summer from June 1986 until August 1994 (Molau,1993a). In 1988, a standard automated weather station was established in a nearby wet meadow. Air temperatures (1.5 m) measured by thermistors (Campbell Scientific model 107B) at 5 minutes intervals were recorded as daily mean, maximum and minimum temperatures on a datalogger (Campbell Scientific CR10).

Two altitudinal gradients on opposing slopes of the valley (Figure 6.1) were chosen: one on the dolomitic South-facing slope and the other on the granitic North-facing slope. Six sites were selected on the dolomitic slope (D1 to D6) and seven on the granitic slope (G1 to G7). Both gradients started near the valley bottom (300 m a.s.l.) and reached 765 m on the dolomitic plateau and 727 m on the granitic mountain ridge (Table 6.1). The chosen sites were relatively large, flat areas with sporadic plant cover and noticeable differences in micro-environmental characteristics due to elevation and aspect.

According to the classification of Edlund and Alt (1989), the plant communities present at these sites ranged from *Dryas-Salix-Saxifraga* barrens (sites G3 and G4) to *Saxifraga*-barrens (sites G1 and D2) and *Saxifraga*-herb barrens (all other sites; Table 6.1). *Papaver radicatum* was present on all sites except G4, which was excluded for the purpose of this study. None of the sites had visible black cryptogamic soil crust (Gold and Bliss, 1995).

6.3.2 Soils

In sparsely vegetated polar deserts, soil development is minimal (Bliss and Svoboda, 1984; Bliss *et al.*, 1984; Bliss *et al.*, 1994). To compare the soil characteristics of both lithologies, random soil samples were collected at each site in 1990 (top 10 cm; n = 30), dried to constant weight at 60°C and sieved with a 2 mm sieve. Fine portions of replicate samples were analyzed from each

Table 6.1: Habitat characteristics of the 13 sites studied and of the 12 sites monitored for phenology along two altitudinal gradients in Sverdrup Pass, Ellesmere Island. Dolomitic gradient was S-facing; granitic gradient was N-facing. VSR = Vascular Species Richness; Cover = mean total vascular plant cover in % of n = 30 random 50 cm x 50 cm quadrats. (Modified from Lévesque and Şvoboda, 1995).

Sites	Altitude (m a.s.l.)	Habitat Description	VSR	Cover (%)	Dominant species
Granitic gradient					
G1	347	main moraine	14	6.7	*Saxifraga tricuspidata*
G2	357	small hill	8	0.9	*Carex nardina*
G3	443	near snow bed, good soil	16	5.7	*Carex nardina* + *Poa arctica*
G4	461	flat plateau (no *Papaver*)	9	7.3	*Salix arctica* + *Dryas integrifolia*
G5	618	boulders	14	2.6	*Saxifraga oppositifolia*
G6	638	boulders	13	2.9	*Saxifraga oppositifolia*
G7	727	boulders	8	1.3	*Saxifraga oppositifolia*
Dolomitic gradient					
D1	335	slope, protected	10	1.2	*Puccinellia bruggemannii* + *Saxifraga oppositifolia*
D2	336	flat and exposed	9	0.3	*Puccinellia bruggemannii* + *Dryas integrifolia*
D3	376	near snow bed	9	0.3	*Saxifraga oppositifolia*
D4	420	flat ridge top	4	0.2	*Braya purpurascens*
D5	684	near snow bed	6	1.4	*Saxifraga oppositifolia*
D6	765	frost boils	4	0.2	*Draba subcapitata* + *Saxifraga oppositifolia*

site, as in Lévesque and Svoboda (1992), for total organic matter content (estimated by loss on ignition method; n = 30), particle size distribution (hydrometric method; n = 8), pH (water-saturated paste; n = 4), available P (extraction by weak HCl solution; n = 4) and exchangeable K and Ca (extraction by neutral-N NH_4OAc; n = 4). Percent N was measured by combustion with a LECO CHN-800 analyzer (n = 3). See Chapter 3 for details.

6.3.3 Ground surface and air temperature, and thawing degree-days (TDD)

Cumulative TDD (above 0°C) in the Sverdrup Pass valley were calculated using the daily mean air temperatures (1.5 m above the ground) measured at the automatic climate station (Molau, 1993a). A summary of the climatic data for 1989 to 1993 is presented in Table 6.2. Since there was no snow cover when the sites were first visited and since it is very difficult to measure the exact number of physiologically active days that plants experience (plants are often warmer than the soil around them; Körner and Larcher, 1988), the length of the potential growing season was calculated as the span of days in the season with daily mean air temperature above the freezing point. The number of days with below freezing temperatures during that period varied between years (Table 6.2).

In 1990, the sucrose inversion (Pallmann) technique (Berthet, 1960) was used along the gradients to determine mean soil surface temperatures and to calculate the seasonal TDD (mean daily temperature in °C x no. of days). Three vials containing 10 ml of buffered 'fast' sucrose solution (pH = 1.3; Denton and Barnes, 1987) were carried on ice to the site, then buried under a fine layer of soil just below the surface. Every 10 days the vials were collected and replaced, and the change of the solution's angle of optical rotation was measured to an accuracy of 0.1°, using a Schmidt-Haensch polarimeter (model 165, type 81176). The results for the particular solutions were read from a standard calibration curve, empirically established, using constant temperatures of 0°, 4°

Table 6.2: Principal climatological characteristics of five growing seasons, at Sverdrup Pass, central Ellesmere Island. Temperatures measured at 1.5 m above the ground in the valley of Sverdrup Pass (79°10'N, 79°30'W). Cumulative precipitation calculated from data collected at the permanent Atmospheric Environment Service (AES) station at Eureka (80°N, 80°W), where solid precipitation was converted to water equivalent, and trace precipitation = 0.01mm (* = 9 days missing in July 1991). 'TDD' represents thawing degree-days.

	1989	1990	1991	1992	1993
First day of phenological recordings	-	June 21	June 14	June 22	June 24
Last day of phenological recording	-	Aug 22	Aug 8	July 27	July 31
First day with daily mean air temperature > 0°C	June 5	May 31	May 19	June 4	May 25
Last day with daily mean air temperature > 0°C	Sept 8	Sept 3	Sept 9	Aug 31	Sept 7
Length of potential growing season (days)	96	96	114	89	106
Number of days in growing season with mean temp. ≤ 0°C	9	7	26	14	17
Annual precipitation (mm)	124	65	88*	70	62.5
June-July-August cumulative precipitation (mm)					
AES (Eureka)	70	17	49*	45	31.2
Highest daily mean temperature (°C) in June-July-August	11.9 July 27	12.3 Jun 29	11.8 Jul 26	11.9 Jul 26	13.9 Jul 15
Lowest daily mean temperature (°C) in June-July-August	-0.5 Jun 5	-3.2 Jun 4	-2.2 Aug 27	-10.3 Jun 1	-0.7 Aug 26
Cumulative TDD during					
Summer months: June	71	158	92	64	120
July	160	198	235	189	298
August	90	119	91	46	41
Total TDD per potential growing season (May to September)	**322**	**476**	**419**	**298**	**462**

and 23°C over periods of up to 7 days. A regression equation ($\text{Log}_{10}\, y = 0.06 \pm 0.00\, x - 1.74 \pm 0.06$; $r^2 = 0.99$) was then applied to convert the optical readings into mean temperature for the 10 day periods. Corrections for the non-linearity of the reaction have been suggested by Lee (1969), but Batten (1987) demonstrated that the correction did not improve the fit between the mean temperatures measured by the Pallmann technique and temperatures recorded with a data-logger in a high arctic study. This was attributed to the moderate diurnal temperature fluctuations at these sites, accordingly, we did not use these corrections and used the standard effective mean (Denton and Barnes, 1987).

From June 22 to August 23, 1990, the total degree-day accumulation measured by the Pallmann technique at the sites ranged from 172 to 522. The seasonal pattern of the soil surface temperatures among the sites and the air temperature at the climate station in the valley were very closely correlated ($r = 0.91$ to 0.98; all with $p < 0.05$; Appendix 6). Therefore, we calculated site-specific regression equations between mean temperature at the valley climate station and mean soil surface temperatures obtained at each site by the Pallmann technique (Appendix 7). These equations were then used to extrapolate daily mean temperatures, degree-day values and potential growing season length at the sites for the 5 growing seasons of 1989-1993.

6.3.4 Plant measurements

The circumpolar herb *Papaver radicatum*, is a mesocorm-chamaephyte (Sørensen, 1941), and is present in a wide range of open and extreme habitats (Porsild and Cody, 1980; Aleksandrova, 1988). In the Canadian High Arctic, it establishes successfully on recently deglaciated terrain (Jones, 1997) as well as on mountain tops (Lévesque and Svoboda, 1992).

At each of the 12 study sites, 15 individuals were randomly selected and labelled on June 22 and 23, 1990, and monitored for four years. Leaf expansion, numbers of flower buds, flowers and ripening seed capsules, as well as the length of the flowering stem, were recorded every 7-10 days. The first and last recording dates varied from year to year according to dates of arrival and departure from the field station (Table 6.2). When a plant was lost due to grazing by arctic hares or muskoxen, it was replaced by choosing another plant in the vicinity. The lower elevation sites, especially those of the granitic gradient, had a relatively large proportion of plants eaten and replaced over the course of this study (*ca.* 50% on G1 and G3; 80% on G2). In addition, at the end of the 1990 growing season, before the fruit capsule broke and the seeds dispersed (*i.e.* from July 19 until August 1 1990), up to 28 specimens per site were collected, pressed and dried to measure the vegetative, reproductive and root biomass. Due to the difficulty in extracting roots from rocky soils (*cf.* Chapter 3; Plate 3.6), only the samples where a large proportion of the roots were retrieved (*i.e.* the main tap root and a number of finer roots, approx. 85% of the total root system biomass) were used in the belowground analysis.

6.3.5 Data and statistical analysis

Site means of each soil parameter were used to test the difference between lithologies using a one-way ANOVA (Systat, 1992). Data were tested for normality using the Kolmogorov-Smirnov test for goodness of fit (Systat, 1992), and for homogeneity of variance using an F_{max}-test (Sokal and Rohlf, 1981).

Repeated measures ANOVA were used to analyze differences in phenological stages between substrates over the 4 year sampling period (MGLH procedure; Systat, 1992). The proportion of plants producing buds, flowers and fruits at each site was transformed using an arcsine transformation (Zar, 1984) and tested for normality and for homogeneity of variance. In these tests each site was used as a replicate.

Dates of flowering were not normally distributed; the differences among years and sites were tested with a nonparametric two-way ANOVA (Zar, 1984), using the ranked differences from the overall mean date of flowering.

Prefloration time (number of days to first flower) relative to the beginning of the growing season (defined as the first day with mean soil surface temperature >0°C) and the cumulative number of degree-days on the day of first flower appearance were calculated for each plant based on the site-specific regressions described above. Flower phenology, the number of flower buds and flowers produced and the length of the largest flowering stem, were used to compare flowering performance among both the years and the sites along the gradients. These variables were not normally distributed and the design did not allow the use of repeated measures ANOVA. Therefore, differences among years within each site and among sites within each year were tested independently using nonparametric ANOVA (Kruskal-Wallis test; Systat, 1992) and nonparametric multiple comparison Tukey-type tests (Zar, 1984). In these tests each plant producing buds and/or flowers was used as a replicate. Replication was unbalanced and the multiple comparison test was adjusted accordingly. The same approach was used to compare differences among sites for the biomass allocation data collected in 1990.

6.4 RESULTS

6.4.1 Soils

On both gradients, the soil pH ranged from neutral to strongly alkaline (pH 6.7 to 8.5). The higher elevations and the granitic sites both had low pH values, but no significant differences were recorded between the substrates (Table 6.3). Soil organic matter content (in < 2 mm fraction) varied but was generally low (ranging from 1 to 12% dwt, Table 6.3). Concentrations of available P were low at all sites (< 10 ppm) and dolomitic sites had significantly lower concentrations

Table 6.3: Soil chemistry and texture from polar desert sites of dolomitic and granitic substrates from altitudinal gradients at Sverdrup Pass, Ellesmere Island. All data are from the small soil fraction (< 2 mm) collected from 0-10 cm depth; means ± SE, from site means, n = 6. Differences between substrates were tested with one-way ANOVA.

Substrate	pH	Total N (%)	Organic matter (%)	Exchangeable cations (ppm)			Texture
				P	K	Ca	
Dolomite	8.0 ± 0.2	0.15 ± 0.07	4.4 ± 1.2	2.1 ± 0.7	20.5 ± 4.8	2175 ± 474	Loamy-Sand
Granite	7.6 ± 0.2	0.21 ± 0.04	6.0 ± 1.7	5.9 ± 1.2	24.8 ± 5.6	1219 ± 411	Sandy-Loam
p-value	0.107	0.402	0.65	0.023	0.481	0.061	

than granitic sites (p = 0.023; Table 6.3). There was no difference in total N nor in exchangeable K, but a nearly significant difference for Ca (p = 0.061; Table 6.3). Overall, the granitic sites had coarse-sandy soils that were very well-drained, warmed quickly and were usually dry on the surface. The dolomitic soils had a larger proportion of silt (from 25% to 50%), retained more moisture and warmed more slowly than the granitic soils.

6.4.2 Year-to-year climate

In the valley of Sverdrup Pass, the 1990 and 1993 seasons were the warmest, while 1992 was the coldest (Figure 6.2). In 1991, the potential growing season was the longest (114 days) because of a few days with above freezing temperatures in May followed by a cold period in late May. Nevertheless, the total number of days with daily mean air temperatures above freezing was similar for most years (87 to 89 days; Table 6.2). The cold year of 1992 was an exception, with only 75 days above freezing. The growing season of 1990 was also exceptional, showing a bimodal temperature curve peaking in June (highest daily mean on June 29; Table 6.2) and again in early August (Figure 6.2). In other years, more than 50% of the heat was received in July.

Total precipitation in the High Arctic is difficult to measure, since most precipitation events do not generate measurable amounts of water and some moisture is deposited as fog and mist (Woo and Steer, 1979). According to the data collected by the Atmospheric Environment Service at Eureka (located on the west coast of Ellesmere Island, *ca.* 100 km North-West of the study site), 1989 was a wet year, with 70 mm of summer precipitation (Table 6.2); July was particularly wet with more than 40 mm. On the other hand, the summer of 1990 was dry, with less than 20 mm of precipitation. Differences in the pattern of precipitation between the coastal Eureka site and the inland Sverdrup Pass site may be expected; however, the partial record of summer precipitation collected at the Sverdrup Pass base camp showed similar patterns (data not shown).

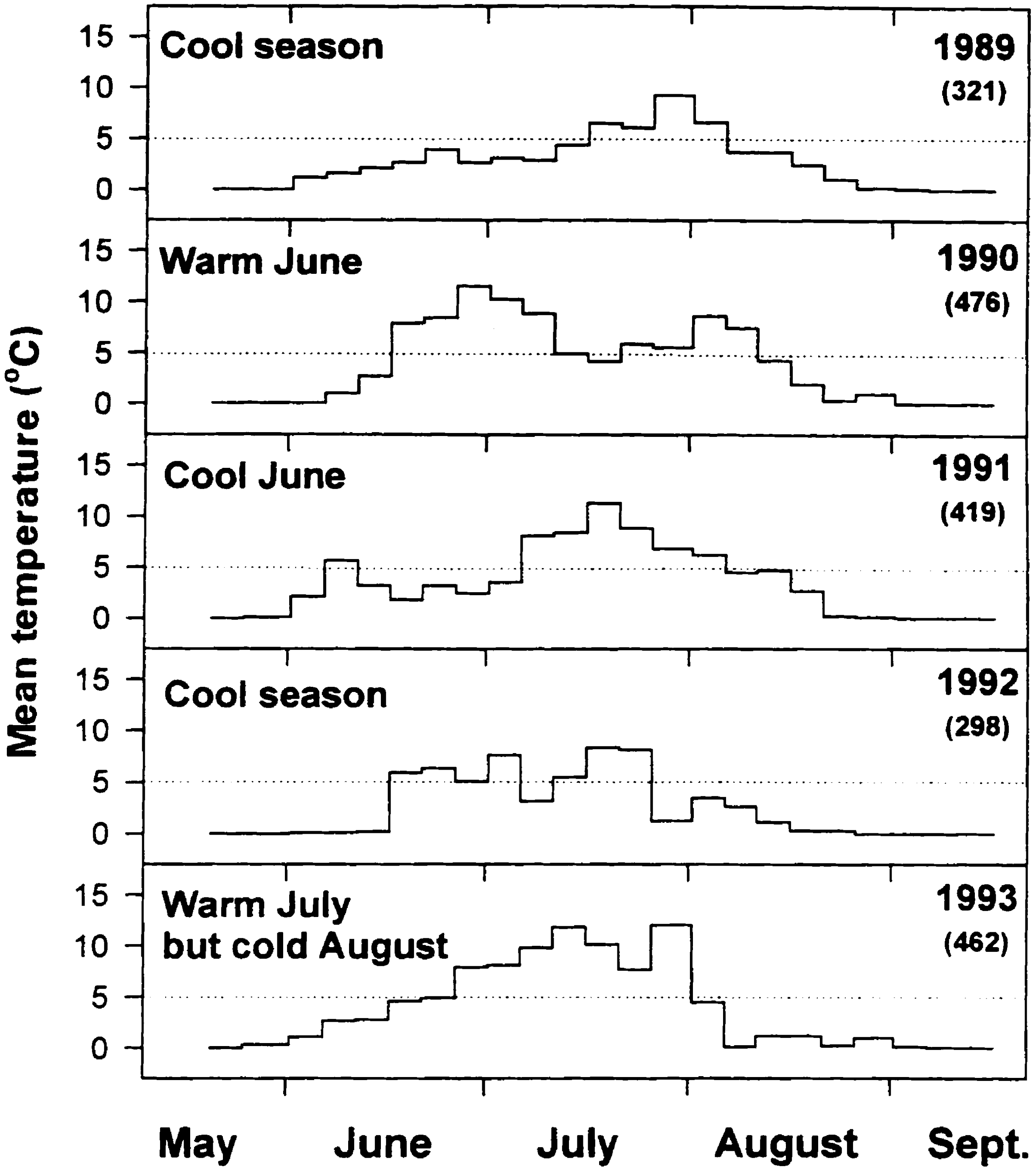


Figure 6.2: Seasonal mean air temperatures (5 day means at 1.5 m above ground) in the valley of Sverdrup Pass, near the divide, Ellesmere Island, Canada. Measured by the automatic weather station (MET). Numbers in parentheses represent the total degree-days (≥ 0°C) for the season.

6.4.3 Microclimate among sites

Each year all 12 sites were free of snow before we arrived in early- to mid- June (Table 6.2). Most sites were exposed, and snow deposition and retention over the winter was probably minimal because of wind. Nevertheless, periodic snowfalls during the summer months were common and affected the length of the actual growing season. The high-elevation sites usually retained new snow for up to 6 or 7 days, while near the valley floor, sites usually did so for no more than 36 hours. This difference may be important for sites where the potential growing season is as little as 60 days (*e.g.* sites D5 and D6 with means of 68 and 63 days, respectively; Figure 6.3b), as it left the total number of days with daily mean surface temperature above the freezing point nearing 40 (46 and 42 days on average for D5 and D6, respectively).

In general, the granitic sites experienced higher temperatures than the dolomitic sites and the temperatures decreased with altitude (Figure 6.3a). In fact, although the granitic gradient was on a north-facing slope, the highest-elevation granitic site G7 (727 m a.s.l.) had temperatures comparable to the lowest-elevation dolomitic site D1 (335 m a.s.l.). This pattern of decrease in total seasonal degree-days with increasing altitude (*ca.* 40 degree-days/100 m), and the strong influence of lithology and exposure, maximised the difference between extreme sites. The lowest granitic site had up to three times more degree-days than the highest dolomitic site (Figure 6.3a).

The length of the potential growing season was slightly less than 100 days on the granitic sites, while it was as low as 50 days on the higher dolomitic sites (Figure 6.3b). The season of 1993 was exceptional, with a warm July followed by a cold August, and although it was one of the two warmest years (Table 6.2, Figure 6.2), the high elevation dolomitic sites experienced one of the shortest potential growing seasons (63 and 47 days for site D5 and D6, respectively).

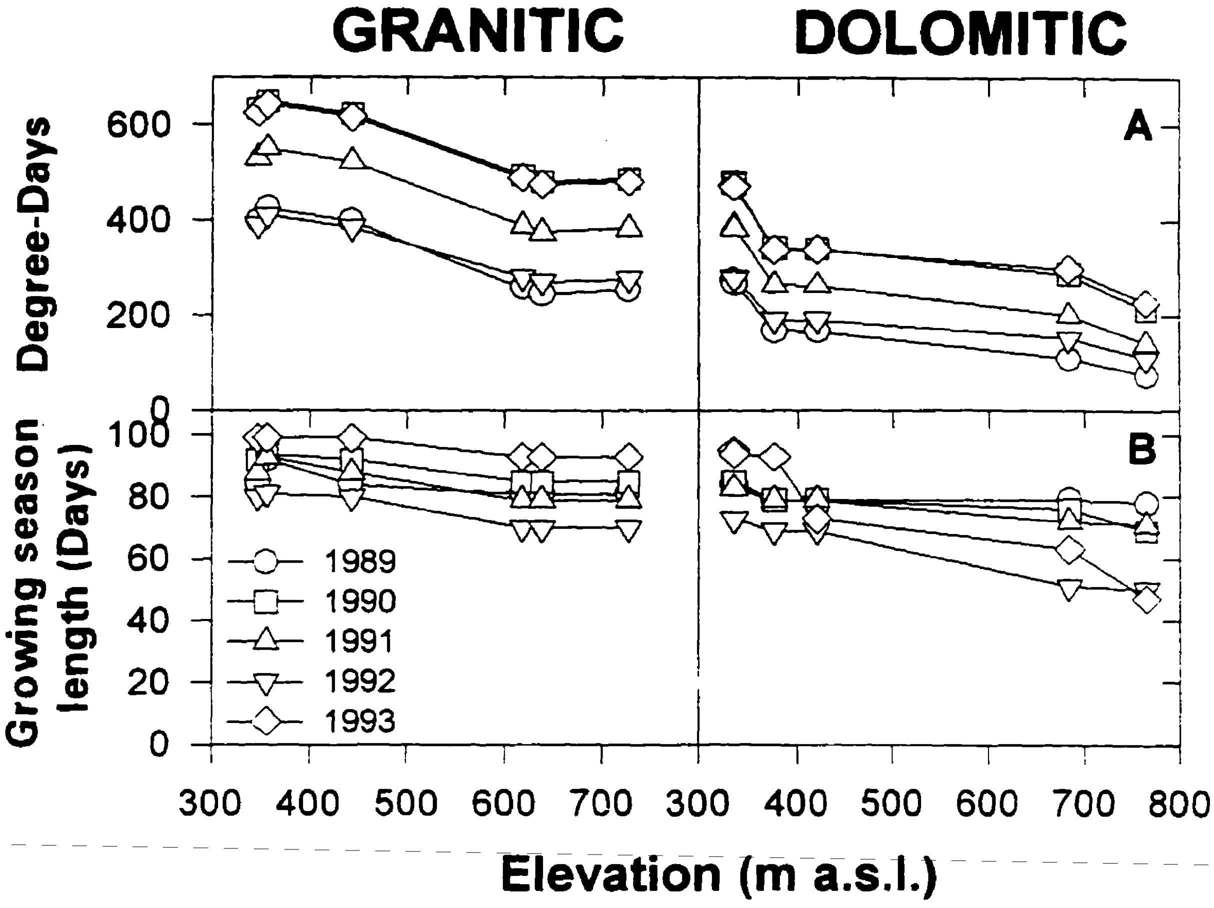


Figure 6.3: Cumulative degree-days (A) and potential growing season length (B) in five consecutive years at 12 sites (surface level) along the granitic and dolomitic gradients, in Sverdrup Pass, Ellesmere Island.

6.4.4 Phenological responses

Among years and between gradients. Leaf set and elongation was observed in nearly all tagged plants at each site, ranging from a low of 60% (Site D4 in 1990) to 100%. However, the production of flower buds, flowers and fruits was more variable: 33% to 93% for buds, and 0% to 73% for flowers and fruits (Figure 6.4). In 1990, at 9 of the 12 sites, all the plants that produced buds also produced flowers. However, in the three subsequent years a large proportion of plants that produced buds did not flower. Plants at the three higher dolomitic sites tended to have the largest proportion of their buds fail to flower. Accordingly, the number of flowering plants was slightly larger on the granitic gradient (Figure 6.4). The number of plants producing seed capsules showed the largest difference between the granitic and dolomitic gradients during the cold summer of 1992 (40 vs 19, respectively).

There was no effect of substrate on the number of plants producing flower buds (Table 6.4). Hence, it appears that the number of plants which pre-form buds was not different between colder or warmer sites in a given year. There was, however, a significant effect of year on bud formation, but the variation among years did not follow a clear pattern. For example, after the cold year of 1992 we may have expected a smaller number of plants producing buds in 1993, but this was not the case. Similarly, site G1, one of the warmest sites, had a marked decrease in flowering in 1991 after a favourable year in 1990 (Figure 6.4).

There was no significant effect of substrate on the number of plants producing flowers and fruits at the level of sampling (Table 6.4). This was associated with the large variation between sites and years. Nevertheless, there was a trend towards a larger proportion of plants on granitic sites completing those phenological events than on the dolomitic gradient (Figure 6.4). Finally, the fruit production showed a nearly significant year effect ($p = 0.064$; Table 6.4).

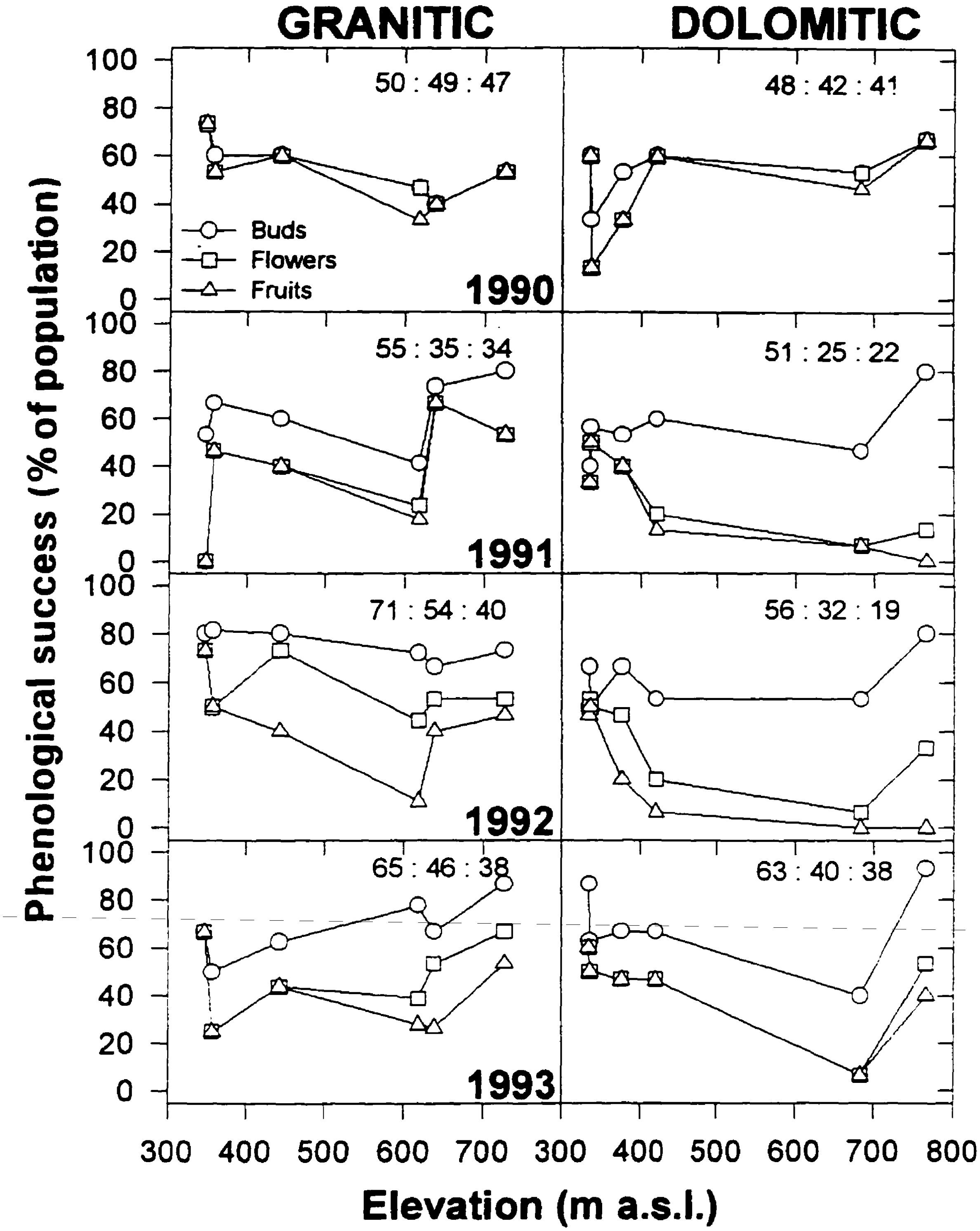


Figure 6.4: Phenological success (percent of tagged plants) in bud, flower and fruit formation of *Papaver radicatum* in four consecutive years, at 12 sites along the granitic and dolomitic altitudinal gradients, in Sverdrup Pass, Ellesmere Island. Yearly total number of plants for each gradient that produced buds, flowers and fruits out of 90 plants monitored (15 per site, six sites on each gradient) is given on the top right corner of the diagrams (buds : flowers : fruits).

Table 6.4: Summary of repeated measures analysis of variance of proportion of plants producing a) buds, b) flowers and c) fruits in two substrates over four years. Values were transformed with Arcsin transformation and tested for normality. For within-subject effects (year), probabilities are Huynh-Feldt estimates[a] (Crowder and Hand, 1990, p. 55).

a) Plants producing buds

Source	df	SS	MS	F	$p > F^a$
Substrate	1	0.032	0.032	0.858	0.376
Error	10	0.374	0.037		
Year	3	0.207	0.069	4.884	0.007
Year x Substrate	3	0.05	0.017	1.178	0.335
Error	30	0.425	0.014		

b) Plants producing flowers

Source	df	SS	MS	F	$p > F^a$
Substrate	1	0.174	0.174	3.719	0.083
Error	10	0.469	0.023		
Year	3	0.326	0.109	2.455	0.093
Year x Substrate	3	0.070	0.023	0.525	0.644
Error	30	1.329	0.044		

c) Plants producing fruits

Source	df	SS	MS	F	$p > F^a$
Substrate	1	0.229	0.229	2.697	0.132
Error	10	0.850	0.085		
Year	3	0.502	0.167	2.818	0.064
Year x Substrate	3	0.192	0.064	1.078	0.370
Error	30	1.780	0.059		

During the late summer of 1991 and the cold summer of 1992 fewer plants produced fruits, especially on the dolomitic gradient (Figure 6.4).

Phenology along gradients within years. Along the dolomitic gradient, there was a trend towards a decrease in the number of flowering and fruiting plants with increasing elevation. The highest dolomitic sites showed a marked decrease in number of plants producing flowers and fruits in the summers of 1991 and 1992 (Figure 6.4). There was no clear, overall trend on the granitic sites.

At all sites in 1990, most flower buds produced flowers and fruits. It was during the cold season of 1992 that the largest discrepancy between the number of buds, flowers and fruits was observed. During that summer most of the flowering events did not start before mid- to late-July (Figure 6.5).

Timing of phenological events. Flowering of *Papaver radicatum* occurred in late-June to mid-July, depending on the year and site elevation (Figure 6.5). There were significant differences among sites ($H = 39.01$; $p < 0.001$) and years in the timing of flowering ($H = 151.41$; $p << 0.001$). Each year, the onset of flowering varied by 10 to 34 days between sites. Generally, the first sites to have flowers were the lower elevation granitic sites (G1, G2, G3) and the last sites were the higher elevation dolomitic sites (D4, D5 and D6). There was almost as much variation in timing of the first flowering event among years within each site as among sites within a year (18 days and 20 days on average, respectively).

On the granitic sites, the colder season of 1992 did not seem to affect the number of plants flowering (Figure 6.4), but flowering was later in the season (Figure 6.5). This trend is also visible for dolomitic sites, except for the highest site (D6) where first flowering occurred latest in 1991, when only two plants flowered in early August. At each site, the time from the first to the last plant to flower varied from one to three weeks. However, the two higher granitic sites

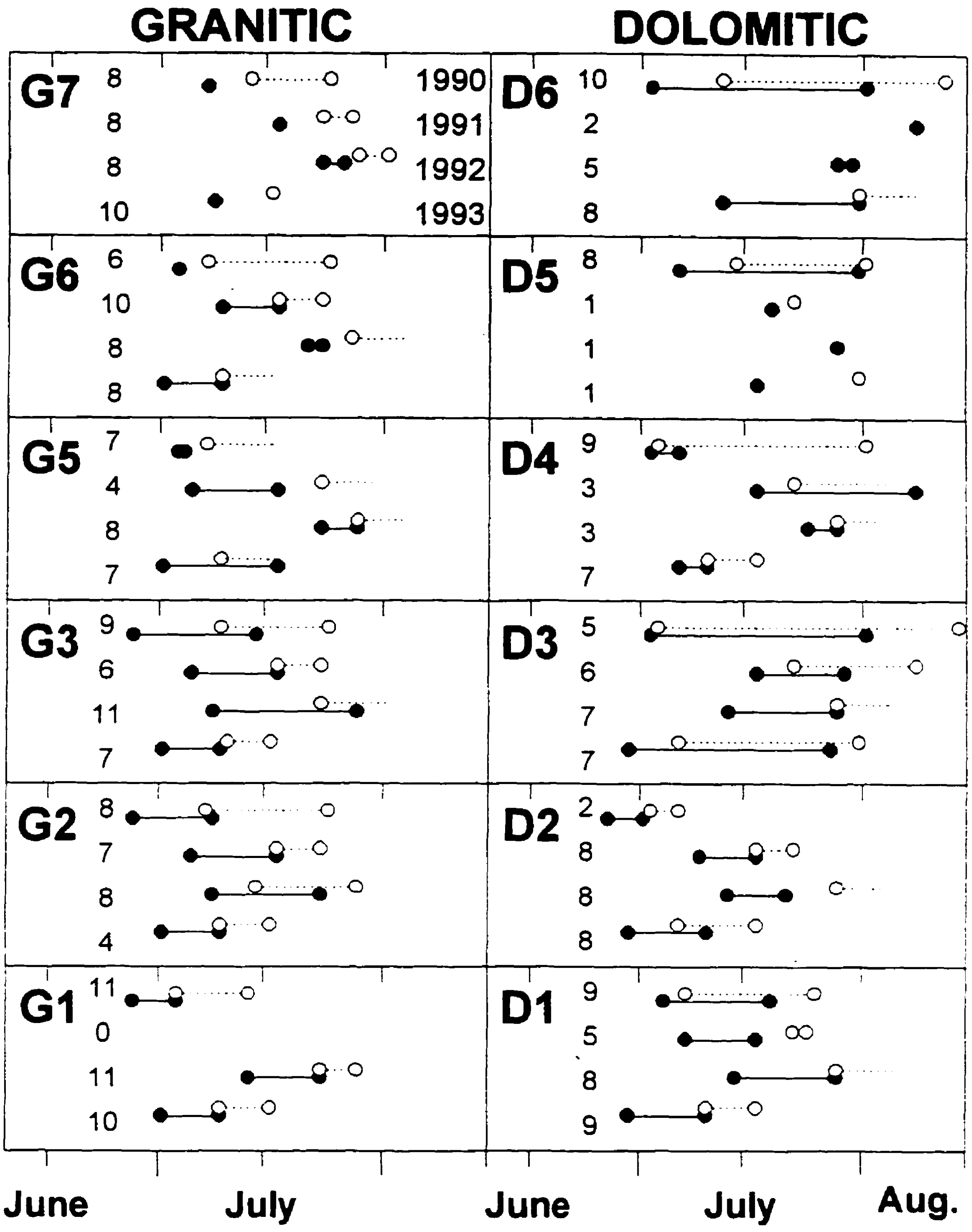


Figure 6.5: Timing of first flower(●) and first fruit (○) of *Papaver radicatum* plants over four seasons, at 12 sites along granitic (G) and dolomitic (D) altitudinal gradients, in Sverdrup Pass, Ellesmere Island. The sites are arranged in descending order of elevation. The number of plants to flower at a particular year out of 15 monitored plants per site is given on the left side of the diagrams.

seemed to have more synchronous flowering, and some of the dolomitic sites had plants flowering over a 7-8 week period (Figure 6.5). The development of the fruits from flowers took on average 7.8 ± 0.3 days on the granitic gradient and 8.5 ± 0.4 days on the dolomitic gradient (Figure 6.5).

Degree-days and flowering. The difference between years in degree-days accumulated at the time of first flowering is less striking (Figure 6.6) than the shift in calendar days (Figure 6.5). Nevertheless, there were significant differences among years for 7 of 12 sites when each site was tested independently (Table 6.5). There was a general trend towards a greater number of degree-days at the granitic sites than at the dolomitic sites. When the 12 sites were compared, the differences were significant only between the lowest and highest sites (Figure 6.6), and no differences were found in 1991 and very few in 1993.

Prefloration time and flowering. There was little variation in the prefloration time among sites within the same year (Figure 6.6). There was no significant difference among the 12 sites in 1990 and only marginal differences in the following years (Figure 6.6). Plants on site D6 took more than 60 days to bloom in 1991, while in 1993 they flowered faster than plants from sites G1, G3, G5 and G6. On the other hand, there were highly significant year-to-year shifts at each site (Table 6.5). Early season temperatures seem to have the strongest impact on timing to attain first flower. For example, June 1991 was cold (Figure 6.2) and thus more calendar days were necessary to reach the minimum degree-days requirement for first bloom (Figure 6.6), even though 1991 as a whole was warm (Figure 6.3).

Bud and flower production. The number of buds and flowers produced per plant over the study period are summarized in Figure 6.7. In spite of the trends outlined above, there was no statistically significant difference in the number of

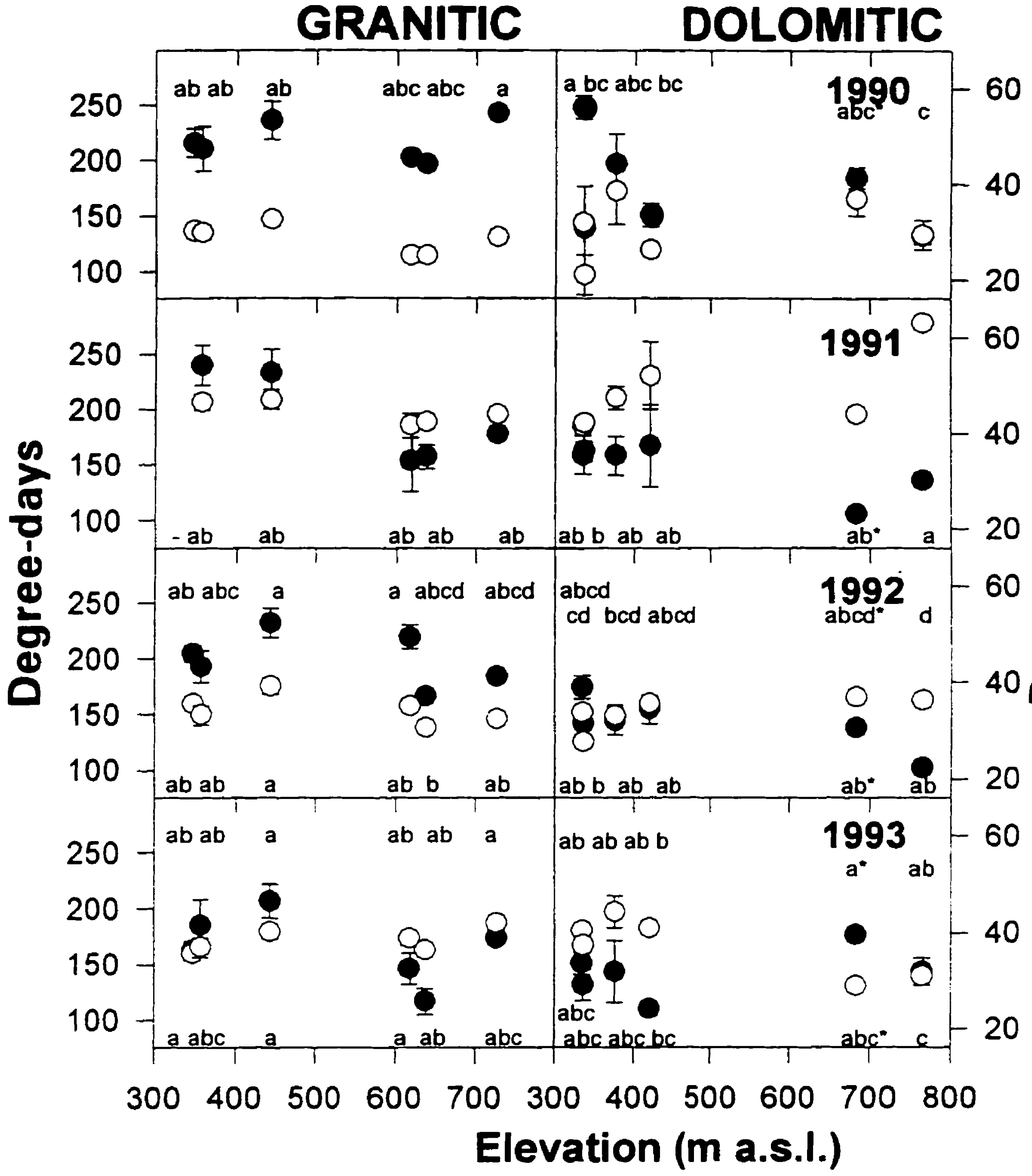


Figure 6.6: Cumulative degree-days (●) and prefloration time in days (○) at date of first flower of *Papaver radicatum* plants in four consecutive years, at 12 sites along granitic and dolomitic altitudinal gradients, in Sverdrup Pass, Ellesmere Island (means ± SE; n = 1 to 11). Overall differences among the sites within years were tested with Kruskal-Wallis test followed by nonparametric multiple comparison. Sites with the same letters are not significantly different ($p < 0.05$). Letters at the top of the diagrams are for degree-days and at the bottom are for calendar days.

Table 6.5: Summary of nonparametric ANOVA (Kruskal-Wallis test) for difference among years within each site for number of buds or flowers per plant, length of flowering stem and number of degree-days and calendar days at time of first flowering of *Papaver radicatum*, monitored during four seasons along two altitudinal gradients in Sverdrup Pass, Ellesmere Island. (* = $p < 0.05$; ** = $p < 0.005$; ns = not significant $p > 0.05$).

Sites	Number of buds/plant	# of flowers/plant	Stem length	Degree-days at first flower	# days at first flower
Granitic gradient					
G1	ns	ns	ns	*	**
G2	ns	ns	ns	ns	**
G3	ns	ns	ns	ns	**
G5	ns	ns	ns	**	**
G6	ns	ns	ns	**	**
G7	ns	ns	**	**	**
Dolomitic gradient					
D1	ns	ns	ns	**	**
D2	ns	ns	*	ns	**
D3	ns	ns	ns	ns	*
D4	ns	ns	*	**	**
D5	ns	ns	ns	ns	ns
D6	ns	ns	**	*	*

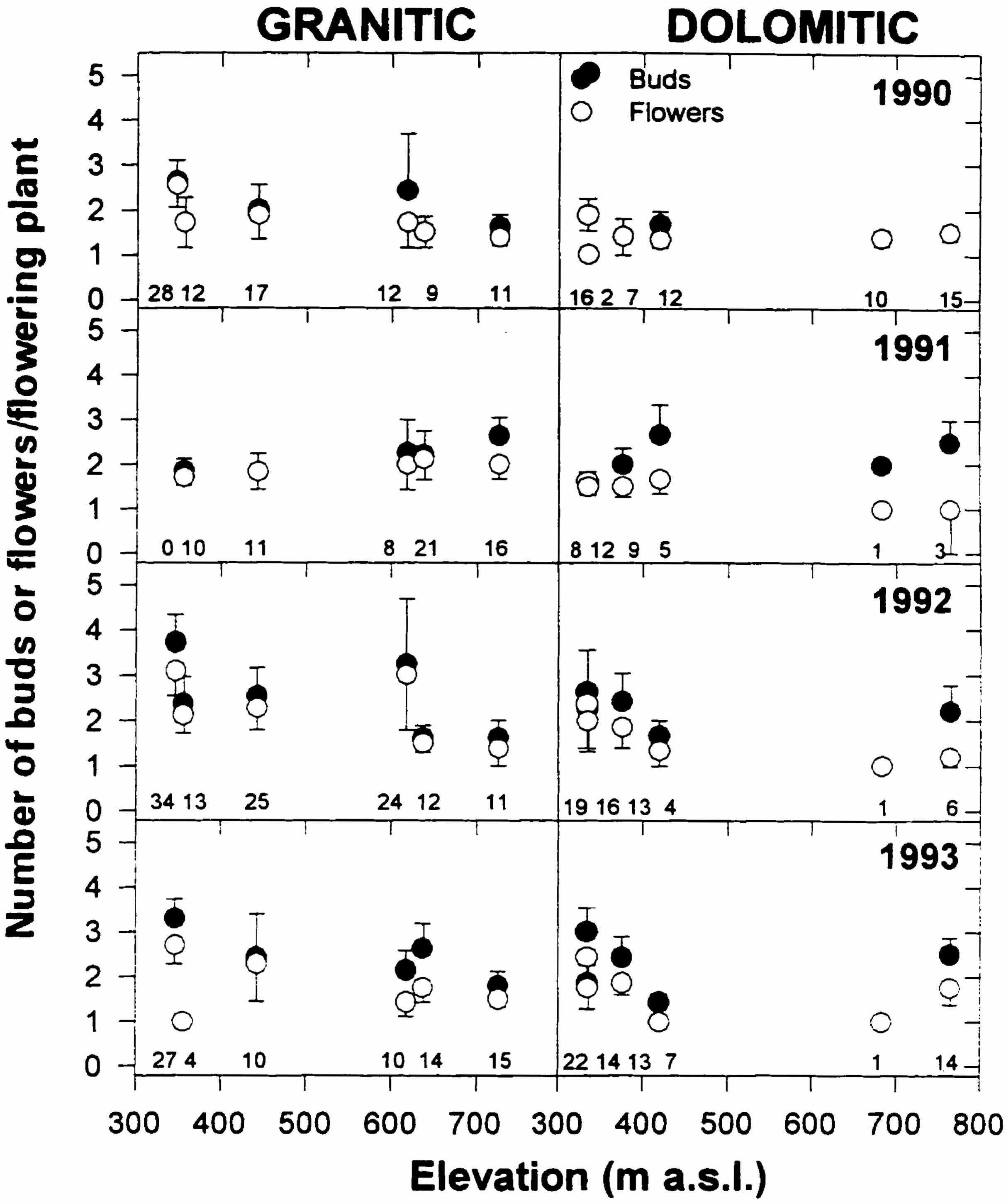


Figure 6.7: Mean number of buds and flowers produced by the flowering plants of *Papaver radicatum* in four consecutive years, at 12 sites along the granitic and dolomitic altitudinal gradients at Sverdrup Pass, Ellesmere Island (means ± SE; n = 1 to 11). The total number of flowers produced annually at each site is given at the bottom of each diagram.

buds or flowers produced per plant among years at any of the sites (Table 6.5). There was also no detectable difference among the sites in the same year (Figure 6.7). Despite these inconclusive statistics, there was a trend towards a decrease in the number of flowers produced per plant with increasing altitude. This pattern is best illustrated by the larger data set of plants collected in 1990 for biomass analysis (Figure 6.8) with 1.6 to 3.4 flowers/plant on the granitic sites and 1.2 to 1.6 flowers/plant on the dolomitic sites. Most plants produced one or two flowers when they bloomed. The production of more than two flowers per plant was rare, and this happened mostly on the warmer lower elevation granitic sites with larger plants. Overall, the plants from the granitic substrate tended to produce slightly more flowers per plant than those on the dolomitic sites.

There was a strong difference in the length of the flower stem between the two gradients (*e.g.* for 1990; Figure 6.8). Plants on the granitic substrate produced markedly longer pedicels than those on dolomitic sites. Consistently, the shortest stems were found on the top of the dolomitic gradient and the longest at the bottom of the granitic gradient.

6.4.5 Biomass and age of plants

There was a decrease in above-ground live biomass with increasing altitude (Figure 6.8). Plants growing on the granitic sites were larger than the ones from the dolomitic sites (total above-ground live biomass per plant ranged from 0.8 to 2.0 g dry weight on granite and from 0.4 to 0.9 g on dolomite; Figure 6.8). Biomass allocation to reproductive structures (*i.e.* stem and flower) followed the same trend, ranging from 0.12 to 0.37 g on granite and from 0.03 to 0.07 g dry weight on dolomite.

There was an increase in investment to belowground structure with altitude on the granitic sites, but relative biomass allocation was similar in plants from dolomitic sites (Figure 6.9). Plants from the granitic gradient invested from

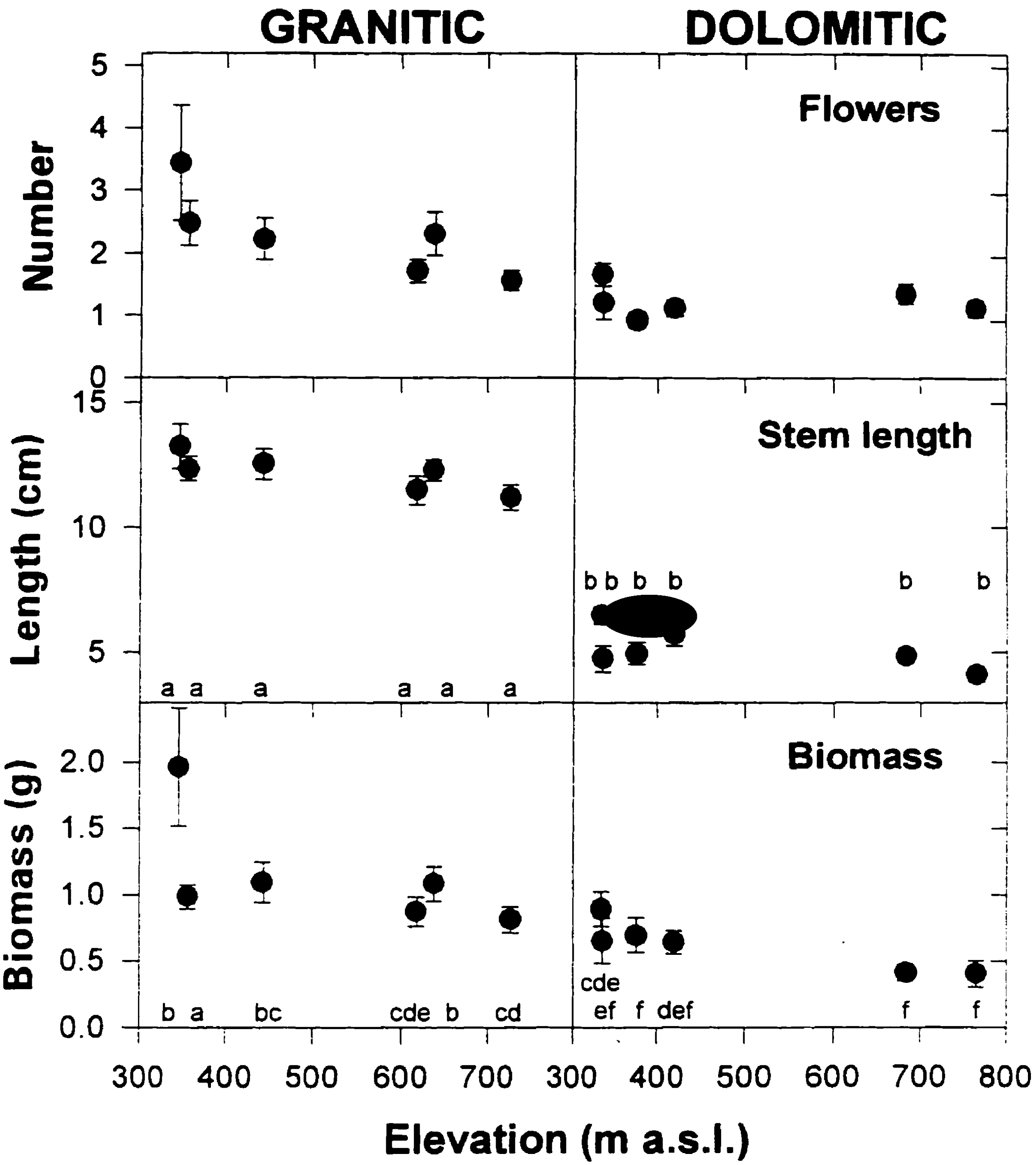


Figure 6.8: Number of flowers produced, length of flowering stems and aboveground live biomass of *Papaver radicatum* in 1990, at 12 sites along the granitic and dolomitic altitudinal gradients, in Sverdrup Pass, Ellesmere Island (means ± SE; n = 15 to 28). Overall differences among the 12 sites were tested with Kruskal Wallis test and nonparametric multiple comparison, letters indicate difference ($p < 0.05$).

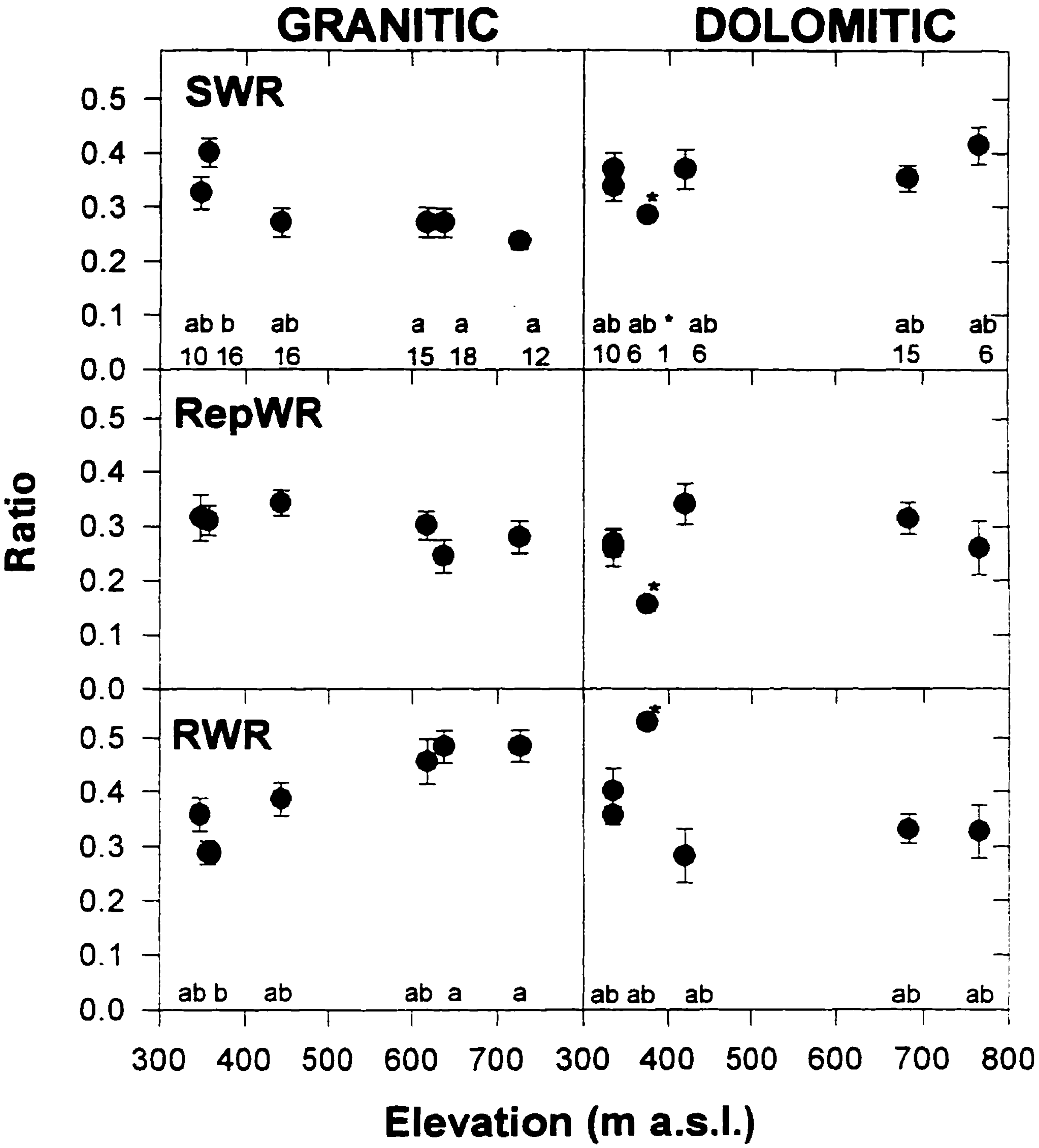


Figure 6.9: Relative total live biomass allocation to shoot (SWR), to reproduction (RepWR) and to root (RWR) of *Papaver radicatum* in 1990, at 12 sites along the granitic and dolomitic altitudinal gradients, in Sverdrup Pass, Ellesmere Island (means ± SE; n = 1 to 18). Overall differences among the 12 sites were tested with Kruskal Wallis test and nonparametric multiple comparison, letters indicate difference ($p < 0.05$).

24 to 40% of their live biomass to shoot, 25 to 34% to reproductive structures and 29 to 48% to roots. Plants along the dolomitic gradient had 34 to 41% of their biomass in shoots, 26 to 34% in reproductive structures and 28 to 40% in roots (values for D3, where only one plant with good roots was analyzed, were excluded for this calculation).

To assess the minimum age of the plants sampled, we assumed that leaf production was similar from year to year and that dead material loss was minimal. We calculated a rough estimate of minimum plant age by dividing the total dead biomass above-ground by the shoot biomass produced during one summer (1990). It is likely that this is an underestimation of true age sincesome dead biomass has probably been lost over the years and the net production may not have been as high in the early days of plant establishment. Despite these simplifications, we estimated that the largest plants were about 30 years old and that the median age of plants on the granitic gradient ranged from 2.0 to 6.2 years compared to 4.4 to 9.4 years on the dolomitic gradient.

6.5 DISCUSSION

6.5.1 Plant performance along altitudinal gradients

Besides the expected decrease in degree-days with elevation, the effect of lithology was striking. The darker granitic substrate absorbed more radiant energy and became warmer than the light-coloured dolomite, in spite of the northern aspect of the granitic slope. In addition to the greater light absorption of granite, the solar azimuth and the 24 h radiation input at high latitudes tend to reduce the diurnal difference in solar input between a north- and south-facing slope (Bliss, 1956). Mølgaard (1982) reported similar temperature patterns at comparable latitudes in Greenland. Drier sandy soils and larger boulder cover may have also contributed to the warmer microclimate at the granitic sites (*cf.*

Chapter 3). In contrast, the finer texture of the dolomitic soil retained more water and increased the heat capacity of these soils, slowing their warming.

There was a difference of 200 degree-days between the colder summers of 1989 and 1992 and the warmer summers of 1990 and 1993. In the High Arctic, where the summer season is already very short (*ca.* 8-12 weeks), even slight temperature variations may result in dramatic shifts in length of the growing season. The warmer summers, however, did not necessarily result in a longer growing season at all sites. The summer of 1993 was one of the warmest, but since August was cold, the higher dolomitic sites experienced one of the shortest growing seasons (63 and 47 days). Therefore, plant growth may be halted at higher sites even during otherwise favourable years.

Despite this wide range of conditions, the number of buds and flowers produced per plant was not different between the gradients, nor among the sites or years. Most plants produced one or two flowers when they bloomed; however, some larger plants at lower granitic sites produced up to 17 flowers. Flower buds of *Papaver radicatum* and other arctic plants are preformed at the end of the previous growing season (Sørensen, 1941; Bell and Bliss, 1980; Shaver and Kummerow, 1992). Sørensen (1941) reported that *Papaver* has a consistent floral periodicity and that many leaf primordia and flower buds are initiated during unfavourable years.

On the other hand, the proportion of plants producing flower buds varied significantly from year to year. For example, during the season following the warm and favourable year of 1990, almost no plants produced buds at the lowest granitic site. Altitude had little effect on the number of plants producing flower buds, despite the lower temperatures at higher elevations. Temperature may not be the most determinant factor in bud preformation. Plants may have their own periodicity, or a limited pool of resources that may be exhausted after a good flowering year. Sørensen (1941) suggested that there might be translocation of photosynthates from aborted flowers. The highest dolomitic site consistently had one of the largest proportion of plants producing flower buds, even though this site was the coldest, had the shortest growing season, and the smallest plants. The relatively low proportion of flowering on this site and its consistently high proportion of bud bearing plants seem to support Sørensen's view.

As expected, there was a slight delay in phenological events with increasing altitude (Bliss, 1956), and there were strong differences among years (Kudo, 1991). At our exposed sites, as in most ecosystems, variation in the timing of flowering was associated with the variation in climate (Walker *et al.*, 1995), and especially with soil surface temperature (Bliss, 1971). Other environmental factors, not measured here, such as soil moisture, may also correlate with flowering and account for some of the variability observed. Plants from the sites with the highest TDD generally flowered earliest and the number of degree-days at first bloom tended to be consistent from year to year. Differences in minimum degree-days to first flower between the two gradients may be related to ecotypic variation (Rathcke and Lacey, 1985). The time period from first frost-free day to first bloom, prefloration time, depended strongly on the temperature early in the season. Given the very short growing season, plants with an early start have better chances to ripen their seeds (Bell and Bliss, 1980; Aleksandrova, 1988), and the more favourable sites had a larger proportion of their population producing fruits. Still, *P. radicatum* periodically produced flowers and even fruits in the least favourable conditions. Hence, inconsistent plant performance from year to year is likely in response to more or less extreme polar desert conditions. A favourable year followed by a series of poor years could induce stagnation or even retrogression at the species and community level (Svoboda and Henry, 1987).

Aleksandrova (1988) reported that some flowers of *P. radicatum* were able to survive the winter under snow and to complete seed development during a second summer; however, we did not observe this at our sites. *P. radicatum* is not a vernal species (Molau, 1993b). Flower development in Sverdrup Pass needed a minimum of three weeks of above freezing temperatures, but if the weather stayed cool, the first bloom was delayed up to 60 days. At our sites, flowers lasted generally less than 10 days and flowering could be completed as early as mid-July. Bliss (1956) found similar results for *Papaver* in northern Alaska.

Flowering stems were consistently longer and plant above-ground live biomass larger at the granitic sites than at the dolomitic sites, where even old plants were small. Limitations in the availability of nutrients and the cooler microclimate were likely responsible for the lower performance on the dolomite. Despite these lithological differences, the proportional allocation of biomass to shoot, root and reproductive structures was very similar at all sites and was almost equally split among the three components. However, results of a preliminary study conducted during the cold summer of 1989 suggest that the proportional allocation may vary between years. *Papaver* from dolomitic and granitic sites had, respectively, 64% and 48% of their live biomass allocated to roots and less than 15% to inflorescences (Lévesque and Svoboda, 1992). Shoot and flower development during the cold summer was limited, which explains the larger proportion of the long-lived root biomass (Bell and Bliss, 1978). Similar analyses, performed at the nearby Alexandra Fiord lowland, revealed only 19% of live biomass allocation to roots (Maessen *et al.*, 1983). In addition to some variation due to sampling error, this difference in allocation may be partly due to the younger age structure of this population (Mølgaard, unpublished) and to the slow growing, long-living root system of *Papaver* (Bell and Bliss, 1978).

The contrast in plant vigour between dolomitic and granitic substrates affected seed viability. Seeds collected in Sverdrup Pass in 1989 from plants in granitic moraines showed up to 80% germination success, while seeds from plants collected on a high dolomitic plateau did not germinate at all (Lévesque and Svoboda, 1992). This suggests that seeds may be produced during most years in 'favourable' polar desert habitats, but on more stressful sites completion of fruit development may be limited to warmer years. Successful germination of seeds of *P. radicatum* derived from seed bank soil collected at some of the gradient sites (Lévesque and Svoboda, 1995) and the clustered pattern of plants found growing on the extreme sites (Chapter 4) suggest periodical on-site production of viable seeds. Under the present climate the on-site seed production might be a rare event at extreme sites, but with the prospects of global change seed ripening might become more frequent (Wookey *et al.*, 1993).

6.5.2 Implications in context global climate change

The study of naturally occurring gradients permits the comparison of plant performance with a wide range of environmental conditions. However, such study is not comparable to experimental investigations where each factor can be controlled. In our case, strong contrasts in temperature and TDD's as well as differences in abiotic (*e.g.* microtopography and moisture availability) and biotic factors (*e.g.* species composition and grazing) were associated with elevation. Manipulating some of these variables, would help discerning the relative importance of individual factors. However, interactions between limiting factors are complex (Walker *et al.*, 1995) and long term community response can not be easily predicted from short term responses to manipulation (Chapin *et al.*, 1995). Over a long period of time, environmental gradients result in integration of plant responses to local conditions and thus their study may be particularly useful in understanding the strategies of survival and reproduction (Kudo, 1991).

In this paper, we have demonstrated that *Papaver* produced flowers on sites with short and cold growing seasons. In contrast, plants transplanted from open tundra into the protected environment of a plastic-covered greenhouse at Alexandra Fiord grew exceedingly well and produced viable seeds (Figure 6.1). This points to an extraordinary plasticity and tolerance of *Papaver* which is able to survive and reproduce over an extensive range of microclimatic and edaphic conditions.

Under a climate warming scenario that would result in warmer and longer growing seasons, increased plant vigour and seed production may be expected

(Wookey *et al.*, 1993). Open-top chambers, designed to emulate seasonal warming, increase the daily mean sub-surface temperature by 1.4°C on average (Johnstone, 1995; Marion *et al.*, 1997). Such manipulation would result in a seasonal increase of approximately 80 to 140 degree-days depending on the site and the length of the particular season. Mølgaard and Christensen (1997), and unpublished results from similar experiments at Alexandra Fiord, show that *P. radicatum* responds strongly even to a slight increase in temperature. A warmer climate would promote many biotic and abiotic processes (*e.g.* pollination, decomposition, nitrification, growth of other species etc.) which in turn would bring about further changes in plant community structure and species interaction (Chapin *et al.*, 1992, 1995).

Soil moisture and nutrient availability also affect growth and phenology (Shaver and Kummerow, 1992; Walker *et al.*, 1995). Savile (1972) observed that the flowering period of *Papaver* was shorter in warm, dry sites, while moist sites had extended flowering both in time and in total number of flowers. In a xeric/mesic semi-desert site at the Alexandra Fiord lowland, the length of budding and flowering time was prolonged for up to two weeks by an irrigation treatment (Woodley and Svoboda, 1994). Extended flowering time and increased flowering density was found in two fertilization experiments at Alexandra Fiord (Henry *et al.*, 1986; Woodley and Svoboda, 1994). If warming (via experiments or actual climate warming) is associated with decreased soil moisture, *Papaver* may not respond favourably to an increase in degree-day accumulation alone. Survival of adult plants may be expected unless drought becomes extreme, but the establishment of new seedlings may be limited (Gold and Bliss, 1995).

If, on the other hand, increased winter precipitation results in later snowmelt, the growing season may not be lengthened but rather shortened or shifted into the early autumn. Such a situation may allow for rapid development of large plants on warmer sites (especially if moisture availability increases), since temperature after snow release critically influences the rate of growth

(Woodley and Svoboda, 1994). On the extreme ends of the microenvironmental spectrum, however, significant reduction of the length of the growing season may threaten the survival of *Papaver* as well as that of many other species.

6.6 CONCLUSIONS

As expected, we found a significant delay in phenological progression associated with altitude. There were also important variations among years. These results were related to the soil surface temperature and thawing degree-days (TDD) available to plant growth. Similarly, biomass per plant decreased with altitude. Smaller plants were found on the higher dolomitic sites which also had colder and shorter growing seasons. Despite their tiny size, some of these plants were estimated to be more than 20 years old. Surprisingly, there was no significant effect of altitude nor of year on the number of flowers per plant produced. This suggests that morphological constraints (Rathcke and Lacey, 1985) may be controlling flower production.

Despite differences in TDD and in soil nutrient availability (in our case P), the proportion of plants producing flowers was not different between the dolomitic and the granitic gradients. However, the size of plants and the length of flowering stems were different. More seeds with high germinability were produced on granitic moraine sites than on dolomitic ridges (Lévesque and Svoboda, 1992). Some plants growing at the highest (coldest) sites were able to flower even in cold years. In such cases flowering occurred late in the season and seed maturation was more at risk to be limited by an early fall.

CHAPTER 7:

GENERAL DISCUSSION

7.1 POLAR DESERT VEGETATION

7.1.1 Vascular species richness and plant community diversity

The apparent barrenness of polar deserts is deceiving. Scarce but persistent vegetation establish in polar landscapes. Vegetated sites were sampled up to 1000 m a.s.l. at 80°N. A total of 41 vascular plant taxa were recorded and several community assemblages were distinguished.

Results, presented in Chapter 3, confirm the preponderance of sparse vascular plant cover in these landscapes. Herbs, *Saxifraga oppositifolia*, *Papaver radicatum*, *Draba subcapitata*, *Draba corymbosa* and *Minuartia rubella* were the five most commonly encountered species and their occurrence was constant across a range of substrate types. In addition, *Phippsia algida* was frequently found colonizing the higher elevation sites with a particularly meagre plant cover, and *Puccinellia bruggemannii* was common on carbonate soils. All the above species (core group) were found frequently in flower or in fruit and appear well adapted to the extreme conditions.

Although plant cover was minimal, species richness and species assemblages varied from site to site. Four groups of plant communities could be distinguished based on the classification analysis (TWINSPAN). Two groups were relatively diverse with frequent occurrences of woody species (*Salix arctica* and *Dryas integrifolia*) and/or sedges (*Carex nardina* or *Kobresia myosuroides*). The two other groups had extremely sparse vegetation dominated by species from the core group described above with only very rare occurrences of woody and sedge species. These two groups were distinguished from each other by a few substrate-specific species (*e.g. Cardamine bellidifolia* and *Puccinellia bruggemannii*).

In addition to the core group of vascular species, many additional species were found exclusively on richer sites (such as *Saxifraga tricuspidata* and *Potentilla pulchella*), while a few species (*e.g. Cardamine bellidifolia* and *Phippsia algida*) colonized the poorer sites. Theoretically, given enough time, plant cover may increase on any site. Some of the stands studied appeared to be advancing in cover and standing crop. Their vascular plant cover was slightly above 5%, and if one adheres strictly to the 5% limit for a polar desert they should be called polar semi-deserts. The consistently low moss and lichen cover is not likely to increase in a foreseeable time unless the soil surface moisture increases.

Unlike this study, Bliss and Svoboda (1984) have described plant communities with a relatively high grass component in the polar barrens of King Christian Island. This suggests that despite the large range of habitats sampled, this study does not encompass the whole vegetational diversity of the polar deserts. In other words, far from being uniform and unvarying, polar landscapes support a wide variety of plant assemblages that developed on different substrates under different conditions. Further sampling from other regions of the Canadian Arctic Archipelago are necessary to draw a more encompassing picture of the polar desert vegetational complexity.

We have uncovered a strong influence of elevation on plant distribution. As expected, the most diverse and abundant plant communities were found at the lower elevations (*cf.* Chapter 3). These sites tend to be warmer, less exposed, and have longer growing seasons. They were most likely released from ice for a longer period of time and are generally closer to seed sources. These conditions make such sites relatively favourable to plant growth. However, exceptions do exist, some low elevation sites had particularly low plant cover (*e.g.* G2) and some were bare (*e.g.* VF3). Possible factors impeding seedling establishment and vegetation development are late lying snow/ice, which can reduce the growing season to just a few days, low soil surface moisture availability (*cf.* Chapter 3) and disturbance by cryoturbation.

This study also reconfirmed that polar desert vegetation is influenced by the type of substrate. More abundant and diverse communities were generally found on granitic substrates. Of the 41 species, 11 (*e.g. Cardamine bellidifolia, Poa arctica* and *Luzula arctica*) were found only on these granitic sites. This may, in part, be due to soil chemical and physical characteristics but, as demonstrated in Chapter 6, ground surface temperature may play a significant role. At equivalent elevations, carbonate sites had lower soil surface temperature than granitic sites. All 'vegetated' sites at the highest elevation had granitic substrates. Only three species were preferentially found on carbonate substrates, *Braya purpurascens*, *Braya thorild-wullfii* and *Melandrium apetalum*.

Although not directly measured in this study, frost activity can influence plant distribution (Raup, 1969). Frost activity is more pronounced on fine textured and moist soils (Washburn, 1989) and in general, soils from carbonate sites are believed to be more active. The rate of movement may, however, be low since only a few freeze-thaw cycles occur every year at these high latitudes and since many sites had a high rock content (Cook and Raiche, 1962). Needle ice disturbance at the soil surface may be particularly damaging to seedling establishment (Anderson, 1996).

In summary, the low plant cover found at the most extreme polar desert sites (mostly on carbonate rocks) may be due to a combination of particularly low temperature and short growing season (snow-free season), high soil pH, low nutrient availability, scant organic matter content, a less stable soil surface and periodic soil surface drought.

7.1.2 Biology of polar desert plants and biotic interactions

The vast majority of the vascular species found in the studied polar deserts reproduce by seeds; including species of the Gramineae, Cyperaceae and Juncaceae families which are characteristic by their caespitose growth forms (Porsild and Cody, 1980). The only exception was *Saxifraga cernua* which reproduces vegetatively by bulbils (Molau and Prentice, 1992). Spores of mosses and liverworts also germinated from our seed bank soil samples. All these modes of reproduction allow for good dispersal and most promote genetic variability which is advantageous in these unpredictable habitats (Murray, 1995).

Seed production may be restricted by the low abundance of pollinators (Tikhmenev, 1984) and obligate entomophiles are absent in the most severe habitats. Many of the core species, however, are able to self-pollinate (*e.g. Draba subcapitata*; Brochmann and Elven, 1992) but most have a higher reproductive success when pollinators are present (*e.g. Saxifraga oppositifolia*; Stenström and Molau, 1992).

The low number of plants of *S. oppositifolia* in the 10 m x 5 m plot studied (*cf.* Chapter 4) and their relatively similar age suggest a periodical rather than regular annual recruitment for this species. Rare occurrences of favourable conditions may have a determinating effect on new recruitments in the plant communities, and consequently, cohorts of similar age groups may prevail in polar deserts. Further work on this subject is required since the present datasets do not allow a precise study of the plant population structure. Although on the polar desert plateau most individuals of *D. subcapitata* produced flowers and fruits during the study years, it was impossible to tell how efficient overall recruitment was. It is possible that, for some species (*e.g. S. oppositifolia*), only a few mature individuals produce most of the viable seeds. What are the conditions necessary for recruitment to take place and how important are these frequent or rare periodic events on plant composition and distribution are pressing questions that should be addressed in future studies.

We assume that grazing by large herbivores (*e.g.* hares and muskoxen) is rare or less destructive in polar deserts and that the return of nutrients by urine and faecal deposition is minimal compared to more frequently utilized habitats (*e.g.* willow fields or wet meadows; Murray, 1991). Nevertheless, certain visited sites were visibly grazed more frequently than others which would affect plant abundance and age structure on these sites (*cf.* Chapter 6). Finally, seed dispersal by herbivores (*e.g.* hares, snow bunting and ptarmigan), even if rare, may be important in these poor marginal habitats since it may facilitate initial plant establishment.

The most frequent biotic interactions of vascular plants are probably with the soil invertebrates and soil microbiota (*e.g.* cryptogamic crust; Gold and Bliss, 1995). Their contribution to N-fixation and organic matter decomposition is critical to plant community development (Heal and Block, 1987; Getsen *et al.*, 1997).

7.1.3 Factors limiting vegetation development

Of the 82 polar desert sites surveyed, 58 had at least some vascular plants present ('vegetated' sites), and 24 did not ('barren' sites). Some of the 'barren' sites supported a low abundance of lichens and mosses (*e.g.* N2 and Q2; *cf.* Chapter 3) in addition to an assumed micro-flora. Although frequently found at high elevation, these 'barren' sites were not distinct from the 'vegetated' sites in their general soil chemical and physical characteristics.

The lack of difference between soil characteristics of 'vegetated' and 'barren' sites suggests that other factors are hindering plant establishment and vegetation development at some sites. These factors likely include, the low availability of empty 'safe' microsites, the shortage of viable seeds, which must reach the 'safe site' from a more or less distant source, and time. Sites which were released from ice only recently may not yet have had the opportunity to be colonized by vascular plants. Over the span of the present study some insight has been gained into the relative importance of these three limiting factors.

Microsite limitations. The microtopography and microsite distribution approach used in our work (*cf.* Chapter 4) was not able to test if seeds could germinate in vacant microsites. Nonetheless our study indicated that, at least in terms of spatial distribution, unoccupied sites similar to those with plants are abundant. Experimental proof supporting these results would require sowing seeds in polar deserts and monitoring seedling recruitment over a period of at least five years. The diversity of the polar desert landscape would further require that such experiments be conducted at a number of sites.

One aspect particularly important to microsite limitation in polar deserts is habitat severity. The microsite proximity to a boulder may result in a slight amelioration (*e.g.* warmer microclimate, deeper active layer), but conditions necessary for successful seedling establishment may, nevertheless, occur only rarely, during exceptionally favourable years (*cf.* Chapter 4). In brief, there are large stretches of open landscape which could be colonized by plants, but sites may be suitable ('safe') for colonization only intermittently when their microclimatic conditions are especially favourable. In other words their actual availability for colonization would be time restricted.

Seed limitations. Germinable seed banks are present in the soil of polar desert stands with as little as 0.1% vascular plant cover. Seed distribution is patchy with higher seed density in proximity to established plants. This clumping was mostly of seeds of the same species, which suggested their local production and a short dispersal range from the established plants (Harper, 1977).

The low plant density compared to the seed bank density points to the low success of germination and/or seedling establishment. Under less favourable conditions seeds would rarely germinate which would result in a slow seed accumulation in the soils (Chapter 5) and an increased seed bank.

At some polar desert sites the number of seeds/m^2 was comparable to densities found at semi-desert sites having much higher plant cover (Freedman *et al.*, 1982). Assuming that seed production is higher or at least equal to that in polar deserts, higher germination in lusher sites would keep the seed bank depleted. The woody species *Salix arctica* and *Dryas integrifolia* produce large quantities of viable seeds (Wookey *et al.*, 1993; Jones, 1995) however, their seeds were not found in the polar desert seed bank, even though their dispersal ability would allow them to reach any of the sites visited. Seeds of these species are wind dispersed, light and perishable (Jones, 1995). These seeds have little chance of being incorporated into the seed bank (Chapin, 1993). Clearly, the extreme polar desert conditions are too severe for these and many other absent species. Edlund and Alt (1989) associate the limit of distribution of these woody species with the 3°C isotherm, thus supporting the previous statement.

Overall, seeds are present in polar desert soils but not abundant. It is likely that the addition of extra seeds would result in more germination. Nevertheless, there is a germinable seed bank at these extreme sites where viable seeds are produced. On rare occasions, species are present in the seed bank but not in the vegetation. Only the most tolerant species succeed in establishment and are present both in the seed bank and in the vegetation.

Time limitations. Time since ice-release is a significant factor in limiting plant development that we were unable to address directly. A careful determination of ice free age of visited sites using a combination of lichenometry, aerial photograph and dating of vascular plants would be invaluable in the study of polar desert vegetation development but was beyond the scope and practicality of our work.

Meagre seed banks and the relative abundance of unoccupied 'safe sites' suggest a youthfulness of many polar desert sites. Some sites could be readily identified as post-Little Ice Age, for example, where recent and on-going ice retreat can be retraced from old aerial photographs and from those showing 'lichen kill' areas. Other relatively young sites can be seen along the coast represented by recently uplifted beaches. These sites were not a focus of our work. While true polar desert communities would remain in their 'stagnant' state of development unless the climate warms, young coastal zones may, in time, develop into more productive plant communities. Studies of plant succession on raised beach ridges at Devon Island (Svoboda, 1977) and a more recent one following glacial retreat at Alexandra Fiord (Jones, 1997) support this prediction.

Overall, many present polar desert sites are still young with meagre vegetation and may in time, if present climatic trends prevail, develop into sites which are more substantially vegetated. On the same note, these sites could be kept from development if the climate deteriorates. As Svoboda and Henry (1987) pointed out, processes of succession are often asymmetric. They progress slowly and retrogress quickly.

7.1.4 Succession potential

According to the information presented so far it appears that plant community development in polar deserts is strongly constrained by the short and cold growing seasons. I have used the Index of Potential Succession proposed in the literature (Bliss and Peterson, 1992) to assess successional potential of some sampled sites.

Assessing successional potential. Of the two indices of succession potential presented in the general introduction (*cf.* Chapter 1), the index of Relative Successional Potential (RSP; Svoboda and Henry, 1987) and its simplified version, the Index of Potential Succession (IPS; Bliss and Peterson, 1992), the latter can be estimated more readily from the information presented in this thesis. This index requires the mean thawing degree days (TDD) for the site and the fraction of the year available to plant growth (*i.e.* mean number of days with temperature above 0°C divided by 365). These values were available for the 13 sites studied along the dolomitic and granitic altitudinal gradients in Sverdrup Pass (Chapter 6). The successional index presented by Svoboda and Henry (1987) requires, in addition, the number of years since deglaciation and the optimal TDD value for the particular species. These two values are difficult to estimate for a majority of the gradient sites. Due to these limitations, the IPS, suggested by Bliss and Peterson (1992) was used to compare the 13 gradient sites with respect to their successional potential.

The IPS values of the gradient sites ranged from 17 for the high elevated site D6 and 124 for G2, near the valley floor (Table 7.1). Bliss and Peterson (1992) arrived at an IPS value of 248 for a low arctic site in Alaska, Umiat (69°N); at Truelove Lowland, Devon Island (76°N) their IPS values were 58 for sites in the central part of the lowland, 44 along the coast and 33 on the plateau (Table 7.1). Our TDD values were measured as soil surface temperatures. Estimates, in the literature are usually derived from the regional climate records where the temperature is measured at 1.5 m above the ground. This difference explains the relatively high IPS values obtained for Sverdrup Pass (79°N).

IPS and vegetation abundance. The IPS values generally increased with increasing vascular plant cover (Figure 7.1) except for site G2 which had a high IPS of 124 and low plant cover of 1.03% (Appendix 4). Clearly, other factors than temperature, such as low moisture availability and/or substrate quality affected the vegetation development on such anomalous sites. The vascular plant cover of the dolomitic sites (D1-D6) remained low despite a four fold increase in IPS down the altitudinal gradient. Moss and lichen cover increased at sites with intermediate IPS values (Figure 7.1). If the two gradients are compared, lichen cover slightly increased with increasing IPS along the dolomitic slope and decreased on the granitic slope (Figure 7.1).

The strongest correlation of the Index of Potential Succession was with the vascular plant diversity (VSD; Figure 7.2). This suggests that with higher temperatures and longer growing seasons more species succeed in establishing at these sites. Plant density, cover and standing crop also tend to increase, but the association with IPS was not as strong (Figure 7.1 and 7.2).

The relationship between VSD and IPS supports our hypothesis that low summer temperatures probably hinder vascular species establishment at the seedling level. *Saxifraga oppositifolia*, *Papaver radicatum*, *Draba subcapitata*,

Table 7.1: Index of Potential Succession (IPS) for some North American Low and High Arctic sites (modified from Bliss and Peterson, 1992) and for 13 gradient sites in Sverdrup Pass, Ellesmere Island. *Growing season represent the proportion of the year* with daily mean temperature above 0°C; TDD represents thawing degree-days above 0°C; n/a indicates that the information is not available.

Site	Latitude	Elevation (m a.s.l.)	Growing season	TDD	IPS
Low Arctic					
Umiat, AK	69°N	n/a	0.25	993	248
Atkasuk, AK	71°N	n/a	0.29	618	179
High Arctic					
Barrow, AK	71°N	0 - 10	0.21	301	63
Truelove Lowland, NWT	76°N				
Central Lowland		10 - 20	0.21	278	58
Coastal site		0 - 10	0.21	210	44
Plateau site		300	0.15	220	33
Sverdrup Pass, NWT	79°N				
Granitic Gradient					
G1		347	0.22	515	115
G2		357	0.23	535	124
G3		443	0.22	508	113
G4		461	0.18	367	68
G5		618	0.18	381	68
G6		638	0.18	369	66
G7		727	0.19	376	70
Dolomitic Gradient					
D1		335	0.21	378	79
D2		336	0.20	374	77
D3		376	0.17	360	45
D4		420	0.17	360	44
D5		684	0.13	209	27
D6		768	0.11	153	17

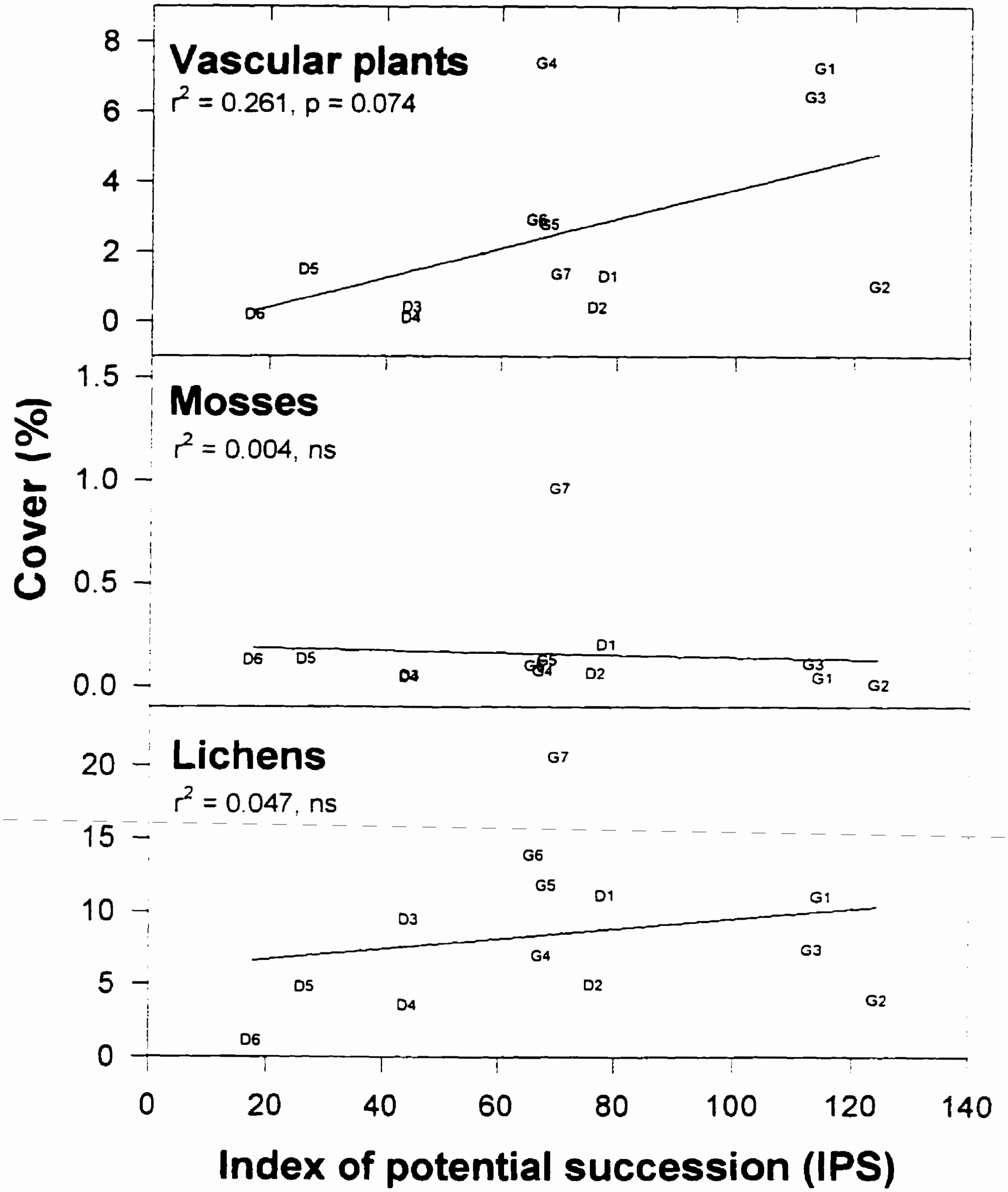


Figure 7.1: Total vascular plant, bryophyte and lichen cover (%) in relation to the Index of Potential Succession (IPS) at 13 polar desert sites in Sverdrup Pass, central Ellesmere Island. Letters identify sites from dolomitic elevation gradient (D1-D6) and granitic elevation gradient (G1-G7); ns stands for non significant, p > 0.1.

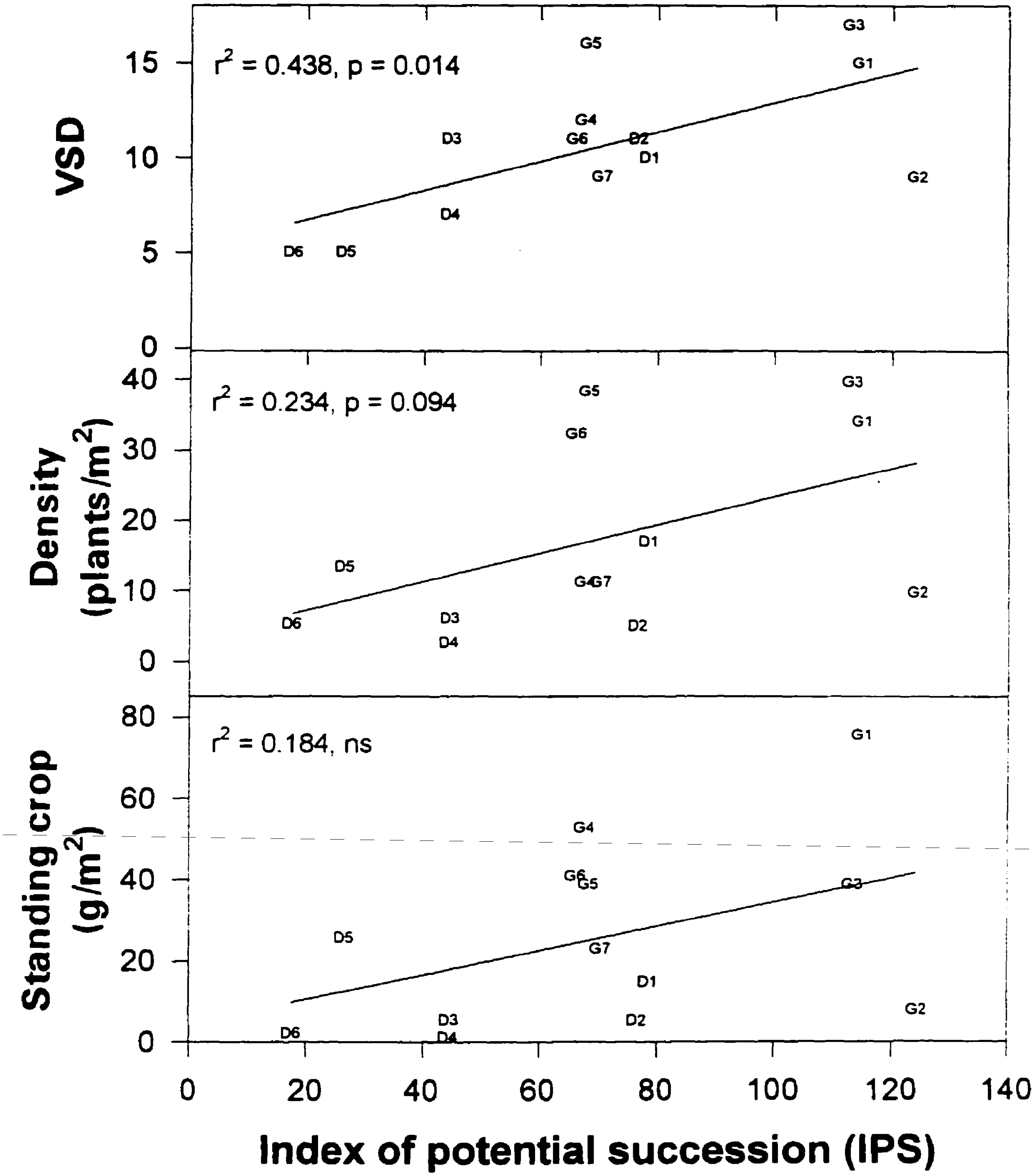


Figure 7.2: Vascular plants species diversity (VSD), density (plants/m^2) and standing crop (g/m^2) in relation to the Index of Potential Succession (IPS) at 13 polar desert sites in Sverdrup Pass, central Ellesmere Island. Letters identify sites from dolomitic elevation gradient (D1-D6) and granitic elevation gradient (G1-G7); ns stands for non significant, $p > 0.1$.

Draba corymbosa, *Puccinellia bruggemannii* and a few others (see Appendix 4) establish successfully on high elevation sites D5 and D6 and represent the core group of species characteristic of polar desert vegetation (Chapter 3). Although arctic plants, in general, are considered well adapted to low temperatures and short growing seasons (Chapin and Shaver, 1985; Billings, 1987), it becomes clear that a handful of species are particularly tolerant of the extreme conditions prevailing in polar deserts.

Integration. Information on the ice-free age of the vegetation on a given site would provide an important determinant for assessment of the colonization and successional processes in these marginal habitats. Inclusion of the time factor into the calculation as in the Index of Relative Successional Potential (RSP; Svoboda and Henry, 1987) may not always be correlated with the actual developmental level of vegetation. This is because the RSP index was designed for levelled mesic habitats and many sites studied were either too wet or too dry or were situated on top of wind-swept ridges, etc. The value of the RSP and IPS indices is in their theoretical assessment of a locality. They represent a reference line from which any departure should be explained on the basis of site-specific conditions.

The RSP of polar deserts is extremely low (Svoboda and Henry, 1987). These sites are frozen for most of the year and remain cold during the short growing season. At many visited sites the time elapsed since release from snow/ice has been surprisingly short, only a few years or decades. Ideally, the question of plant colonization could be addressed experimentally, especially with regard to seed germination and seedling establishment. To encompass a longer period of time, plant colonization experiments would need to be used in combination with a chronosequence approach (*e.g.* Matthews and Whittaker, 1987; Jones, 1997) where sites and plants would be aged.

7.2 FUTURE PROSPECTS

This work has expanded our knowledge about the flora, vegetation, and plant colonization of polar desert vegetation in central Ellesmere Island, Canada, yet much remains to be learned about the ecology of these marginal systems. A survey and classification of the vegetation covering a wider geographical range of sites (*i.e.* other Islands of the Canadian Arctic Archipelago, Greenland and/or Eurasian High Arctic) would be mandatory in order to fully comprehend the vegetation diversity of polar deserts and their developmental trends. Further, experimentation and analysis of the influence of environmental factors (*e.g.* temperature, soil moisture and nutrient availability) on the early stages of species invasion and plant community development is particularly needed. Aging of plants and sites would discriminate between the young and the extremely poor older sites. Establishment of permanent plots and a direct monitoring of changes over a long period of time, 20 or more years, appears to be an indispensable part of the solution. These long-term monitoring approaches may not be immediately rewarding for the researcher establishing such plots but would be invaluable if continued, since they would offer insight into the variability and complexity of this natural system (*e.g.* the work of Tamm in Sweden 1948, 1956 and later).

The arctic regions are expected to be most affected by ongoing climatic change (Maxwell, 1992). It is suggested that with global temperature rising, plant growth in temperate and northern latitudes would increase. This may be true in regions and localities with sufficient moisture, where an increase in TDD may readily promote growth. As a result nutrient mineralization and all biotic interactions would be affected and consequently changes in community structure could be expected. At dry localities, however, higher temperatures would promote more evaporation and the negative water balance may become a liability to plant growth; more particularly, seedling establishment may be hindered. It is unknown whether the climate amelioration will be associated with an increase or a decrease in precipitation (Maxwell, 1992). In the High Arctic, snow is the main source of moisture and its increase would be viewed as beneficial. However, if higher snow accumulation prolonged the spring snowmelt past the summer solstice, its effect may be detrimental by reducing the already short growing season (Chapin *et al.*, 1992).

A schematic summary of this scenario is presented in Table 7.2. Positively affected sites (*e.g.* mesic sites) would have slightly longer and warmer growing seasons, which would promote plant community expansion. Negatively affected sites (*e.g.* dry sites) would see their vegetation stagnate, even dying out. Overall, climate amelioration would promote plant growth, reproduction and new species recruitment at a larger scale in polar deserts, except at sites where there is drought or extended snow cover.

There is, however, another less often discussed scenario of the potential effect of global warming on arctic regions, northern climate cooling (Svoboda, 1996). During the last 20 years the northeastern American Arctic has actually experienced lower temperatures with higher snow deposition (Gullett and Skinner, 1992). If this trend should continue, plant growth, reproduction and species recruitment would be reduced (Table 7.2) and plant dieback and large scale community retrogression could be expected.

Recent satellite data, using 'normalized difference vegetation index' (NDVI) suggest an increased plant growth in the northern high latitudes from 1981-1991 (Myneni *et al.*, 1997). Alaska, northwestern Canada and northern Eurasia showed a particularly strong change in NDVI amplitude associated with earlier disappearance of snow in spring (Myneni *et al.*, 1997). In the two first regions, vegetation density was already high. In northern Eurasia, however, the NDVI values rose sharply during their sampling period, suggesting more important vegetation changes in this region (Myneni *et al.*, 1997). The Eastern Canadian Arctic Archipelago and Greenland, on the other hand, showed little change (Myneni *et al.*, 1997) which is consistent with the cooling trends reported

Table 7.2: Summary of potential impact of two climate warming and two climate cooling scenarios on polar desert 'favourable' and 'unfavourable' sites. ↑ indicates an increase; ↑↓ indicates unpredictable response; ↓ indicates a decrease.

	WARMING		COOLING	
	early snowmelt	late snowmelt	early snowmelt	late snowmelt
Unfavourable site	↑ growth ↑ reproduction ↑ recruitment	↑↓ growth ↑↓ reproduction ↑↓ recruitment ** Depending on growing season length	↓ growth ↓ reproduction ↓ recruitment	↓↓ growth ↓↓ reproduction ↓↓ recruitment ** Risk of Dieback
Favourable site	↑↑ growth ↑↑ reproduction ↑ recruitment ** Risk of summer drought	↑↓ growth ↑↓ reproduction ↑ recruitment ** Risk of delayed season	↑↓ growth ↑↓ reproduction ↑↓ recruitment ** Occasional success	↑↓ growth ↑↓ reproduction ↑↓ recruitment ** Occasional success

over this region (Gullett and Skinner, 1992; Chapman and Walsh, 1993; Kumar *et al.*, 1994).

The greening trends observed by Myneni *et al.* (1997) highlight regional diversity and the rapid response of vegetation to change. Ground proofing of such trends is difficult yet necessary (Fung, 1997) and the regional differences observed at high latitudes may offer unique opportunities to study and compare the effect of the warming and of the cooling on arctic plant communities. Polar desert vegetation is sensitive to climatic fluctuation and in this open landscape even slight changes may have a dramatic impact.

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APPENDIX 1:

LIST OF VASCULAR PLANTS FOUND ON THE STUDIED POLAR DESERT SITES, CENTRAL ELLESMERE ISLAND, CANADA.

Generally, the taxonomy and nomenclature follow Porsild and Cody (1980). Deviations from this flora are discussed under the particular genus or species. The taxa are listed alphabetically.

Braya purpurascens (R. Br.) Bunge
Braya thorild-wulffii Ostenf.
Cardamine bellidifolia L.
Carex misandra R. Br.

Carex nardina Fr./*Kobresia myosuroides* (Vill.) Fiori & Paol

When in flower or fruit these species can be easily distinguished. Both occur at site G3. However, on most sites studied they occurred only in the vegetative state when it is impossible to reliably distinguish them. Consequently most records are reported as *Carex nardina/Kobresia myosuroides*. On the sites where identification was possible *Carex nardina* was more abundant.

Cassiope tetragona (L.) D. Don

Cerastium cf arcticum Lange *s.l.*

The material of the *Cerastium alpinum/arcticum* complex was treated as one taxon *Cerastium arcticum* Lge. following descriptions given by Porsild, 1964, and in accordance to recent work done in Northern Greenland (Bay, 1992). The specimens collected were uniform, low, densely caespitose, hirsute but not glandular-viscid. This taxon is endemic to the Arctic Archipelago and to northernmost Greenland (Porsild, 1964).

Cystopteris fragilis (L.) Bernh.

Genus *Draba*, comments on species identification:

The work by Mulligan (1966, 1972, 1974) and Mulligan *et al.* (1970) on the genus *Draba* describes the group as polyploid and apomictic and as generally able to self-pollinate and produce viable seeds. Intensive population and genetic studies of 15 taxa of nordic *Draba* (including all the taxa described in this work) from northern Norway and Svalbard confirm these findings (Brochmann, 1992a, 1992b, 1993). Brochmann and Elven (1992) also relate polyploidy to ecological amplitude and strategies (based on Grime, 1979) and discuss its genetic consequences.

In this study, nomenclature follows Mulligan (1976). Taxonomic key and criteria used to distinguish the taxa are based on Mulligan (1974, 1976), with a simplified key focusing on high arctic taxa, reworked by Ball (pers. comm.). In addition to flower colour and petal size and shape Mulligan (1976) stresses the crucial importance of the presence, abundance and shape of hairs on silique (or ovary) and on underside of leaves for speciation in this group. Flowering and/or fruiting specimens were found from most sites. Vegetative specimens were identified by careful comparison of vegetative characters with those of the flowering specimens. Notes on general habit of the plants and on key distinguishing features are included below.

More detailed information on reproductive strategies, pollen and seed morphology and ecology can be found in: Brochmann, 1992; Brochmann, 1993 and Brochmann and Elven (1992).

Draba alpina L.

Yellow flowered with siliques mostly glabrous and usually broadest below the middle. Relatively few sparse forked hairs on leaves. The presence of simple hairs on the blade (not on the margin or the mid-vein, compare with *D. corymbosa* and *D. subcapitata*) is characteristic. Relatively rarely found on mountain tops but rather on scree slopes. Like *D. corymbosa* and *D. subcapitata*, specimens generally small with often only 1 or 2 rosettes branching from a common root.

Draba cinerea Adams

Siliques with stellate and forked hairs. Leaves with stellate hairs larger (> 0.2 mm) and less regular than *D. nivalis*. Distinct from *D. oblongata* which has a mixture of hairs on the leaves. Relatively common on certain lower elevation slope sites, but uncommon on the more exposed sites. This hexaploid species was found only on 'gradient sites' of the Sverdrup Pass valley.

Draba corymbosa R. Br.

Siliques of this yellow flowered species were always hairy. Leaves with forked or stellate hairs. If some simple hairs present, only on margin or mid-vein (not on blade, compare with *D. alpina*). Hairs present on the whole surface of the leaf (compare with *D. subcapitata*). Leaves generally broader than *D. subcapitata* and with more hairs than *D alpina*. Often found on mountain sites. This species is a 16-ploid (Brochmann and Elven, 1992), frequently found with *D. subcapitata* and is often very small (see *D. alpina*).

Draba lactea Adams

Rarely encountered on mountain sites, frequent along river beds; few, distinct, many forked hairs at tip of leaves. Siliques glabrous and stem usually glabrous. Very distinct from other *Draba* sp found in this study.

Draba nivalis Liljebl.

Siliques with stellate hairs. Both leaf surfaces with small (< 0.2 mm) evenly distributed stellate hairs give a grey appearance to the rosette. Found only on two granitic sites; very distinct from other *Draba* sp found in this study.

Draba oblongata R.Br. *ex* DC.

Siliques with stellate and cruciform hairs. Leaves with a dense mixture of mostly forked hairs, including simple hairs (compare to *D. cinerea*). White flowers generally open on an already elongating stem (compare to *D. subcapitata*). Relatively uncommon on the most extreme sites. Depauperate vegetative specimens are sometimes difficult to distinguish from *D. subcapitata* but generally the abundance of hairs is characteristic. Remnants of flowering stems is also a good indicator since this species frequently has stem longer than 2 cm and the flower head is less compact. This species was found only on 'gradient sites' of the Sverdrup Pass valley.

Draba subcapitata Simm.

Siliques mostly glabrous, purplish and elongated (very distinctive). Leaves with relatively few hairs (compared to *D. corymbosa* and *D. oblongata*); some forked hairs (generally 1-2 forked, mostly at the tip of the leaf) and long simple marginal hairs (compared to *D. alpina*). Leaves often narrow with a prominent mid-vein. Minute plants, white flowers bloom within the rosette of leaves. Hairy scape rarely longer than 2 cm (compare with *D. oblongata*) elongates when the siliques start to form. Regularly found on exposed mountain sites, seeds often present in seed bank (Lévesque and Svoboda, 1995).

Dryas integrifolia M. Vahl
Erysimum pallasii (Pursh) Fern.

Festuca hyperborea Holmen

Closely related to *Festuca brachyphylla* Schultes, *Festuca hyperborea* was identified as a distinct species by Holmen (1957) who described specimens from Greenland. More recently this taxon has received more attention, being recognised and described by Markgraf-Dannenberg (1980) in Flora Europaea. Canadian specimens were described and the distribution mapped by Aiken and Darbyshire (1990). A key distinguishing the two species for the Queen Elizabeth Island (McLachlan *et al.*, 1989) was used in this study. Allozyme and morphological comparisons between the species are also available (Aiken *et al.*, 1994).

Luzula arctica Blytt
Luzula confusa Lindeb.
Melandrium affine J. Vahl
Melandrium apetalum (L.) Fenzl
Minuartia rubella (Wahlenb.) Hiern
Oxyria digyna (L.) Hill
Papaver radicatum Rottb. *s. lat.*

Pedicularis cf arctica R. Br.:

This species occurred only as immature leaves on two polar desert sites. Identification was made by comparison of the foliage with herbarium specimens. The species was however relatively common at the nearby lowland.

Phippsia algida (Sol.) R. Br.
Poa abbreviata R. Br.
Poa arctica R. Br.
Potentilla hyparctica Malte
Potentilla pulchella R.,Br.
Puccinellia bruggemannii Th. Sør.

Salix arctica Pall.

Saxifraga caespitosa L. *s. lat.*

Saxifraga cernua L.

Saxifraga nivalis L.

Saxifraga oppositifolia L.

Saxifraga rivularis L. *s. lat.*

Saxifraga tricuspidata Rottb.

Stellaria longipes Goldie

APPENDIX 2:

GENERAL SITE DESCRIPTION OF POLAR DESERT SITES SAMPLED IN CENTRAL ELLESMERE ISLAND, CANADA.

The following 14 pages present the general site characteristics (date of sampling, longitude, latitude, elevation (m a.s.l.), substrate type (carbonate, C; granitic, G; sandstone, S), slope angle and aspect (in degrees)) of 82 polar desert sites, (54 'vegetated', 28 'barren'). Certain sites were surveyed briefly while others were sampled in detail. Microtopography, soil physical and chemical variables and plant presence and/or abundance are given wherever available. Microtopography (roughness, scale 1 to 5 (*cf.* Chapter 3); percent cover of fines (< 4 mm), pebbles and boulders (> 10 cm)), soil physical (sand, silt and clay content) and chemical variables (pH, organic matter content (OM), available phosphorus (P), extractable potassium and calcium (K and Ca)). Vascular species (VS) diversity, cover (%), density (plants/m^2) and standing crop (live and dead aboveground attached biomass; g/m^2); ground covering bryophyte and lichen cover and total plant cover (%; BC stands for black crust); litter and feces cover (%). The total number of quadrats sampled to investigate bryophyte, lichen and vascular plant cover is also given.

Reference number refers to the region around major landscape features, following the presentation given in Figure 3.1; for details on sampling approaches and analyses, see section 3.3 Methods; for detailed vascular species diversity, cover and frequency, see Appendix 4.

Alexandra Fiord: **1**, N1-N5 and **2**, E1, S1, AG, AD
Bache Peninsula: **3**, B1
Hayes Fiord and Jokel Fiord: **4**, H1 and **5**, J4
Beitstad Fiord: **6**, Z1, ZL, BT1-BT6
Sverdrup Pass: **7**and **8**, carbonate sites (LM0-LM5, VP1, VP2, TT, DG1-DG3, WM, DP, D1-D6); granitic and sandstone sites (KM, GB1, G1-G9 and EM1)
Mount Lawson: **9**, M1, LB, LG, P1-P6
Mount Moore: **10**, MM1-MM4
Vendom Fiord: **11**, VF1-VF3; **12**, C1, C2, CL; **13**, Q1, Q2; **14**, R2-R4
Princess Marie Bay: **15**, PMB
Judge Daly Promontory: **16**, W1, W2, WL and X1

SITE	E1	S1	AG	AD	N1	N2
REFERENCE NUMBER	2	2	2	2	1	1
General characteristics						
Date	21/07/90	22/07/90	04/07/92	04/07/92	28/07/93	28/07/93
Latitude (°N)	78°51'	78°48'	78°50'	78°51'	78°46'12"	78°46'14"
Longitude (°W)	75°38'	75°58'	76°01'	76°00'	75°14'32"	75°17'47"
Elevation (m a.s.l.)	818	786	540	540	1000	962
Substrate type	G	G	G	D	G	G
Slope angle (°)						
Slope aspect (°)	5					
Microtopography and soils						
Roughness	-	2.47	1.92	2.32		3.40
Boulders (%)	21.4	19.5	14.4	10.3		21.6
Pebbles (%)	39.8	48.0	3.7	54.3		58.9
Fines (%)	37.2	26.0	76.2	28.7		26.2
Sand (%)	82.8	67.0	57.6	60.5		80.6
Silt (%)	11.5	25.4	29.4	32.7		13.1
Clay (%)	5.6	7.7	13.0	6.9		6.3
OM (%)	1.5	1.7	3.7	4.8		1.1
P (ppm)	5.96	6.49	2.85	1.39		3.67
K (ppm)	10	19	16	9		8
Ca (ppm)	108	219	479	924		84
pH	5.03	5.20	5.56	7.57		6.20
Vegetation						
VS Diversity A	11	8	12	8		0
VS Diversity B						
VS Cover (%)	1.94	0.45	11.18	5.18	0	0
VS Density (plants/m^2)		9.07	66.40	27.20		0
VS Standing crop (g/m^2)	13.17	6.51	66.43	47.21		0
Bryophyte cover (%)	14.37	0.08	3.48	0.09	p	0.93
Lichen cover (%)	33.01	0.22	50.28	3.31	p	2.19
Total plant cover (%)	49.32	0.75	64.94	8.58		3.12
Litter cover (%)	0.43	0	2.24	0.40		0
Feces cover (%)	0	0	0.03	0		0
Number of quadrats sampled						
Vasculars	93	15	25	25		38
Moss	66	15	25	25		20
Lichen	66	15	25	25		20

SITE	N3	N4	N5	B1	J4	H1
REFERENCE NUMBER	1	1	1	3	5	4
General characteristics						
Date	28/07/93	28/07/93	28/07/93	16/07/90	10/0792	10/07/92
Latitude (°N)	78°44'55"	78°44'55"	78°44'55"	79°03'	78°58'31"	78°43'03"
Longitude (°W)	75°06'00"	75°06'00"	75°06'00"	75°00'	77°07'26"	78°12'14"
Elevation (m a.s.l.)	812	855	1003	608	870	912
Substrate type	G	G	G	D	G	S
Slope angle (°)						
Slope aspect (°)						
Microtopography and soils						
Roughness	3.47			3.19	2.64	1.70
Boulders (%)	25.9			9.5	1.6	17.1
Pebbles (%)	48.4			75.5	54.2	43.3
Fines (%)	28.5			15.0	44.8	39.8
Sand (%)	78.7		72.9	39.6	68.9	55.4
Silt (%)	15.9		22.4	49.8	25.2	39.0
Clay (%)	5.4		4.7	10.6	5.9	5.6
OM (%)	2.5		1.4	3.1	2.4	4.7
P (ppm)	10.29		13.92	0.52	3.32	4.15
K (ppm)	17		9	8	11	12
Ca (ppm)	583		35	1750	366	1053
pH	6.30		5.17	7.97	6.77	7.56
Vegetation						
VS Diversity A	9			8	17	11
VS Diversity B						
VS Cover (%)	0.52	p	0	0.49	3.32	0.72
VS Density (plants/m^2)	6.64			16.53	30.64	21.30
VS Standing crop (g/m^2)	8.47			3.95	45.37	6.92
Bryophyte cover (%)	0.18	p	p	tr	0.53	0.32
Lichen cover (%)	2.57	p	0	0.21	38.36	14.69
Total plant cover (%)	3.27			0.70	42.21	15.73
Litter cover (%)	0.04			0.05	1.00	0.31
Feces cover (%)	0			0.02	0.01	0.02
Number of quadrats sampled						
Vasculars	129			30	87	41
Moss	105			17	53	40
Lichen	105			17	53	40

SITE	Z1	ZL	BT1	BT2	BT3	BT4
REFERENCE NUMBER	6	6	6	6	6	6
General characteristics						
Date	11/07/93	11/07/93	04/08/92	04/08/92	04/08/92	04/08/92
Latitude (°N)	79°02'10"	79°02'30"	79°05'13"	79°05'13"	79°05'13"	79°05'13"
Longitude (°W)	78°04'26"	78°27'00"	78°48'08"	78°48'08"	78°48'08"	78°48'08"
Elevation (m a.s.l.)	970	648	824	833	860	906
Substrate type	G	D	G	GS	GS	SG
Slope angle (°)					1	
Slope aspect (°)					32	
Microtopography and soils						
Roughness	2.89					
Boulders (%)	19.1					
Pebbles (%)	52.3					
Fines (%)	28.7					
Sand (%)	72.1				92.6	97.9
Silt (%)	22.8				3.6	0.0
Clay (%)	5.1				3.8	2.1
OM (%)	1.7				0.8	0.5
P (ppm)	4.40				2.00	1.00
K (ppm)	16				6	26
Ca (ppm)	131				64	23
pH	5.95				6.00	6.00
Vegetation						
VS Diversity A	5					
VS Diversity B						
VS Cover (%)	0.39	p	8+	p	p	p
VS Density (plants/m^2)	7.57					
VS Standing crop (g/m^2)	5.80					
Bryophyte cover (%)	0.33				tr	
Lichen cover (%)	6.74				BC	
Total plant cover (%)	7.46					
Litter cover (%)	0.04					
Feces cover (%)	< 0.01					
Number of quadrats sampled						
Vasculars	94					
Moss	30					
Lichen	30					

SITE	BT5	BT6	LMO	LM1	LM2	LM3
REFERENCE NUMBER	6	6	7	7	7	7
General characteristics						
Date	04/08/92	04/08/92	18/07/91	18/07/91	18/07/91	18/07/91
Latitude (°N)	79°05'13"	79°05'13"	79°09'	79°09'	79°09'	79°09'
Longitude (°W)	78°48'08"	78°48'08"	79°18'	79°18'	79°18'	79°18'
Elevation (m a.s.l.)	900	836	885	827	865	915
Substrate type	GS	GS	D	D	D	D
Slope angle (°)	0-2	2-3				
Slope aspect (°)	32	25				
Microtopography and soils						
Roughness				2.90		
Boulders (%)		20		34.4		
Pebbles (%)		20-40		17.9		
Fines (%)		60		40.4		
Sand (%)				63.5	60.6	46.7
Silt (%)				22.6	10.9	37.5
Clay (%)				13.9	28.5	15.9
OM (%)				9.7	13.8	7.2
P (ppm)				5.40	5.68	4.28
K (ppm)				17	30	35
Ca (ppm)				2339	2251	2547
pH				7.53	7.66	7.73
Vegetation						
VS Diversity A				6		
VS Diversity B						
VS Cover (%)	p	p	0	0.38	p	0
VS Density (plants/m^2)				3.53		
VS Standing crop (g/m^2)				2.78		
Bryophyte cover (%)				0.95		
Lichen cover (%)	BC	BC		5.76		
Total plant cover (%)				7.09		
Litter cover (%)				0.02		
Feces cover (%)				0		
Number of quadrats sampled						
Vasculars				93		
Moss				52		
Lichen				52		

SITE	LM4	LM5	VP1	VP2	TT	DG1
REFERENCE NUMBER	7	7	7	7	7	8
General characteristics						
Date	18/07/91	18/07/91	22/06/93	22/06/93	22/06/93	12/07/91
Latitude (°N)	79°09'	79°09'	79°10'16"	79°10'16"	79°10'	79°08'
Longitude (°W)	79°18'	79°18'	79°02'02"	79°02'02"	79°15'	80°42'
Elevation (m a.s.l.)	947	993	818	818	703	664
Substrate type	D	D	D	D	D	D
Slope angle (°)				3-5		
Slope aspect (°)				27		
Microtopography and soils						
Roughness			2.74	2.60		3.27
Boulders (%)			21.2	13.9		15.5
Pebbles (%)			42..1	54.1		64.3
Fines (%)			22.6	23.1		15.0
Sand (%)	34.1	34.9	66.9	58.8		49.1
Silt (%)	42.2	54.9	22.8	29.2		35.4
Clay (%)	23.8	10.2	10.3	12.0		15.5
OM (%)	9.7	4.6	3.4	2.8		6.4
P (ppm)	4.10	0.54	3.69	2.91		2.90
K (ppm)	26	6	10	16		16
Ca (ppm)	2298	1986	1257	1919		1800
pH	7.87	7.93	8.13	7.98		7.75
Vegetation						
VS Diversity A			2	4		5
VS Diversity B						
VS Cover (%)	0	0	0.08	0.12	p	0.11
VS Density (plants/m^2)			0.30	1.43		1.77
VS Standing crop (g/m^2))			0.74	1.00		1.38
Bryophyte cover (%)			0.18	0.07		0.02
Lichen cover (%)			3.62	2.18		1.46
Total plant cover (%)			3.88	2.37		1.59
Litter cover (%)			0	0.01		0.02
Feces cover (%)			0.01	< 0.01		0
Number of quadrats sampled						
Vasculars			53	70		122
Moss			40	35		52
Lichen			40	35		52

SITE	DG2	DG3	WM	DP	D1	D2
REFERENCE NUMBER	8	8	8	7	7	7
General characteristics						
Date	12/07/91	12/07/91	27/07/90	22/06/90	10,11/07/90	11,12/07/90
Latitude (°N)	79°08'	79°08'	79°08'30"	79°11'30"	79°09'	79°08'30"
Longitude (°W)	80°42'	80°42'	80°20'00"	79°35'00"	79°43'	79°44'48"
Elevation (m a.s.l.)	800	852	970	909	335	336
Substrate type	D	D	D	D	D	D
Slope angle (°)					12	5
Slope aspect (°)					18	20
Microtopography and soils						
Roughness					3.63	2.49
Boulders (%)					17.8	7.7
Pebbles (%)					72.9	62.3
Fines (%)					9.4	29.8
Sand (%)					67.2	68.3
Silt (%)					29.1	25.2
Clay (%)					3.7	6.5
OM (%)					5.6	4.7
P (ppm)					4.85	0.82
K (ppm)					27	25
Ca (ppm)					2110	2810
pH					8.20	8.00
Vegetation						
VS Diversity A					10	11
VS Diversity B					10	12
VS Cover (%)	0	0	0	0	1.29	0.42
VS Density (plants/m^2)					16.93	5.00
VS Standing crop (gm^2)					14.96	5.43
Bryophyte cover (%)					0.20	0.06
Lichen cover (%)					11.10	4.95
Total plant cover (%)					12.59	5.43
Litter cover (%)					0.34	0.43
Feces cover (%)					0.15	0.05
Number of quadrats sampled						
Vasculars					30	60
Moss					30	30
Lichen					30	30

SITE	D3	D4	D5	D6	KM	GB1
REFERENCE NUMBER	7	7	7	7	7	8
General characteristics						
Date	30/07/90	02/08/90	14/08/90	14/08/90	25/0791	27/07/90
Latitude (°N)	79°09'	79°09'30"	79°10'	79°10'30"	79°07'	79°04'30"
Longitude (°W)	79°45'	79°43'30"	79°43'	79°40'30"	79°40'	80°12'00"
Elevation (m a.s.l.)	376	420	684	765	792	939
Substrate type	D	D	D	D	G	G
Slope angle (°)	0-5	5	0-5	0-2		
Slope aspect (°)	27	18	27	18		36
Microtopography and soils						
Roughness	3.20	2.95	3.33	2.98		3.85
Boulders (%)	12.0	11.3	14.5	7.3		21.4
Pebbles (%)	57.3	71.9	71.5	88.5		39.8
Fines (%)	22.5	20.1	11.1	10.1		37.2
Sand (%)	44.6	55.3	53.9	41.9		66.9
Silt (%)	50.2	39.5	39.5	46.7		28.4
Clay (%)	5.2	5.2	6.6	11.4		4.8
OM (%)	3.3	3.3	5.8	3.4		1.3
P (ppm)	1.10	1.13	4.04	0.94		14.20
K (ppm)	18	19	14	20		10
Ca (ppm)	1490	1860	2570	2220		68
pH	8.50	8.40	7.40	7.60		5.25
Vegetation						
VS Diversity A	11	7	5	5		7
VS Diversity B	11	9	6	9		
VS Cover (%)	0.41	0.11	1.49	0.20	p	0.34
VS Density (plants/m^2)	6.18	2.67	13.44	5.31		1.94
VS Standing crop (g/m^2)	5.55	1.15	25.72	2.22		2.12
Bryophyte cover (%)	0.05	0.04	0.13	0.13		1.71
Lichen cover (%)	9.47	3.54	4.79	1.13		27.38
Total plant cover (%)	9.93	3.69	6.41	1.46		29.43
Litter cover (%)	0.04	0.03	0.07	0.04		< 0.01
Feces cover (%)	0.01	0.05	0.05	0.02		0
Number of quadrats sampled						
Vasculars	57	66	50	58		173
Moss	30	30	30	30		66
Lichen	30	30	30	30		66

SITE	G1	G2	G3	G4	G5	G6
REFERENCE NUMBER	7	7	7	7	7	7
General characteristics						
Date	26/07/90	11/08/90	06/08/90	08/08/90	10/08/90	10/08/90
Latitude (°N)	79°08'06"	78°08'12"	79°07'48"	79°08'	79°07'18"	79°07'
Longitude (°W)	79°38'00"	79°37'30"	79°35'30"	79°35'	79°32'00"	79°33'
Elevation (m a.s.l.)	347	357	443	461	618	638
Substrate type	G	G	G	G	G	G
Slope angle (°)	0	0	3	0-2	0-1	0
Slope aspect (°)	0	0	27	25	20	0
Microtopography and soils						
Roughness	4.43	2.43	3.07	2.00	3.60	2.73
Boulders (%)	43.4	18.0	22.3	9.0	26.1	18.4
Pebbles (%)	22.9	33.3	33.4	41.1	51.6	39.2
Fines (%)	24.3	41.1	43.3	48.6	25.3	34.3
Sand (%)	79.9	76.0	82.5	77.9	82.5	83.1
Silt (%)	20.1	20.0	16.2	19.1	17.5	12.0
Clay (%)	0.0	6.9	1.3	2.9	0.0	4.8
OM (%)	12.5	4.8	9.6	5.9	3.0	4.3
P (ppm)	4.72	7.28	8.06	1.99	2.01	3.58
K (ppm)	42	32	34	20	8	23
Ca (ppm)	2690	1450	2020	1660	340	650
pH	7.90	7.90	7.50	8.20	7.90	7.88
Vegetation						
VS Diversity A	15	9	17	12	16	11
VS Diversity B	15	9	20	14	16	11
VS Cover (%)	7.28	1.03	6.43	7.40	2.78	2.93
VS Density (plants/m^2)	34.00	9.73	39.60	11.20	38.27	32.27
VS Standing crop (g/m^2)	75.58	7.93	38.88	52.87	38.93	40.92
Bryophyte cover (%)	0.04	<0.01	0.11	0.08	0.13	0.10
Lichen cover (%)	11.03	3.92	7.37	6.96	11.77	13.85
Total plant cover (%)	18.35	4.97	13.91	14.44	14.68	16.88
Litter cover (%)	1.51	0.56	1.21	0.22	0.60	0.44
Feces cover (%)	0.03	0.17	0.41	0.19	0.06	0.09
Number of quadrats sampled						
Vasculars	30	30	30	45	30	30
Moss	30	30	30	30	30	30
Lichen	30	30	30	30	30	30

SITE	G7	G8	G9	EM1	M1	LB
REFERENCE NUMBER	7	7	7	7	9	9
General characteristics						
Date	09/08/90	17/07/90	17/07/90	27/07/90	14/07/91	14/07/91
Latitude (°N)	79°06'48"	79°06'48"	79°06'30"	79°09'	79°09'	79°09'
Longitude (°W)	79°33'12"	79°36'30"	79°36'00"	79°29'	81°58'	81°58'
Elevation (m a.s.l.)	727	811	973	636	703	745
Substrate type	G	G	G	S	D	D
Slope angle (°)	0					
Slope aspect (°)	0					
Microtopography and soils						
Roughness	3.77	3.53		3.75	2.57	
Boulders (%)	31.1	33.0		16.2	34.4	
Pebbles (%)	46.7	10.2		49.4	36.7	
Fines (%)	26.9	47.5		32.9	31.3	
Sand (%)	88.7	79.4		86.8	46.4	51.9
Silt (%)	9.4	11.7		9.3	20.7	24.9
Clay (%)	1.9	9.0		3.9	33.0	14.9
OM (%)	1.7	4.0		0.4	9.6	14.4
P (ppm)	9.84	19.15		1.44	3.48	2.90
K (ppm)	10	12		4	20	16
Ca (ppm)	170	117		45	2439	1800
pH	6.67	4.98		5.88	7.46	7.75
Vegetation						
VS Diversity A	9	5		12	4	
VS Diversity B	9					
VS Cover (%)	1.36	0.14	0	0.48	0.28	0
VS Density (plants/m^2)	11.20	11.73		1.84	7.56	
VS Standing crop (g/m^2)	23.08	0.37		8.72	1.76	
Bryophyte cover (%)	0.96	0.55		0	0.27	
Lichen cover (%)	20.57	0.55		5.60	0.22	
Total plant cover (%)	22.89	1.24		6.08	0.77	
Litter cover (%)	0.11	0.10		0.04	0.07	
Feces cover (%)	0.03	0		0	0	
Number of quadrats sampled						
Vasculars	30	15		176	64	
Moss	30	15		15	42	
Lichen	30	15		15	42	

SITE	LG	P1	P2	P3	P4	P5
REFERENCE NUMBER	9	9	9	9	9	9
General characteristics						
Date	14/07/91	14/07/91	14/07/91	14/07/91	14/07/91	14/07/91
Latitude (°N)	79°09'	79°09'	79°09'	79°09'	79°09'	79°09'
Longitude (°W)	81°58'	81°58'	81°58'	81°58'	81°58'	81°58'
Elevation (m a.s.l.)	745	891	723	727	745	908
Substrate type	D	D	D	D	D	D
Slope angle (°)						
Slope aspect (°)						
Microtopography and soils						
Roughness						
Boulders (%)						
Pebbles (%)						
Fines (%)						
Sand (%)	60.7					63.9
Silt (%)	27.3					26.1
Clay (%)	12.0					9.9
OM (%)	4.0					6.0
P (ppm)	2.90					2.90
K (ppm)	16					16
Ca (ppm)	1800					1800
pH	7.75					7.75
Vegetation						
VS Diversity A						
VS Diversity B						
VS Cover (%)	0	0	0	0	0	0
VS Density (plants/m^2)						
VS Standing crop (g/m^2)						
Bryophyte cover (%)						
Lichen cover (%)						
Total plant cover (%)						
Litter cover (%)						
Feces cover (%)						
Number of quadrats sampled						
Vasculars						
Moss						
Lichen						

SITE	P6	MM1	MM2	MM3	MM4	MM4P
REFERENCE NUMBER	9	10	10	10	10	10
General characteristics						
Date	14/07/91	15/07/91	15/07/91	15/07/91	15/07/91	15/07/09
Latitude (°N)	79°09'	79°17'	79°17'	79°17'	79°17'	79°17'
Longitude (°W)	81°58'	81°42'	81°42'	81°42'	81°42'	81°42'
Elevation (m a.s.l.)	1025	873	788	788	790	790
Substrate type	D	D	D	D	D	D
Slope angle (°)				5	5	
Slope aspect (°)				20	22	
Microtopography and soils						
Roughness				1.78	2	
Boulders (%)				2.2	2.2	
Pebbles (%)				62.5	62.5	
Fines (%)				35.6	35.6	
Sand (%)	27.5	38.0	33.0	35.7	36.3	35.4
Silt (%)	17.4	32.1	32.7	31.5	34.1	32.5
Clay (%)	5.1	29.9	34.3	32.8	29.6	32.2
OM (%)	8.2	4.9	4.8	4.1	3.2	3.1
P (ppm)	2.90	1.19	3.00	2.32	1.35	2.48
K (ppm)	16	26	25	20	17	26
Ca (ppm)	1800	2547	2997	2713	2479	2275
pH	7.75	7.62	7.68	7.78	7.82	7.55
Vegetation						
VS Diversity A				3	4	
VS Diversity B						
VS Cover (%)	0	0	p	0.04	0.09	p
VS Density (plants/m^2)				0.91	1.93	
VS Standing crop (g/m^2)				0.24	0.50	
Bryophyte cover (%)				0.45	0.03	
Lichen cover (%)				0.70	0	
Total plant cover (%)				1.19	0.12	
Litter cover (%)				0	0.01	
Feces cover (%)				0	0	
Number of quadrats sampled						
Vasculars				22	29	
Moss				10	5	
Lichen				10	5	

SITE	VF1	VF2	VF3	C1	C2	CL
REFERENCE NUMBER	11	11	11	12	12	12
General characteristics						
Date	21/07/93	21/07/93	21/07/93	22/07/93	22/07/93	22/07/93
Latitude (°N)	78°07'39"	78°07'39"	78°07'39"	78°23'19"	78°23'19"	78°23'21"
Longitude (°W)	82°18'09"	82°18'09"	82°18'09"	82°08'55"	82°08'55"	82°03'53"
Elevation (m a.s.l.)	550	550	552	758	661	909
Substrate type	D	D	D	D	D	D
Slope angle (°)						
Slope aspect (°)						
Microtopography and soils						
Roughness		2.83		2.95	2.68	
Boulders (%)		14.3		4.9	1.8	
Pebbles (%)		52.1		63.3	62.9	
Fines (%)		31.7		34.1	33.1	
Sand (%)		33.0	37.7	30.7	35.5	
Silt (%)		54.7	46.5	59.7	56.3	
Clay (%)		12.3	15.8	9.6	8.1	
OM (%)		2.8	4.1	4.9	5.1	
P (ppm)		4.53	6.03	4.47	3.56	
K (ppm)		21	19	13	12	
Ca (ppm)		1224	1665	681	562	
pH		7.87	7.51	7.77	7.58	
Vegetation						
VS Diversity A		8		2	10	
VS Diversity B						
VS Cover (%)	p	0.15	0	< 0.01	0.37	0
VS Density (plants/m^2)		2.63		<0.01	6.48	
VS Standing crop (g/m^2)		1.08		0.10	3.66	
Bryophyte cover (%)		0.26		0.06	0.19	
Lichen cover (%)		4.32		1.36	4.18	
Total plant cover (%)		4.73		1.42	4.74	
Litter cover (%)		0.02		0	0.02	
Feces cover (%)		< 0.01		0	< 0.01	
Number of quadrats sampled						
Vasculars		123		24	87	
Moss		59		20	60	
Lichen		59		20	60	

SITE	Q1	Q2	R2	R3	R4	PMB
REFERENCE NUMBER	13	13	14	14	14	15
General characteristics						
Date	23/07/93	23/07/93	23/07/93	23/07/93	23/07/93	25/07/93
Latitude (°N)	78°27'21"	78°27'21"	79°28'	79°28'	79°28'	79°28'
Longitude (°W)	81°03'58"	81°03'58"	75°55'	75°55'	75°55'	75°55'
Elevation (m a.s.l.)	842	977	770	803	833	645
Substrate type	G	G	G	G	G	D
Slope angle (°)						
Slope aspect (°)						
Microtopography and soils						
Roughness	3.00	3.05				2.92
Boulders (%)	15.4	24.1				4.8
Pebbles (%)	52.1	41.0				56.1
Fines (%)	32.3	40.8				40.1
Sand (%)	73.2	62.8	85.0			47.7
Silt (%)	19.2	29.2	8.0			39.8
Clay (%)	7.6	8.0	7.0			12.6
OM (%)	1.8	1.9	1.9			4.4
P (ppm)	2.37	39.00	15.04			1.07
K (ppm)	28	12	11			12
Ca (ppm)	533	57	49			1950
pH	6.33	5.23	4.77			7.35
Vegetation						
VS Diversity A	5	0				6
VS Diversity B						
VS Cover (%)	0.34	0	0	0	0	0.64
VS Density (plants/m^2)	14.22	0				13.30
VS Standing crop (g/m^2)	2.17	0				5.99
Bryophyte cover (%)	0.59	0.78	p			0.25
Lichen cover (%)	3.03	2.63	p			8.56
Total plant cover (%)	3.96	3.41				9.45
Litter cover (%)	0.30	0.04				0.11
Feces cover (%)	< 0.01	0				< 0.01
Number of quadrats sampled						
Vasculars	74	34				58
Moss	60	20				50
Lichen	60	20				50

SITE	W1	W2	WL	X1
REFERENCE NUMBER	16	16	16	16
General characteristics				
Date	10/08/92	10/08/92	10/08/92	09/08/93
Latitude (°N)	80°12'20"	80°12'20"	80°15'09"	80°12'08"
Longitude (°W)	71°01'13"	71°01'13"	71°05'07"	70°18'27"
Elevation (m a.s.l.)	852	848	1121	803
Substrate type	D	D	D	D
Slope angle (°)	4-5			
Slope aspect (°)	16	~16		
Microtopography and soils				
Roughness		2.33		2.53
Boulders (%)		0		23.2
Pebbles (%)		20		29.3
Fines (%)		80		40.1
Sand (%)	42.2	43.5		26.7
Silt (%)	33.8	35.4		31.1
Clay (%)	24.0	21.1		42.3
OM (%)	6.0	6.2		4.1
P (ppm)	0.64	0.67		8.57
K (ppm)	28	21		14
Ca (ppm)	2360	1794		2537
pH	7.08	7.18		7.37
Vegetation				
VS Diversity A		10		16
VS Diversity B				
VS Cover (%)	p	1.91	0	0.76
VS Density (plants/m^2)		30.00		24.67
VS Standing crop (g/m^2)		28.48		4.56
Bryophyte cover (%)		0.14		0.22
Lichen cover (%)		0.13		0.01
Total plant cover (%)		2.18		0.99
Litter cover (%)		0.06		0.17
Feces cover (%)		0		0.03
Number of quadrats sampled				
Vasculars		30		30
Moss		30		30
Lichen		30		30

APPENDIX 3:

EQUATIONS FOR CONVERSION OF COVER VALUES TO STANDING CROP

Species specific equations (coefficient ± standard error) established from vascular plants collected at Sverdrup Pass, Ellesmere Island. For details see Method section in Chapter 3.

Species	x coefficient	intercept	n	r^2
Braya sp.[1]	8.46 ± 2.22	-0.0145 ± 0.099	11	0.618
Cerastium sp.	4.36 ± 0.70	0.0379 ± 0.0572	17	0.721
Draba sp.[2]	7.32 ± 2.78	0.0306 ± 0.067	69	0.919
**Dryas integrifolia*[3]	9.00 ± 0.73	0	25	0.700
Erysimum pallasii	5.40 ± 1.00	0.0553 ± 0.1414	16	0.674
Graminae[4]	5.47 ± 0.52	- 0.0177 ± 0.125	50	0.696
Melandrium sp.[5]	3.91 ± 0.27	0.0011 ± 0.0363	21	0.917
Minuartia rubella	5.81 ± 0.75	0.0007 ± 0.0412	35	0.643
Papaver radicatum[6]	5.40 ± 0.63	0.0420 ± 0.214	32	0.708
Potentilla sp.[7]	6.84 ± 0.79	0.0733 ± 0.1072	22	0.788
**Salix arctica*	4.72 ± 0.44	0	31	0.751
Saxifraga caespitosa	12.58 ± 0.66	-0.0142 ± 0.0847	10	0.979
Saxifraga nivalis[8]	1.645 ± 1.217	0.0768 ± 0.0370	17	0.109
**Saxifraga oppositifolia*	18.77 ± 0.83	0	31	0.930
**Saxifraga tricuspidata*	12.63 ± 1.10	0	26	0.746
Stellaria longipes	3.32 ± 0.66	0.0035 ± 0.0568	22	0.559

* Regression equation forced through zero to make the values near zero more realistic and without changing much the overall r^2.

The equations given above were used for the following species:

[1] *Braya purpurascens, Braya thorild-wulffii*

[2] *Cardamine bellidifolia, Draba alpina, D. cinerea, D. corymbosa, D. nivalis, D. oblongata, D. subcapitata*

[3] *Cassiope tetragona, Carex nardina/Kobresia myosuroides, Dryas integrifolia*

[4] *Carex misandra, Festuca hyperborea, Luzula arctica, L. confusa, Phippsia algida, Poa abbreviata, P. arctica, Puccinellia bruggemannii*

[5] *Melandrium affine, M. apetalum*

[6] *Papaver radicatum, Pedicularis cf. arctica*

[7] *Potentilla hyparctica, P. pulchella*

[8] *Oxyria digyna, Saxifraga cernua, S. nivalis*

APPENDIX 4:

VASCULAR PLANT COVER (%) AND FREQUENCY (%) AT 58 POLAR DESERT SITES SAMPLED IN CENTRAL ELLESMERE ISLAND, CANADA.

The following 14 pages present the detailed, site specific vascular plant cover and frequency of 58 polar desert stands where at least a few vascular plants were recorded. Data are presented as percentage of total number of quadrats sampled during the 5 to 8 hours survey sampling; 'c' represents percent cover and 'f' frequency of occurrence (%); 'tr' represents species found on site but not in sampled quadrats; 'x' was used for species encountered during subsequent sampling along the altitudinal gradients along Sverdrup Pass. A few sites were visited more briefly, though an exhaustive list can not be presented, a minimal list of species encountered is presented (as indicated by 'p').

Reference number refers to the region around major landscape features, following the presentation given in Figure 3.1; sites characteristics are given in Appendix 2; nomenclature follows Porsild and Cody, 1980 except for a few taxa specified in Appendix 1.

Alexandra Fiord: **1**, N3, N4 and **2**, E1, S1, AG, AD
Bache Peninsula: **3**, B1
Hayes Fiord and Jokel Fiord: **4**, H1 and **5**, J4
Beitstad Fiord: **6**, Z1, ZL, BT1-BT6
Sverdrup Pass: **7** and **8**, carbonate sites (LM1, LM2, VP1, VP2, TT, DG1, D1-D6);
    granitic and sandstone sites (KM, GB1, G1-G8 and EM1)
Mount Lawson: **9**, M1
Mount Moore: **10**, MM2-MM4
Vendom Fiord: **11**, VF1, VF2; **12**, C1, C2; **13**, Q1
Princess Marie Bay: **15**, PMB
Judge Daly Promontory: **16**, W1, W2 and X1

SITE	E1		S1		AG		AD	
REFERENCE NUMBER	2		2		2		2	
SPECIES	C	F	C	F	C	F	C	F
Braya purpurascens								
Braya thorild-wulffii								
Cardamine bellidifolia	0.08	4.3	0.02	6.7				
Carex misandra								
C. nardina/Kobresia myosuroides								
Cassiope tetragona			tr	tr				
Cerastium cf arcticum			tr	tr	0.02	8.0		
Cystopteris fragilis								
Draba alpina								
Draba cinerea								
Draba corymbosa	0.01	1.1	0.02	6.7				
Draba lactea	tr	tr						
Draba nivalis	0.01	1.1						
Draba oblongata								
Draba subcapitata					0.03	12.0	0.08	32.0
Dryas integrifolia					0.02	8.0	0.65	36.0
Erysimum pallasii								
Festuca hyperborea								
Luzula arctica	0.43	7.5			0.20	60.0		
Luzula confusa			0.13	20.0	0.69	84.0	0.01	4.0
Melandrium affine								
Melandrium apetalum								
Minuartia rubella								
Oxyria digyna					0.04	16.0		
Papaver radicatum	0.75	8.6	tr	tr	0.04	16.0	0.01	4.0
Pedicularis cf arctica					0.01	4.0	tr	tr
Phippsia algida					0.47	80.0		
Poa abbreviata								
Poa arctica	0.08	1.1			0.30	4.0		
Potentilla hyparctica								
Potentilla pulchella								
Puccinellia bruggemannii								
Salix arctica	0.01	1.1			8.49	100.0	3.03	96.0
Saxifraga caespitosa							tr	tr
Saxifraga cernua	0.31	6.5						
Saxifraga nivalis			tr	tr				
Saxifraga oppositifolia	0.26	17.2	0.28	13.3	0.87	56.0	1 40	96.0
Saxifraga rivularis								
Saxifraga tricuspidata	tr	tr						
Stellaria longipes								

SITE	N3		N4		B1		J4	
REFERENCE NUMBER	1		1		3		5	
SPECIES	C	F	C	F	C	F	C	F
Braya purpurascens					0.05	20.0		
Braya thorild-wulfffii								
Cardamine bellidifolia	< 0.01	1.6		p			0.02	9.2
Carex misandra								
C. nardina/Kobresia myosuroides							0.09	4.6
Cassiope tetragona								
Cerastium cf arcticum					0.03	13.3		
Cystopteris fragilis								
Draba alpina							0.01	5.8
Draba cinerea								
Draba corymbosa					0.12	46.7	< 0.01	1.2
Draba lactea								
Draba nivalis								
Draba oblongata								
Draba subcapitata	0.04	14.0			0.14	50.0	0.03	11.5
Dryas integrifolia								
Erysimum pallasii								
Festuca hyperborea							tr	tr
Luzula arctica							0.01	2.3
Luzula confusa	tr	tr					0.16	2.8
Melandrium affine								
Melandrium apetalum								
Minuartia rubella	0.01	0.8			0.02	6.7	0.03	8.1
Oxyria digyna								
Papaver radicatum	0.07	14.0		p	0.02	6.7	0.08	17.2
Pedicularis cf arctica								
Phippsia algida	tr	tr		p				
Poa abbreviata							tr	tr
Poa arctica								
Potentilla hyparctica							tr	tr
Potentilla pulchella								
Puccinellia bruggemannii					0.08	23.3		
Salix arctica								
Saxifraga caespitosa								
Saxifraga cernua	< 0.01	1.6		p			0.01	3.5
Saxifraga nivalis	tr	tr					0.10	18.4
Saxifraga oppositifolia	0.40	34.1		p	0.04	16.7	1.25	52.9
Saxifraga rivularis								
Saxifraga tricuspidata							1.52	2.3
Stellaria longipes							< 0.01	1.5

SITE	H1		Z1		ZL		BT1	
REFERENCE NUMBER	4		6		6		6	
SPECIES	C	F	C	F	C	F	C	F
Braya purpurascens								
Braya thorild-wulfffii								
Cardamine bellidifolia			0.01	3.2				
Carex misandra								
C. nardina/Kobresia myosuroides								
Cassiope tetragona								
Cerastium cf arcticum								p
Cystopteris fragilis								
Draba alpina	0.01	2.5						
Draba cinerea								
Draba corymbosa	0.21	68.3						
Draba lactea								
Draba nivalis			0.01	3.2				
Draba oblongata								
Draba subcapitata	0.04	17.1	0.10	36.2		p		
Dryas integrifolia								
Erysimum pallasii								
Festuca hyperborea								
Luzula arctica								
Luzula confusa								
Melandrium affine								
Melandrium apetalum								
Minuartia rubella	tr	tr						
Oxyria digyna								
Papaver radicatum	0.02	2.4	0.03	11.7		p		p
Pedicularis cf arctica								
Phippsia algida	0.23	58.5						
Poa abbreviata								
Poa arctica								
Potentilla hyparctica								
Potentilla pulchella								
Puccinellia bruggemannii	0.01	2.4						
Salix arctica								
Saxifraga caespitosa	tr	tr						
Saxifraga cernua	0.02	7.3						
Saxifraga nivalis								
Saxifraga oppositifolia	0.18	43.9	0.25	24.5		p		p
Saxifraga rivularis								
Saxifraga tricuspidata								
Stellaria longipes	tr	tr						

SITE	BT2		BT3		BT4		BT5	
REFERENCE NUMBER	6		6		6		6	
SPECIES	C	F	C	F	C	F	C	F
Braya purpurascens								
Braya thorild-wulfffii								
Cardamine bellidifolia		p						
Carex misandra								
C. nardina/Kobresia myosuroides								
Cassiope tetragona								
Cerastium cf arcticum								
Cystopteris fragilis								
Draba alpina								
Draba cinerea								
Draba corymbosa				p				
Draba lactea								
Draba nivalis								
Draba oblongata								
Draba subcapitata								
Dryas integrifolia								
Erysimum pallasii								
Festuca hyperborea								
Luzula arctica		p						
Luzula confusa		p		p				
Melandrium affine								
Melandrium apetalum								
Minuartia rubella								
Oxyria digyna								
Papaver radicatum				p				
Pedicularis cf arctica								
Phippsia algida								
Poa abbreviata								
Poa arctica								
Potentilla hyparctica								
Potentilla pulchella								
Puccinellia bruggemannii								
Salix arctica								
Saxifraga caespitosa								
Saxifraga cernua				p				
Saxifraga nivalis								
Saxifraga oppositifolia				p		p		p
Saxifraga rivularis								
Saxifraga tricuspidata								
Stellaria longipes								

SITE	BT6		LM1		LM2		VP1	
REFERENCE NUMBER	6		7		7		7	
SPECIES	C	F	C	F	C	F	C	F
Braya purpurascens								
Braya thorild-wulffii								
Cardamine bellidifolia		p						
Carex misandra								
C. nardina/Kobresia myosuroides								
Cassiope tetragona								
Cerastium cf arcticum								
Cystopteris fragilis								
Draba alpina								
Draba cinerea								
Draba corymbosa			0.02	6.5				
Draba lactea								
Draba nivalis								
Draba oblongata								
Draba subcapitata			0.01	1.1				
Dryas integrifolia								
Erysimum pallasii								
Festuca hyperborea								
Luzula arctica		p						
Luzula confusa		p						
Melandrium affine								
Melandrium apetalum								
Minuartia rubella		p						
Oxyria digyna								
Papaver radicatum		p	0.05	6.5				
Pedicularis cf arctica								
Phippsia algida		p	0.26	21.5		p	0.06	3.8
Poa abbreviata								
Poa arctica								
Potentilla hyparctica								
Potentilla pulchella								
Puccinellia bruggemannii								
Salix arctica								
Saxifraga caespitosa								
Saxifraga cernua			0.01	2.2				
Saxifraga nivalis								
Saxifraga oppositifolia		p	0.04	4.3			0.02	5.7
Saxifraga rivularis		p						
Saxifraga tricuspidata								
Stellaria longipes								

SITE	VP2		TT		DG1		D1	
REFERENCE NUMBER	7		7		8		7	
SPECIES	C	F	C	F	C	F	C	F
Braya purpurascens							0.08	33.3
Braya thorild-wulffii								
Cardamine bellidifolia								
Carex misandra								
C. nardina/Kobresia myosuroides							tr	tr
Cassiope tetragona								
Cerastium cf arcticum							tr	tr
Cystopteris fragilis							tr	tr
Draba alpina								
Draba cinerea								
Draba corymbosa	tr	tr			0.03	11.5	tr	tr
Draba lactea								
Draba nivalis								
Draba oblongata							0.05	20.0
Draba subcapitata	0.01	1.4			0.03	9.0	0.03	13.3
Dryas integrifolia							tr	tr
Erysimum pallasii								
Festuca hyperborea								
Luzula arctica								
Luzula confusa								
Melandrium affine								
Melandrium apetalum							tr	tr
Minuartia rubella							0.08	20.0
Oxyria digyna								
Papaver radicatum				p	0.01	3.3	0.06	16.7
Pedicularis cf arctica								
Phippsia algida	0.09	18.6			< 0.01	0.8		
Poa abbreviata								
Poa arctica								
Potentilla hyparctica								
Potentilla pulchella							0.01	3.3
Puccinellia bruggemannii							0.44	80.0
Salix arctica							tr	tr
Saxifraga caespitosa								
Saxifraga cernua								
Saxifraga nivalis								
Saxifraga oppositifolia	0.02	1.4			0.04	4.1	0.53	23.3
Saxifraga rivularis								
Saxifraga tricuspidata								
Stellaria longipes								

SITE	D2		D3		D4		D5	
REFERENCE NUMBER	7		7		7		7	
SPECIES	C	F	C	F	C	F	C	F
Braya purpurascens	0.02	8.3	0.03	12.3	0.05	21.2		
Braya thorild-wulfffii						x		
Cardamine bellidifolia								
Carex misandra								
C. nardina/Kobresia myosuroides								
Cassiope tetragona								
Cerastium cf arcticum			0.02	3.5	< 0.01	1.5		
Cystopteris fragilis								
Draba alpina								
Draba cinerea	x	x						
Draba corymbosa	< 0.01	1.7	0.01	3.5	x	x	tr	tr
Draba lactea								
Draba nivalis								
Draba oblongata	x	x						
Draba subcapitata	0.01	5.0	0.01	3.5	0.01	3.0	0.12	48.0
Dryas integrifolia	0.11	5.0	tr	tr				
Erysimum pallasii								
Festuca hyperborea								
Luzula arctica								
Luzula confusa								
Melandrium affine								
Melandrium apetalum			tr	tr				
Minuartia rubella	0.02	6.7	0.02	5.3	0.01	3.0		
Oxyria digyna								
Papaver radicatum	0.01	5.0	0.01	3.5	< 0.01	1.5	0.06	24.0
Pedicularis cf arctica								
Phippsia algida							0.01	4.0
Poa abbreviata	< 0.01	1.7	< 0.01	1.8	0.01	4.5		
Poa arctica								
Potentilla hyparctica								
Potentilla pulchella								
Puccinellia bruggemannii	0.04	15.0	0.08	7.0	x	x	tr	tr
Salix arctica	< 0.01	1.7	tr	tr				
Saxifraga caespitosa								
Saxifraga cernua							tr	tr
Saxifraga nivalis								
Saxifraga oppositifolia	0.20	16.7	0.23	33.3	0.02	6.1	1.30	64.0
Saxifraga rivularis								
Saxifraga tricuspidata	tr	tr						
Stellaria longipes			tr	tr				

SITE	D6		KM		GB1		G1	
REFERENCE NUMBER	7		7		8		7	
SPECIES	C	F	C	F	C	F	C	F
Braya purpurascens								
Braya thorild-wulffii								
Cardamine bellidifolia					tr	0.6		
Carex misandra							0.08	16.7
C. nardina/Kobresia myosuroides							1.39	63.3
Cassiope tetragona								
Cerastium cf arcticum								
Cystopteris fragilis								
Draba alpina							0.01	3.3
Draba cinerea							0.02	6.7
Draba corymbosa	< 0.01	1.7			tr	0.6		
Draba lactea								
Draba nivalis								
Draba oblongata							0.05	20.0
Draba subcapitata	0.10	34.5		p	0.04	11.0	0.02	6.7
Dryas integrifolia							1.13	20.0
Erysimum pallasii							0.03	3.3
Festuca hyperborea								
Luzula arctica								
Luzula confusa					0.15	2.9		
Melandrium affine								
Melandrium apetalum								
Minuartia rubella	x	x					0.05	20.0
Oxyria digyna								
Papaver radicatum	0.03	13.8		p	0.08	11.6	0.01	3.3
Pedicularis cf arctica								
Phippsia algida	x	x						
Poa abbreviata	tr	tr			0.08	2.9	0.09	20.0
Poa arctica							tr	tr
Potentilla hyparctica								
Potentilla pulchella							0.01	3.3
Puccinellia bruggemannii	x	x						
Salix arctica								
Saxifraga caespitosa								
Saxifraga cernua	x	x						
Saxifraga nivalis					tr	tr		
Saxifraga oppositifolia	0.07	3.4		p			1.24	80.0
Saxifraga rivularis								
Saxifraga tricuspidata							3.16	63.3
Stellaria longipes								

SITE	G2		G3		G4		G5	
REFERENCE NUMBER	7		7		7		7	
SPECIES	C	F	C	F	C	F	C	F
Braya purpurascens					0.07	28.9		
Braya thorild-wulfffii								
Cardamine bellidifolia							0.01	3.3
Carex misandra			0.01	3.3				
C. nardina/Kobresia myosuroides	0.38	20.0	3.09	63.3	tr	tr	0.14	13.3
Cassiope tetragona								
Cerastium cf arcticum							tr	tr
Cystopteris fragilis								
Draba alpina					tr	tr		
Draba cinerea			0.04	16.7	0.02	6.7	0.01	3.3
Draba corymbosa			0.03	13.3	0.03	13.3	0.01	3.3
Draba lactea								
Draba nivalis								
Draba oblongata	0.03	13.3	0.06	23.3	0.05	20.0		
Draba subcapitata	0.07	26.7	0.03	13.3	0.02	8.9	0.15	60.0
Dryas integrifolia			1.36	26.7	3.26	15.6		
Erysimum pallasii								
Festuca hyperborea			x	x				
Luzula arctica								
Luzula confusa			x	x			0.04	10.0
Melandrium affine			0.10	40.0				
Melandrium apetalum								
Minuartia rubella	0.03	13.3	0.04	16.7	0.04	17.8	0.03	10.0
Oxyria digyna								
Papaver radicatum	0.02	6.7	0.02	6.7			0.07	20.0
Pedicularis cf arctica								
Phippsia algida								
Poa abbreviata			0.12	26.7	0.05	15.6	0.43	70.0
Poa arctica	0.21	43.3	0.26	63.3	0.02	4.4	0.03	3.3
Potentilla hyparctica							0.03	3.3
Potentilla pulchella								
Puccinellia bruggemannii			x	x	x	x		
Salix arctica	0.01	3.3	tr	tr	3.60	20.0		
Saxifraga caespitosa			0.03	10.0			0.02	6.7
Saxifraga cernua								
Saxifraga nivalis			tr	tr			tr	tr
Saxifraga oppositifolia	0.29	33.3	1.13	53.3	0.22	22.2	1.78	80.0
Saxifraga rivularis								
Saxifraga tricuspidata	tr	tr	0.03	6.7			0.01	3.3
Stellaria longipes	tr	tr	0.09	20.0			0.04	10.3

SITE	G6		G7		G8		EM1	
REFERENCE NUMBER	7		7		7		7	
SPECIES	C	F	C	F	C	F	C	F
Braya purpurascens								
Braya thorild-wulfffii								
Cardamine bellidifolia			0.01	3.3	tr	tr	tr	0.6
Carex misandra								
C. nardina/Kobresia myosuroides	0.10	6.7	tr	tr				
Cassiope tetragona							tr	tr
Cerastium cf arcticum							tr	tr
Cystopteris fragilis								
Draba alpina							tr	tr
Draba cinerea								
Draba corymbosa	x	x					tr	tr
Draba lactea								
Draba nivalis								
Draba oblongata								
Draba subcapitata	0.08	33.3	0.11	43.3			0.01	2.8
Dryas integrifolia								
Erysimum pallasii								
Festuca hyperborea								
Luzula arctica							tr	tr
Luzula confusa	tr	tr	tr	tr	tr	tr		
Melandrium affine								
Melandrium apetalum								
Minuartia rubella			0.01	3.3			tr	0.6
Oxyria digyna								
Papaver radicatum	0.05	20.0	0.08	26.7	tr	tr	0.02	5.7
Pedicularis cf arctica								
Phippsia algida								
Poa abbreviata	0.18	33.3			tr	tr	tr	tr
Poa arctica	0.03	6.7	tr	tr	tr	tr		
Potentilla hyparctica	0.02	6.7						
Potentilla pulchella								
Puccinellia bruggemannii								
Salix arctica								
Saxifraga caespitosa								
Saxifraga cernua							0.01	1.1
Saxifraga nivalis	0.01	3.3	0.01	3.3				
Saxifraga oppositifolia	1.43	60.0	1.14	53.3			0.44	19.3
Saxifraga rivularis					0.13	53.3		
Saxifraga tricuspidata	0.93	20.0	tr	tr				
Stellaria longipes	0.11	13.3						

SITE	M1		MM2		MM3		MM4	
REFERENCE NUMBER	9		10		10		10	
SPECIES	C	F	C	F	C	F	C	F
Braya purpurascens								
Braya thorild-wulfffii								
Cardamine bellidifolia								
Carex misandra								
C. nardina/Kobresia myosuroides								
Cassiope tetragona								
Cerastium cf arcticum								
Cystopteris fragilis								
Draba alpina								
Draba cinerea								
Draba corymbosa								
Draba lactea								
Draba nivalis								
Draba oblongata								
Draba subcapitata	0.12	31.3						
Dryas integrifolia								
Erysimum pallasii								
Festuca hyperborea								
Luzula arctica								
Luzula confusa								
Melandrium affine								
Melandrium apetalum								
Minuartia rubella								
Oxyria digyna								
Papaver radicatum				p	tr	tr	0.01	3.5
Pedicularis cf arctica								
Phippsia algida	0.09	26.6		p	0.03	13.6	0.08	6.9
Poa abbreviata							tr	tr
Poa arctica								
Potentilla hyparctica								
Potentilla pulchella								
Puccinellia bruggemannii								
Salix arctica								
Saxifraga caespitosa								
Saxifraga cernua	0.06	20.3						
Saxifraga nivalis								
Saxifraga oppositifolia	0.01	1.6		p	tr	tr	tr	tr
Saxifraga rivularis								
Saxifraga tricuspidata								
Stellaria longipes								

SITE	MM4P		VF1		VF2		C1	
REFERENCE NUMBER	10		11		11		12	
SPECIES	C	F	C	F	C	F	C	F
Braya purpurascens								
Braya thorild-wulfffii								
Cardamine bellidifolia								
Carex misandra								
C. nardina/Kobresia myosuroides								
Cassiope tetragona								
Cerastium cf arcticum					tr	tr		
Cystopteris fragilis								
Draba alpina								
Draba cinerea								
Draba corymbosa				p	0.03	4.1	tr	tr
Draba lactea								
Draba nivalis								
Draba oblongata								
Draba subcapitata				p	0.04	15.5		
Dryas integrifolia								
Erysimum pallasii								
Festuca hyperborea								
Luzula arctica								
Luzula confusa								
Melandrium affine								
Melandrium apetalum								
Minuartia rubella								
Oxyria digyna								
Papaver radicatum		p			tr	tr	tr	tr
Pedicularis cf arctica								
Phippsia algida		p			0.01	4.9		
Poa abbreviata		p						
Poa arctica								
Potentilla hyparctica								
Potentilla pulchella								
Puccinellia bruggemannii					0.04	2.4		
Salix arctica								
Saxifraga caespitosa								
Saxifraga cernua					0.02	8.1		
Saxifraga nivalis								
Saxifraga oppositifolia		p		p	< 0.01	1.6	tr	tr
Saxifraga rivularis								
Saxifraga tricuspidata								
Stellaria longipes								

SITE	C2		Q1		PMB		W1	
REFERENCE NUMBER	12		13		15		16	
SPECIES	C	F	C	F	C	F	C	F
Braya purpurascens								
Braya thorild-wulfffii								
Cardamine bellidifolia			0.01	2.7				
Carex misandra								
C. nardina/Kobresia myosuroides								
Cassiope tetragona								
Cerastium cf arcticum	0.02	1.2						p
Cystopteris fragilis								
Draba alpina					0.13	44.8		
Draba cinerea								
Draba corymbosa	0.01	3.5			0.15	41.4		
Draba lactea								
Draba nivalis								
Draba oblongata								
Draba subcapitata			0.11	39.2	0.15	48.3		
Dryas integrifolia								
Erysimum pallasii								
Festuca hyperborea								
Luzula arctica								
Luzula confusa								
Melandrium affine								
Melandrium apetalum								
Minuartia rubella								
Oxyria digyna								
Papaver radicatum	0.04	10.3	0.21	59.5	0.09	25.9		
Pedicularis cf arctica								
Phippsia algida	0.17	41.4			< 0.01	1.7		
Poa abbreviata								p
Poa arctica								
Potentilla hyparctica								
Potentilla pulchella								
Puccinellia bruggemannii								p
Salix arctica								
Saxifraga caespitosa	tr	tr						
Saxifraga cernua	0.02	6.9	0.02	9.5				
Saxifraga nivalis	< 0.01	1.2						
Saxifraga oppositifolia	0.10	10.3	tr	tr	0.12	27.6		p
Saxifraga rivularis	tr	tr						
Saxifraga tricuspidata								
Stellaria longipes	tr	tr						

SITE	W2		X1	
REFERENCE NUMBER	16		16	
SPECIES	C	F	C	F
Braya purpurascens				
Braya thorild-wulfffii	0.19	70.0		
Cardamine bellidifolia				
Carex misandra				
C. nardina/Kobresia myosuroides				
Cassiope tetragona				
Cerastium cf arcticum	tr	tr	tr	tr
Cystopteris fragilis				
Draba alpina				
Draba cinerea				
Draba corymbosa	0.04	10.0		
Draba lactea				
Draba nivalis				
Draba oblongata				
Draba subcapitata	0.10	30.0	0.18	60.0
Dryas integrifolia				
Erysimum pallasii				
Festuca hyperborea				
Luzula arctica				
Luzula confusa				
Melandrium affine				
Melandrium apetalum				
Minuartia rubella	0.01	3.3		
Oxyria digyna	0.07	10.0		
Papaver radicatum	0.10	26.7	0.46	90.0
Pedicularis cf arctica				
Phippsia algida			0.12	40.0
Poa abbreviata	tr	tr		
Poa arctica				
Potentilla hyparctica				
Potentilla pulchella				
Puccinellia bruggemannii	0.10	40.0	tr	tr
Salix arctica				
Saxifraga caespitosa				
Saxifraga cernua				
Saxifraga nivalis				
Saxifraga oppositifolia	1.30	93.3	tr	tr
Saxifraga rivularis				
Saxifraga tricuspidata				
Stellaria longipes				

APPENDIX 5:

DETAILED SAMPLE AND SPECIES GROUPS OF TWINSPAN ANALYSIS OF 38 POLAR DESERT SITES FROM CENTRAL ELLESMERE ISLAND, CANADA.

The analysis include 38 vegetated polar desert sites indicated by vertical letters at the top of each column. Location of these sites is given in Figure 4.1, site characteristics in Appendix 1 and detailed species cover and frequency in Appendix 4. The main four sample groups are represented by letters at the top of the table (A, B, C and D) and by double spaces between the columns. The next division is indicated by numbers (*e.g.* A1 and A2). Single spaces divide columns to the 5th level of division where 14 noda were recognized (*cf.* Chapter 3). The dendrogram of this analysis is presented in Figure 3.8.

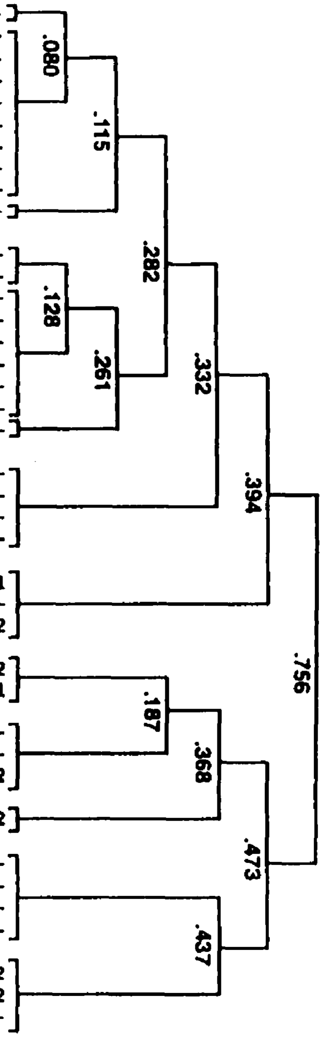
Species are identified by the first three letters of the genus and the first four letters of the species, complete species names are available in Appendix 2. The abundance of the species is presented according to the cover abundance scale presented in Chapter 2 (*e.g.* 1 represents < 0.5% cover and 9 > 75%); + indicates species present on site but not in quadrat sampling (see Method Chapter 3). Species groups are identified from 1 to 7. The division of the groupings and the corresponding eigenvalues are presented at the right end of the table. A summary of this detailed table in presented in Chapter 3 (Table 3.7).

```
SITE GROUPS:              A1  A2      B1    B2  C1  C2        D1          D2

              SITES:                             G E     MM  DP      VV L  V
                          GGG JGGG W BDDDD G AA  E BS MNQZ MMC GMD XD MPP MHCF
SPECIES:                  123 4567 2 12341 4 DG  1 11 1311 341 1B6 15 112 1122
GROUP 1
   37  STE LONG           -12 222- - --1-- - --  - -- ---- --- --- -- --- -11-
    4  CAR MISA           2-2 ---- - ----- - --  - -- ---- --- --- -- --- ----
    5  CAR NARD           425 2221 - ----1 1 --  - -- ---- --- --- -- --- ----
    8  DRA CINE           2-2 -2-- - ----- 2 --  - -- ---- --- --- -- --- ----
   15  ERY PALL           2-- ---- - ----- - --  - -- ---- --- --- -- --- ----
   16  FES HYPE           --+ 1--- - ----- - --  - -- ---- --- --- -- --- ----
   19  MEL AFFI           --2 ---- - ----- - --  - -- ---- --- --- -- --- ----
   28  POT HYPA           --- 122- - ----- - --  - -- ---- --- --- -- --- ----
   36  SAX TRIC           512 4231 - -1--- - --  1 -- ---- --- --- -- --- ----
   12  DRA OBLO           222 ---- - -+--2 2 --  - -- ---- --- --- -- --- ----

   14  DRY INTE           4-4 ---- - -21-1 5 32  - -- ---- --- --- -- --- ----
   29  POT PULC           2-- ---- - ----2 - --  - -- ---- --- --- -- --- ----
    1  BRA PURP           --- ---- - 22222 2 --  - -- ---- --- --- -- --- ----
    2  BRA THOR           --- ---- 2 ---+- - --  - -- ---- --- --- -- --- ----
   20  MEL APET           --- ---- - --1-1 - --  - -- ---- --- --- -- --- ----
   22  OXY DIGY           --- ---- 2 ----- - -2  - -- ---- --- --- -- --- ----
   24  PED ARCT           --- ---- - ----- - 12  - -- ---- --- --- -- --- ----
   31  SAL ARCT           -21 ---- - -21-1 5 56  2 -- ---- --- --- -- --- ----
   26  POA ABBR           2-2 122- 1 -222- 2 --  - 2- 1--- -1- --1 -- --- ----
GROUP 2
   18  LUZ CONF           --+ 2211 - ----- - 23  - 22 -1-- --- --- -- --- ----
   27  POA ARCT           122 -221 - ----- 2 -2  2 -- ---- --- --- -- --- ----
   32  SAX CEAS           --2 -2-- - ----- - 1-  - -- ---- --- --- -- --- -11-
   34  SAX NIVA           --1 2122 - ----- - --  - 11 -1-- --- --- -- --- --2-
GROUP 3
    6  CER ARCT           --- -1-- 1 2-221 - -2  - -1 1--- --- --- 1- --- --21
   21  MIN RUBE           222 22-2 2 22222 2 --  - -- 12-- --- --+ -- --- -1--
   30  PUC BRUG           --+ ---- 2 222+2 + --  - -- ---- --- --+ 11 --- -2-2
GROUP 4
   13  DRA SUBC           222 2222 2 22222 2 22  - 2- 2222 --- 222 22 2-2 22-2
   23  PAP RADI           222 2222 2 22222 - 22  3 21 2222 121 222 22 --- 2221

    7  DRA ALPI           2-- 2--- - ----- 1 --  - -- 1--- --- -2- -- --- -2--
   17  LUZ ARCT           --- 2--- - ----- - -2  2 -- 1--- --- --- -- --- ----
   35  SAX OPPO           424 4444 4 22223 2 43  2 -2 2212 111 222 14 222 2222
GROUP 5
    9  DRA CORY           --2 22+- 2 222+1 2 --  2 12 1--- --1 222 -1 --1 2222
GROUP 6
    3  CAR BELL           --- 22-2 - ----- - --  2 12 1222 --- --- -- --- ----
   10  DRA LACT           --- ---- - ----- - --  1 -- ---- --- --- -- --- ----
   11  DRA NIVA           --- ---- - ----- - --  2 -- ---2 --- --- -- --- ----
   39  CAS TETR           --- ---- - ----- - --  - -1 1--- --- --- -- --- ----
GROUP 7
   25  PHI ALGI           --- ---- - ----- - -2  - -- -1-- 22- 22+ 22 222 2222
   33  SAX CERN           --- 2--- - ----- - --  2 -- 222- --- --+ -1 2-- 2222
   38  SAX RIVU           --- ---- - ----- - --  - -- ---- --- --- -- --- --1-
```

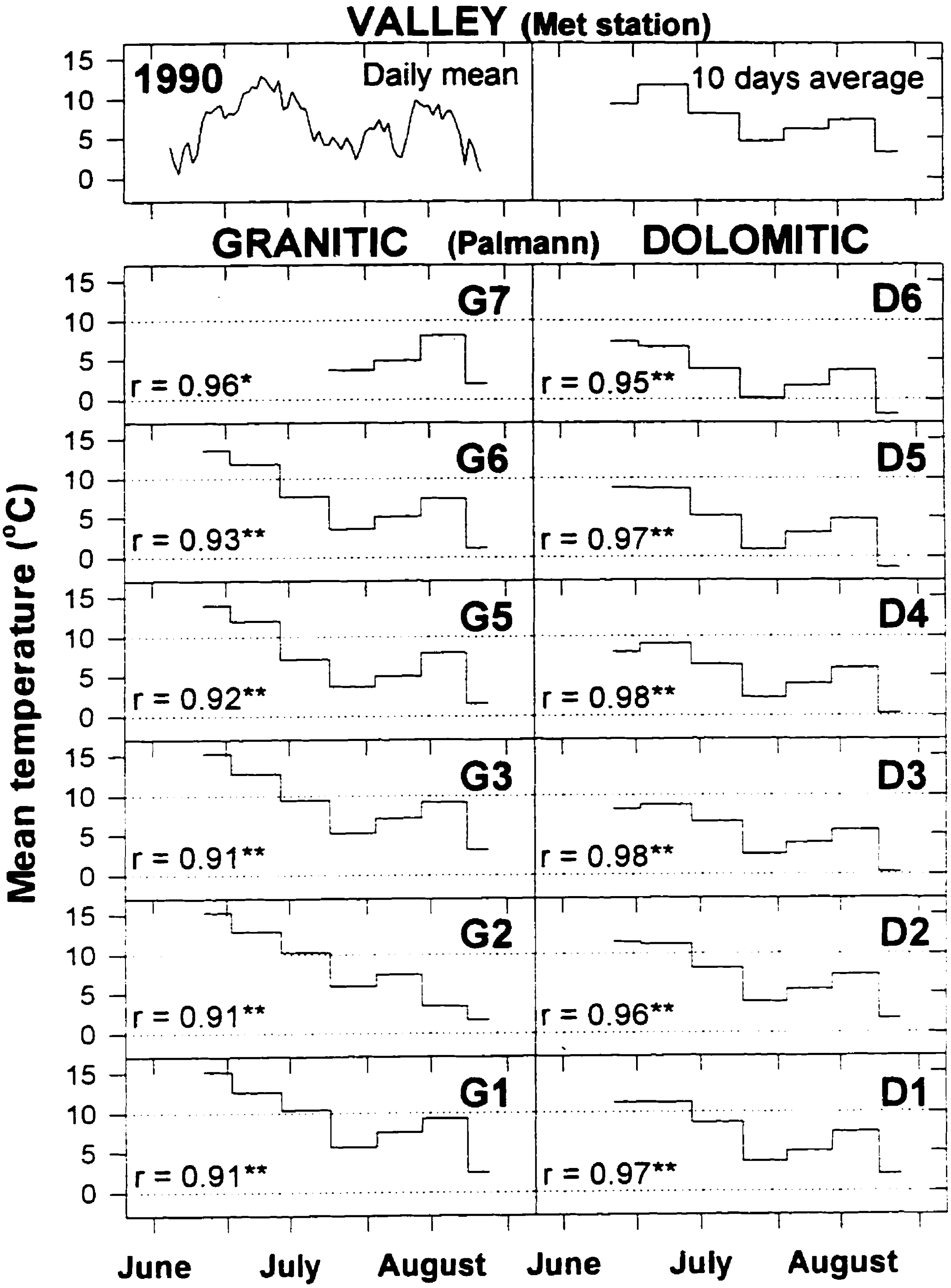


APPENDIX 6:

CORRESPONDENCE OF THE SOIL SURFACE TEMPERATURE TO THE VALLEY TEMPERATURE DATA

Seasonal temperature patterns in 1990 in the valley and along two altitudinal gradients in Sverdrup Pass, Ellesmere Island, Canada. Daily and 10 day temperature means as measured continuously at 1.5 m by the automated station in the valley ('MET' station; upper diagrams) and soil surface temperatures measured using the Pallmann technique at the gradient sites (lower diagrams). 'r' represents the Pearson correlation coefficient between the mean temperatures at the gradient sites and the valley mean temperatures and * indicates the level of significance: * $p \leq 0.05$ and ** $p \leq 0.005$. For details see Method section in Chapter 6.

N.B. Only 6 of the 7 gradient sites were represented on the following figure. Site G4 also had a significant correlation: $r = 0.90$ and $p < 0.005$.


VALLEY (Met station)
1990
Daily mean
10 days average
GRANITIC (Palmann) DOLOMITIC
G7
r = 0.96*
D6
r = 0.95**
G6
r = 0.93**
D5
r = 0.97**
G5
r = 0.92**
D4
r = 0.98**
G3
r = 0.91**
D3
r = 0.98**
G2
r = 0.91**
D2
r = 0.96**
G1
r = 0.91**
D1
r = 0.97**
Mean temperature (°C)
0
5
10
15
June
July
August
June
July
August

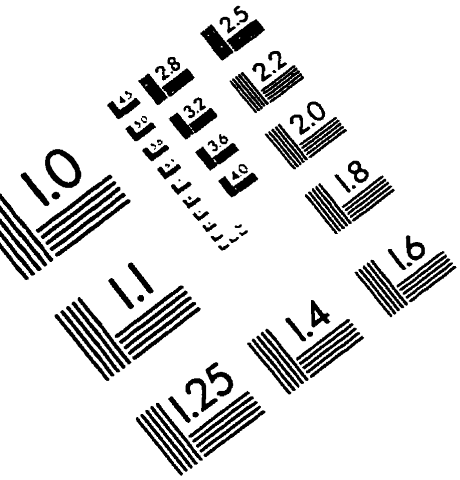
APPENDIX 7:

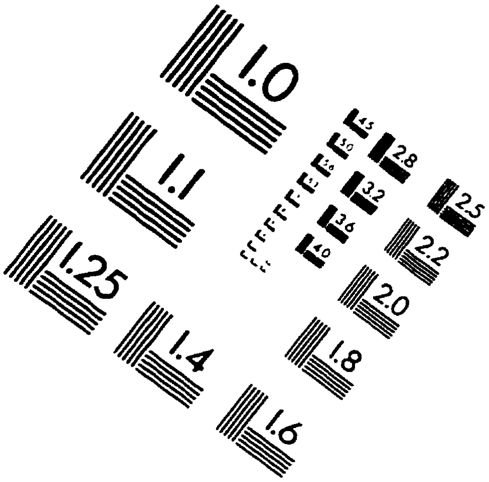
SITE-SPECIFIC EQUATIONS FOR CONVERSION OF VALLEY TEMPERATURE DATA

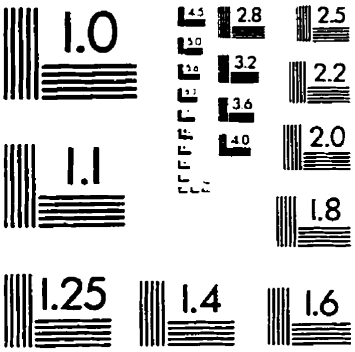
Site specific regression equations (coefficient ± standard error) established between the microclimate temperatures measured continuously at 1.5 m in the valley and the soil surface temperatures measured with the Pallmann technique, in 1990, at 6 dolomitic and 7 granitic sites along the two altitudinal gradients at Sverdrup Pass, Ellesmere Island. adj r^2, represents adjusted r^2. For details see Method section in Chapter 6.

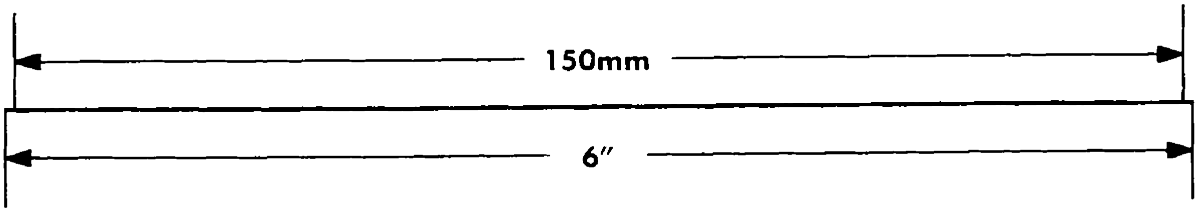
Site	x coefficient	intercept	n	adj r^2
Granitic sites				
G1	1.336 ± 0.266	-0.572 ± 2.048	7	0.80
G2	1.281 ± 0.255	-0.052 ± 1.962	7	0.80
G3	1.313 ± 0.266	-0.547 ± 2.046	7	0.80
G4	1.343 ± 0.297	-2.163 ± 2.285	7	0.76
G5	1.395 ± 0.275	-2.676 ± 2.116	7	0.80
G6	1.400 ± 0.243	-2.891 ± 1.868	7	0.84
G7	1.369 ± 0.270	-2.606 ± 1.490	4	0.89
Dolomitic sites				
D1	1.189 ± 0.140	-1.541 ± 1.073	7	0.92
D2	1.204 ± 0.148	-1.675 ± 1.138	7	0.92
D3	1.045 ± 0.105	-2.390 ± 0.805	7	0.94
D4	1.056 ± 0.088	-2.474 ± 0.676	7	0.96
D5	1.247 ± 0.147	-4.672 ± 1.129	7	0.92
D6	1.091 ± 0.159	-4.814 ± 1.222	7	089

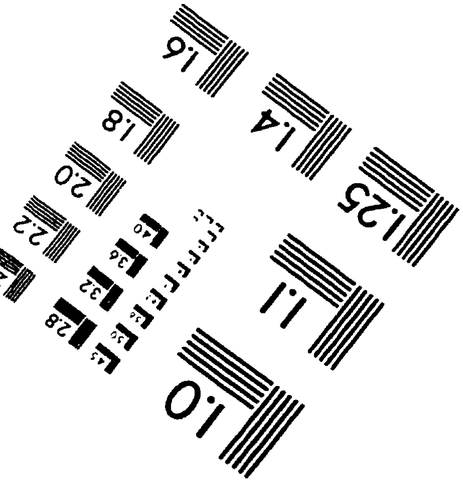
IMAGE EVALUATION
TEST TARGET (QA-3)

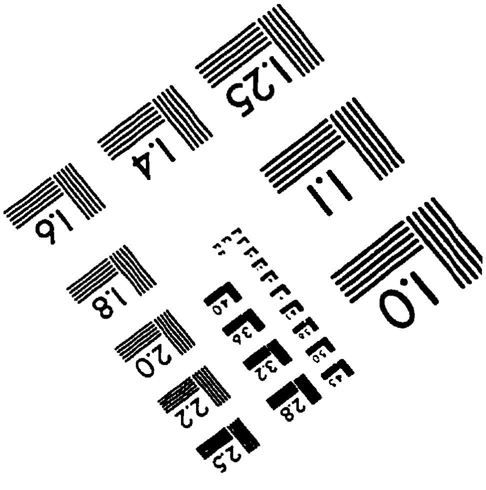












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