Scientific paper

Phytosociological classification and ecological characterization of high arctic vegetation of Canada with some remarks in relation to vegetation of Svalbard

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Abstract: An attempt was made to classify vegetation of the High Arctic of Canada at the higher level of syntaxonomy. Provisionally, one class, two orders and four alliances in addition to unclassified "polar desert complex" were distinguished. They were: the Salicetea arcticae, incorporating the Saxifragetalia oppositifoliae and the Caricetalia stantis. The Saxifragetalia oppositifoliae comprised of three alliances, i.e., Papaverion lapponici, Dryado-Salicion arcticae, and Cassiopion tetragonae, in addition to the "polar desert complex". Under the Caricetalia stantis, one alliance Caricion stantis was recognized. Vegetation of the Canadian High Arctic was compared with that of Svalbard. The most striking difference between the two regions was a presence/absence of Cassiope tetragona in the zonal phytogeocoenoses. The Cassiopedominating communities are fairly common in Svalbard whereas they are generally limited in the Canadian High Arctic. Such difference was explained primarily by climatic characteristics and concomitant soil properties in such a manner that a highly continental climate of the Canadian High Arctic decelerates the soil leaching and eluviation to maintain generally high base status of soils. On the other hand, a strongly oceanic climate of Svalbard promotes soil leaching to result in a soil acidification. Cassiope tetragona is known to be acidophilous and thrives better in acidic soils. In the Canadian High Arctic, development of the Cassiope-dominating communities is rather restricted to the areas where soils are generally acidic. Such a climate-soil-vegetation interaction regulates development of zonal phytogeocoenoses to determine biogeoclimatic characteristics of the respective regions.

key words: biogeoclimatic processes, High Arctic Canada, Svalbard, syntaxonomy vegetation classification

1. Introduction

In Canada, the Arctic biome occupies approximately 2.4 million km², *i.e.*, ca. 27% of the total land area of the country. It extends ca. 3500 km in a south-north direction, approximately from 52° N to 83° N, from southern end of James Bay to the northern tip

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of Ellesmere Island, and 4700 km in an east-west direction from 60°W to 141°W, *i.e.*, east coast of Labrador to Alaska-Yukon border. Because of the broad geographical extent, physical environment varies to a considerable extent from region to region within the Canadian Arctic, so do the vegetation characteristics.

The present paper attempts to classify vegetation of the High Arctic of Canada by means of phytosociology (Braun-Blanquet, 1965), to provide a tentative syntaxonomical hierarchy at higher levels, to characterize the vegetation based on the environmental conditions, and to compare vegetation characteristics of the Canadian High Arctic with those of Syalbard.

2. Physical and biological environment of the Canadian Arctic

In this article, the Arctic is defined as a circumpolar biome north of tree-line. Hence, the southern boundary of the Arctic generally coincides with the Nordenskjord line (Nordenskjord and Mecking, 1928). Vegetation physiognomy is, therefore, represented by extensive treeless tundra and polar desert landscapes.

Climate of the Canadian Arctic is extremely cold and generally dry. Mean annual temperature ranges approximately from -9°C to -20°C with a general mean of -12.8°C . Mean monthly temperature of the warmest month, usually July, ranges from 3°C to 12°C with a general mean of 7.0°C , and that of the coldest month, mostly February, ranges from -25°C to -39°C with a general mean of -29.6°C . Number of months of mean monthly temperature above 0°C is usually two and that of above 10°C is usually zero, or rarely and at most one. There is a geographical "cold belt", which is located roughly in the northern central region of the Arctic Archipelago along an imaginary line connecting Alert, Eureka, Resolute, Pond Inlet, Igloolik and Hall Beach. Precipitation is generally low. Annual total precipitation ranges from 76 mm (at Eureka) to 603 mm (at Cape Dyer) with an overall average of 229 mm. Precipitation tends to concentrate in summer months. According to Thornthwaite's calculation (Thornthwaite, 1948), potential evapotranspiration much exceeds the precipitation to result in potential water deficit unless melting water is supplied from thaw of permafrost, nearby snow beds and/or glaciers.

In terms of the physiographic regions, majority of the Canadian Arctic belongs to the Borderlands that are divided into the Arctic Coastal Plains, Arctic Lowlands and Innuitian Regions (Bostock, 1970). Arctic Coastal Plains and Arctic Lowlands consist generally of gentle and flat relief. Innuitian Regions, on the other hand, comprise a series of plateaus and relatively rugged mountain chains of the northern Arctic. This is the region where the "cold belt" locates. Geologically, Arctic Lowlands are represented by Ordovician to Devonian sedimentary rocks, predominantly of calcareous nature including limestone, dolomite, shale, and conglomerates, which overlying Precambrian basement. Arctic Coastal Plains are characterized by extensive occurrences of sedimentary of Tertiary and Quaternary, which is made up of less consolidated gravel, sand, silt, and wood debris. Innuitian Regions basically consist of Jurassic to Cretaceous sedimentary rocks with occasional occurrences of Ordovician (Thornsteinsson and Tozer, 1970). A small portion of the eastern Arctic Archipelago belongs to the Canadian Shield, its division Davis Region, which consists of elevated highlands with

deeply dissected landscapes. Geology of the region consists predominantly of granitic gneiss of Proterozoic (Stockwell et al., 1970).

Regarding soils, entire area of the Canadian Arctic is represented by Cryiosol (CSSC, 1977, 1978). A rate of physical weathering much exceeds chemical weathering processes due to low temperature and low precipitation. Cryoturbation is intense and is a dominant agent that prevents soil horizon differentiation. Such pedogenic conditions result in an extensive development of regosolic soils in the Arctic. Periglacial structured ground is a common feature. Chemical characteristics vary greatly reflecting local pedogenic conditions and kinds of parent material. In the Canadian Arctic, soil pH widely ranges from 4.5 to 8.9. (Barrett, 1972; Woo and Zoltai, 1977; Walker and Peters, 1977; Batten and Svoboda, 1994; Muc *et al.*, 1994; Kojima, 1999). Alkaline soils often develop where calcareous geology predominates. Depth of active layer is generally found to be 20–90 cm.

Floristically, the entire area of the Canadian Arctic belongs to Arctic Tundra Floral Region (Scoggan, 1978). It is characterized by a paucity of vascular species. In fact, number of species occurring in the Arctic (A+a of Scoggan) is 573, *i.e.*, 17% of total vascular species in Canada. Another characteristic feature is a presence of a large number of species of circumpolar distribution. For instance, 106 species out of 144 growing in the High Arctic Canada have circumpolar distribution occurring both in the North American and Eurasian continents (Scoggan, 1978). Yurtsev (1994, 2004) recognized four floristic divisions for the Canadian Arctic. They were subprovinces of IVA (Central Canada subprovince), IVB (West Hudsonian subprovince), IVE (Ellesmere-North Greenland subprovince) and V (Baffin-Labrador province), all of which are distinguished by the presence of characterizing taxa.

Vegetation and environmental characteristics of the Arctic of North America is thoroughly reviewed by Bliss (1988). General characterization and comprehensive discussions as to the circumpolar Arctic vegetation are provided by Bliss and Matveyeva (1992) and Walker *et al.* (1994).

3. Ecological zonation of the Canadian Arctic

There are several schemes of ecological division of the Canadian Arctic at the zonal level (Table 1). As early as 1898, Merriam designated the areas north and above of the tree lines as the Arctic or Arctic-Alpine zone, which were characterized by the presence of arctic poppy, dwarf willow, various saxifrages and gentians, though gentians better represent the alpine environment rather than the Arctic. Walter and Box (1976) denominated the north of tree lines of northern high latitudes as Zonobiome IX (Arctic). Bailey (1996) called the extreme high latitudes of the earth "Polar Domain" and divided it into six "Ecoregions", i.e., Ice Cap, Ice Cap Regime Mts., Tundra, Tundra Regime Mts., Subarctic, and Subarctic Regime Mts. Of them, the first four categories may correspond to the Canadian Arctic.

It was Polunin (1951), however, who first made ecological division of the Arctic, demarcating it from the Subarctic by an imaginary line approximately 80 km north of continuous forest of macrophanerophytic growth of trees of 2–8 m tall. He divided the Arctic further into three sections, *i.e.*, Low-Arctic, Mid-Arctic, and High-Arctic based

	Polunin (1951)	Π	Zoltai (1977)		Blis	s (1977)		CCELC (1989)	CAVM (2003)		Alek	ova (1971)	
	High Arcite		High Arctic		tic	Polar Desert Polar		High Arctic	Subzone A		Pol Des	ar sert	northern
•			no complex		Semi-desert complexes of	Arctic	Arctic Oceanic	Subzone B			ra		
Arctic	Mid-Arctic	c Arctic Mid-Arctic		Arctic	H	sedge meadows and polar semi- desert		Mid-Arctic	Subzone C			ic Tundra	northern
	Low Arctic		Low Arctic			Low Arctic		Low Arctic	Subzone D	Arctic	'a	Arctic	southern
								Moist	Subzone E		Tundra	Tundra	northern
								Low Arctic					middle
S	Subarctic		Subarctic	Subarctic				Subarctic				Subarctic	southern

Table 1. Some schemes of ecological zonation of the Canadian Arctic.

on the degree of vegetative cover and floristic characteristics.

Aleksandrova (1971) presented a somewhat different scheme for the northern regions of the Eurasian continent. She included the subarctic biome (sensu Polunin) into the Arctic and divided the Arctic into two sections primarily based on the physiognomy, i.e., tundra region and polar desert region. Tundra region was the area with higher vegetative cover but lacking trees whereas the polar desert encompassed the areas of extremely low vegetative cover in the high north.

Bliss (1977) recognized two basic zones for the Canadian Arctic, *i.e.*, Low Arctic and High Arctic, amalgamating the Mid Arctic (*sensu* Polunin) with High Arctic. Then, he further subdivided the High Arctic into three sections, *i.e.*, Polar Desert, Polar Semi-desert, and Complexes of sedge-meadows and Polar Semi-desert.

Zoltai (1977, 1978), basically following the Polunin's scheme, divided the Arctic of Canada into three divisions, *i.e.*, Low Arctic, Mid Arctic, and High Arctic, based on the degree of vegetative cover. The basic framework of this system was adopted and further developed to the classification scheme of CCELC (1989) (Fig. 1). Based on climatic and vegetational characteristics, CCELC recognized ten Ecoclimatic Provinces for the entire Canada. "Arctic Ecoclimatic Province" was identified for the Canadian Arctic, which was further subdivided into five "Ecoclimatic Regions" as: Oceanic High Arctic (HAo), High Arctic (HA), Mid Arctic (MA), Low Arctic (LA), and Moist Low Arctic (LAm). Wiken (1986) proposed a somewhat different zonation system for the Canadian Arctic, dividing it into three sections, *i.e.*, Southern Arctic, Northern Arctic and Arctic Cordillera. The Arctic Cordillera encompasses the areas of east coast of Ellesmere Island, Devon Island, and Baffin Island. It is the area where a series of mountain chains develops.

The latest version of the circumpolar arctic vegetation zonation and mapping was published by CAVM Team (2003), in which the Canadian Arctic was divided into five subzones (Subzone A~E) in the order of harshness of climate.

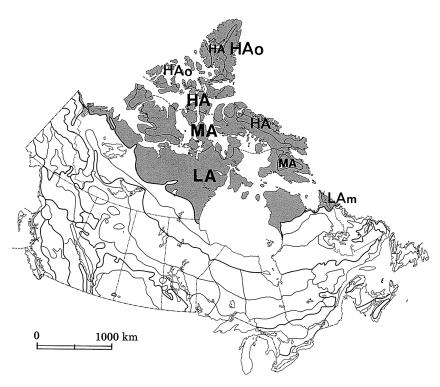


Fig. 1. Ecoclimatic Regions of the Arctic Canada (from CCELC, 1989). Shaded area indicates the Arctic Biome. LA: Low Arctic, LAm: Moist Low Arctic, MA: Mid-Arctic, HA: High Arctic, HAo: Oceanic High Arctic.

4. Vegetation classification and hierarchy of the Canadian High Arctic

For the High Arctic of Canada, a phytosociological classification was first attempted by Barrett (1972) and a syntaxonomical hierarchy was proposed for the lowlands of Devon Island, in which seven orders, seven alliances and nine associations were recognized. In this article, however, an additional attempt was made to classify and systematize the vegetation of the Canadian High Arctic at higher level, covering much broader geographical area. There were numerous studies conducted to describe and characterize the High Arctic vegetation of Canada. From them, the following papers were selected for the present study to synthesize the vegetation hierarchy. They were: Barrett (1972), Sheard and Geale (1983), Bergeron and Svoboda (1989), Kojima (1991, 1999), Batten and Svoboda (1994). These were the papers that provided complete description of vegetation structure on the stand basis, hence, served as a database for the vegetation synthesis. Furthermore, plant communities described in those papers were, by and large, those on the well-advanced and stable stage of vegetation succession. From the papers listed above, a total of 331 stands were selected and processed. However, for the present article, only vascular species were employed. It was no question that cryptogams were vitally important components of the Arctic

vegetation. But they were not included in this classification because listing and treatments of cryptogams were not necessarily consistent or complete throughout the literatures cited here. Tidal salt marsh communities were also excluded because they were the vegetation highly affected by edaphic conditions and did not represent necessarily the zonal vegetation.

An overall vegetation synthesis table was constructed based on the 40 vegetation groups, comparable to plant association, made up of 331 stands described variously from the High Arctic of Canada (Table 2). In the table, only such species were included as those showing the constancy class more than III in any of the 40 vegetation groups and those appearing more than five groups in the table regardless the constancy class. Based on the synthesis table, one Class, two Orders and four Alliances with one unclassified "polar desert complex" were provisionally recognized. Below the alliances, however, many plant associations should develop reflecting site-specific local conditions. Table 3 presents a summary of the syntaxonomical hierarchy with characteristic combinations of species for the units. Figure 2 illustrates general landscapes of the five syntaxonomic units. Following are brief descriptions of the syntaxa.

Class: Salicetea arcticae class nov.

The Class Salicetea arcticae represents the highest level of vegetation synthesis of the High Arctic of Canada, covering the entire vegetation of the High Arctic. It reflects extremely harsh physical environment of the North American High Arctic. It is characterized floristically best by the presence and common occurrence of Salix arctica. Other major characteristic species include Draba alpina (sensu lato), Stellaria longipes, Luzula arctica (sensu lato), and Alopecurus alpinus. In fact, Salix arctica is the most ubiquitous and often dominating species throughout the Canadian High Arctic, occurring in a wide spectrum of habitat conditions. Physiognomically, the class incorporates various kinds of ecosystems, e.g. polar desert, vegetation of earth hummocks, arctic heath, mesic meadows, sedge meadows, and so forth. The Class may be divided into two orders. The Class incorporates two Orders, i.e., Saxifragetalia oppositifoliae and Caricetalia stantis.

Order I. Saxifragetalia oppositifoliae Kojima 1991

The Saxifragetalia oppositifoliae is best characterized by the common occurrence of Saxifraga oppositifolia. It represents vegetation of xeric to mesic habitats of various soil chemistry from alkaline to slightly acidic conditions. Physiognomically, it represents most kinds of ecosystems of the High Arctic except for those of the poorly drained habitats. This order incorporates four kinds of alliances.

Alliance 1. Papaverion lapponici Kojima 1991

The Papaverion lapponici is floristically characterized by the presence of *Papaver lapponicum* (sensu lato incl. radicatum), often accompanied by Saxifraga caespitosa, Minuartia rubella, Poa arctica, and Cerastium alpinum (incl. arcticum). Besides the characteristic species of the class and order, such species as Poa abbreviata, Festuca baffinensis (incl. brachyphylla), Minuartia rossii, Parrya arctica often associate with this alliance. Landscape is typically polar-desert with low vegetative cover, usually less

Table 2. Vegetation synthesis table representing higher

Vegetation group #	B3	B4	C4	B5	B7	<u>A1</u>	S1	<u>S2</u>	SE	<u>A3</u>	C2	Cl	C3	B1	SF	S3
Species/ Number of stands	13	8	6	20	13	10	5	10	7	2	7	8	5		10	12
Class															************	
Salix arctica ***,*	II	II	V	II	V	I		II	V	V		I	II		V	V
Draba alpina/oblongata	I	I	II	I	I	I	IV	IV	I	I	V	Ш	IV	I	Ш	II
Stellaria longipes	I	I	II	I		I		Ш	Ш		I	II	III		Ш	II
Luzula arctica/nivalis		I	I	II		Ш			Ш	V		II	Ш			
Alopecurus alpimus				I	II			I	I		II				II	
Order											Saxif	rageta	ilia o	posi	tifolia	e
Saxifraga oppositifolia **	II	Ш	V			IV	v	V	V	IV	V	III	V	IV	II	III
Alliance	"	Polar	deser	t com	plex"				Papav	erion	lappe	onici				
Papaver lapponicum/radicatum *	I	II	П			I	V	III	Ш	Ш	V	V	V	II	I	I
Saxifraga caespitosa	I	П			I		Ш	II	II		I	\mathbf{v}	II	п		
Poa arctica	١.					I			I	I	IV	\mathbf{v}	Ш			
Cerastium arcticum/alpinum	I	I		I		I			II	II	Ш	II	ΙV	п		
Minuartia rubella	I						I	IV	I	I				1		
Poa abbreviata		I					IV	\mathbf{v}	V					п	Ш	Ш
Festuca baffinensis/brachyphylla		I				I			I	IV			\mathbf{v}	I	I	
Minuartia rossii	.I	I	II								Ш	IV	IV	I		
Cerastium regelii	I	I	I	I							II	II	II			
Parrya arctica											Ш	II	II	ا.		
Saxifraga tricuspidata						1		V	V					.		I
Dryas integrifolia*						I		Ш	V						IV	v
Pedicularis hirsuta									I						I	
Carex rupestris									II						I	
Carex misandra			I					I								II
Oxyria digyna	I	II							I	II				.	II	
Carex nardina								Ш	II						I	
Cassiope tetragona*						I			Ш	I				٦.	II	II
Silene acaulis						I								.		
Carex stans **,*																
Juncus biglumis	II		Ш		I	[II			III	I		I	
Polygonum viviparum			I		I											I
Saxifraga cernua		I		I			I		II	I	Ш	Ш		I		
Dupontia fisheri			I	II												
Saxifraga hirculus				I												
Melandrium apetalum	I	I		I												
Eriophorum scheuchzeri														.		
Eriophorum triste						l										

^{#:} Vegetation groups: A(1~6): Alexandra Fiord (Batten & Svoboda, 1994); B(1~7): Bathurst Island (Sheard & Gaele, 1983); C(1~7): Cornwallis Island (Kojima, 1991); D(1~8): Devon island (Barrett, 1972); S(1~6): Sverdrup Pass (Kojima, 1999); S(D~F): Sverdrup Pass (Bergeron & Svoboda (1989)

than 5%. This alliance represents vegetation of well drained xeric to subxeric habitats. Substrate is predominantly of coarse gravels of sorted and structured ground. Soils are generally coarse to medium-textured and slightly to strongly alkaline in reaction. Besides the cold climate, extensive occurrence of calcareous geology seems to be another factor to develop this type of vegetation.

This alliance may incorporate the following vegetation types variously described in the High Arctic of Canada: *Papaver-Draba* community, *Saxifraga-Draba* community, *Saxifraga-Papaver* community of Woo and Zoltai (1977) from Somerset and Prince of

^{***} characteritic species of the class, ** characteristic species of the order, * characteritic species of the alliance

syntaxonomical	units of the	Canadian	High Arctic	vegetation.
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SD2	C5	D2	D1	D4	D5	A4	A6			SD1	A2	A5	D3	D7	S6	SA	SB	D6		C6			S5
18	10	7	11	6	10	2	2	6	10	6	3	6	8	12	10	6	14	7	4	8	7	5	10
			cticae																				
V	V	V	V	V	V	Ш	V	II	V	V	I	v	\mathbf{v}	V	V	V	V	V	V	IV	V	Ш	V
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•	•	V	•	Ш	V	•	I	•	I	•	I	I	IV	V	Ш	•	•	III	II	V	V		Ш
		V	•	•	V	•	IV			II	Ш	Ш	IV	IV	•	•	I	II		II	IV		•
I		III					I		IV			I					11			IV			
																	Caric			is			
<u>V</u>	V	IV	V	V	V	V	III	III	IV	III	IV	II	V	V			II	III	V				I
Drya	do-Sa	licior	arcti	cae			_			Cassi	opion	tetraș	gonae				Caric	ion st	antis				
-	Ш	V	I	III	V				II	I	I	I	V	V						I	I		
	Ш	Ш			II									V						I		I	
		V			II		I			I	п	I		v									
		Ш	п		V					-	I	Ī	v	v									
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Wales Islands; Purple saxifrage plains of Thompson (1980) from Boothia Peninsula; Saxifraga oppositifolia barrens of Edlund (1980) from Lougheed Island; Barren Heath Subtype and Dwarf Shrub-Sedge Type of Zoltai et al. (1981) from Axel Heiberg Island; the cluster 1 of Sheard and Geale (1983) from Bathurst Island; Saxifraga caespitosa-Poa arctica type, Saxifraga oppositifolia-Draba bellii type, and Saxifraga oppositifolia-Festuca baffinensis type of Kojima (1991) from Cornwallis Island; Vegetation of plateau above Truelove Lowland, Devon Island, and that of plateau above Alexandra Fiord, Ellesmere Island of Bliss et al. (1994); Luzula-dominated Community of Batten and Svoboda (1994) from Alexandra Fiord, Ellesmere Island; Saxifraga oppositifolia Community type and Saxifraga tricuspidata Community type of Kojima (1999) from Sverdrup Pass, Ellesmere Island.

Table 3. A summary table of syntaxonomical hierarchy and major species characterizing and differentiating the syntaxonomical units.

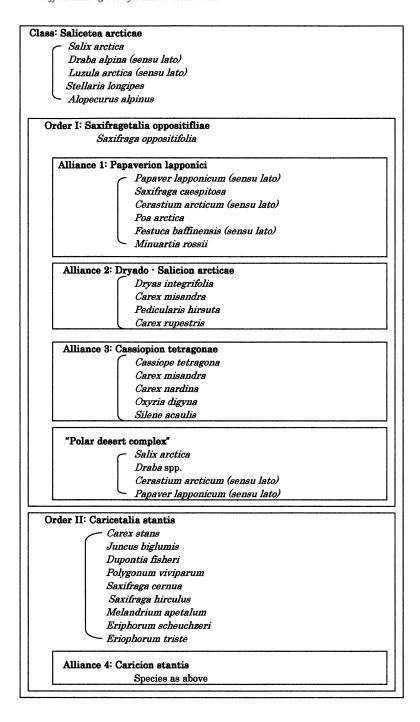




Fig. 2. Photographs showing general physiognomy of the syntaxonomic units of the High Arctic Canada.

1: General landscape of the High Arctic, 2: "Polar desert complex", 3: Papaverion lapponici, 4:

Dryado-Salicion arcticae, 5: Cassiopion tetragonae, 6: Caricion stantis (photo credit: S. Kojima).

Alliance 2. Dryado–Salicion arcticae all. nov. (*cf.* Luzulo–Salicion arcticae Barrett, 1972; Salicion arcticae Kojima 1991)

The Dryado-Salicion arcticae is characterized by high dominancy of *Dryas integrifolia*. Besides the characteristic species of the class and order, other major components of this alliance include *Carex misandra*, *Carex nardina*, *Poa abbreviata*, *Papaver lapponicum* (sensu lato) and *Polygonum viviparum*. Vegetative cover is moderate to high as it reaches as high as 100% in some instances, e.g. dwarf willow community developing on earth hummocks. This alliance represents vegetation developing in

moderately drained mesic habitats in a gentle topography such as slope bases near valley bottom, hummocky moraines, alluvial terraces, and so on. Soils are generally fine-to medium-textured of calcareous to circum-neutral nature. This alliance is considered to be the best representative of the zonal phytogeocoenoses of the Canadian High Arctic. It may be comparable to vegetation of the Dryadion integrifoliae and Luzulo–Salicion arcticae of Barrett (1972).

This alliance may incorporate the following vegetation types variously described: Tetragono–Dryadetum integrifoliae, Pedicularo–Dryadetum integrifoliae and Pogonato–Luzulo–Salicetum arcticae of Barrett (1972) from Devon Island; Salix–Dryas Community and Saxifraga–Polyblastia Community of Woo and Zoltai (1977) from Somerset and Prince of Wales Islands; Lichen–Dryas plateaus of Thompson (1980) from Boothia Peninsula; the cluster 2 of Sheard and Geale (1983) from Bathurst Island; the Dryas integrifolia dominated community type (nodum C) and the Salix arctica dominated community (nodum F) of Bergeron and Svoboda (1989) from Sverdrup Pass, Ellesmere Island; Saxifraga oppositifolia–Dryas integrifolia type of Kojima (1991) from Cornwallis Island; Dryas barrens Community and Dryas–Carex Community of Batten and Svoboda (1994) from Alexandra Fiord, Ellesmere Island; Lichen–Cushion Plant–Dwarf Shrub community and Deciduous Dwarf Shrub and Graminoid Community of Muc et al. (1994) from Alexandra Fiord, Ellesmere Island; Dryas integrifolia–Salix arctica Community type of Kojima (1999) from Sverdrup Pass, Ellesmere Island.

Alliance 3. Cassiopion tetragonae Barrett, 1972

The Cassiopion tetragonae is best characterized by the presence and high dominancy of Cassiope tetragona. Besides the characteristic species of the class and order, other components of this alliance include Dryas integrifolia, Carex misandra, C. nardina, Papaver lapponicum, Poa arctica and Arctagrostis latifolia. Vegetative cover is high as it attains 100% in most instances. It develops in gentle topography of alluvial terrace, valley bottom, and base of scree and talus slopes and moraine. The habitats are frequently associated with late snowbeds and snow banks. It is reported that acidic parent material promotes the establishment of this type of vegetation (Woo and Zoltai, 1977; Nams and Freedman, 1994; Kojima, 1999). Soils are moist and generally acidic. Well developed Cassiope tetragona dominated communities seem to be confined to the eastern part of the High Arctic of Canada, mainly eastern drainages of Ellesmere Island, Devon Island, and Banks Island (CAVM Team, 2003). In the central and western part of the High Arctic, this kind of communities is extremely scarce. This alliance is somewhat resemble to the Dryado-Salicion arcticae discussed previously. It is, however, clearly distinguished by the preponderant occurrence of Cassiope tetragona and generally acidic soils.

This alliance may incorporate the following vegetation types variously described at a plant association level: Sphaerophoro-Rhacomitrio-Cassiopetum tetragonae of Barrett (1972) from Devon Island; Cassiope-Cetraria Communitty Type of Woo and Zoltai (1977) from Somerset and Prince of Wales Islands; a part of the Dryas integrifolia-dominated community type (nodum D) of Bergeron and Svoboda (1989) from Sverdrup Pass, Ellesmere Island; Cassiope-dominated Community and Salix arctica-Cassiope tetragona Dwarf-shrub Community of Batten and Svoboda (1994) from

Alexandra Fiord, Ellesmere Island; Dwarf Shrub-Cushion Plant (DS-CP) type of Muc et al. (1994) from Alexandra Fiord, Ellesmere Island; Cassiope tetragona Community type of Kojima (1999) from Sverdrup Pass, Ellesmere Island.

"Polar desert complex"

In addition to the three alliances discussed above, "polar desert complex" may be discussed here. This complex does not have any particular characteristic species of vascular plants with high dominancy except Salix arctica. Other species such as Papaver lapponicum, Saxifraga caespitosa, Cerastium regelii, Cerastium arcticum (incl. alpinum) may often associate with this complex though their coverage is not necessarily high. This is a vegetation complex to represent a typical polar desert landscape. Species diversity is low, so is the vegetative cover of vascular species as usually less than 5%, though cryptogams particularly some lichens may show comparatively high coverage. Physiognomy is typically desolate polar desert landscape with widely scattered small patches of Salix arctica interwoven with other components. It develops in xeric habitats of exposed ridge tops, upper slopes, terraces, plateaus and level topography. Substrate consists of various types of material, including glacial deposits, shattered rocks, mass wasting, sorted stone plains and talus deposits. Habitats are excessively drained. Soils are coarse-textured and generally highly calcareous. There is a tendency that occurrence of the complex is more localized in the central to western part of the High Arctic of Canada, particularly in the western to central part of the Queen Elizabeth Islands.

This complex may include the following vegetation types variously described: Saxifraga-Salix Community of Woo and Zoltai (1977) from Somerset and Prince of Wales Islands; Dryas Barren Subtype of Zoltai et al. (1981) from Axel Heiberg Island; the clusters 3,4,5,7 of Sheard and Geale (1983) from Bathurst Island; Saxifraga oppositifolia-Salix arctica type of Kojima (1991) from Cornwallis Island; Saxifraga oppositifolia-Luzula based Community of Batten and Svoboda (1994) from Alexandra Fiord, Ellesmere Island.

Order II. Caricetalia stantis Kojima 1991 (cf. Caricetalia fuscae Barrett, 1972)

The Caricetalia stantis is characterized best by the presence and high dominance of *Carex stans*. It represents vegetation of poorly drained hygric to hydric habitats of lowlands and is widely distributed throughout the High Arctic of Canada. Physiognomically, it represents sedge and graminoid meadows developing in topographical flats and depressions. This order consists of one alliance.

Alliance 4. Caricion stantis Kojima 1991 (=Caricion aquatilis Barrett, 1972)

The Caricion stantis represents vegetation occurring in poorly drained habitats. Floristically, it is a very distinct vegetation unit characterized best by Carex stans. Other major characteristic species include Juncus biglumis, Polygonum viviparum, Saxifraga cernua, Melandrium apetalum, Eriophorum scheuchzeri, E. triste, and Pedicularis hirsuta. Vegetative cover is high as it attains 100% in most instances. Soils are always saturated with water and neutral to acidic in reaction. There is a tendency of peat accumulation at the top of the solum, if not very prominent. This alliance usually develops in a level

to slightly depressed topography of valley bottoms, terraces and plateaus. Because of lush growth of vegetation, such a landscape is often called "polar oasis" (Svoboda and Freedman, 1994).

This alliance incorporates the following vegetation types variously described: Carisetum stantis of Barrett (1972) from Devon Island; Carex-Drepanocladus Community Type of Woo and Zoltai (1977) from Somerset and Prince of Wales Islands; Sedge Meadow Subtype of Zoltai et al. (1981) from Axel Heiberg Island; the cluster 6 of Sheard and Geale (1983) from Bathurst Island; Carex aquatilis-Eriophorum triste meadow community type (nodum A) and Carex aquatilis meadow community type (nodum B) of Bergeron and Svoboda (1989) from Sverdrup Pass, Ellesmere Island; Carex stans type and Dupontia fisheri-Alopecurus alpinus type of Kojima (1991) from Cornwallis Island; Carex meadow Community of Batten and Svoboda (1994) from Alexandra Fiord, Ellesmere Island; Sedge-Cushion Plant-Dwarf Shrub (S-CP-DS) type of Muc et al. (1994) from Alexandra Fiord; Carex meadows, Dupontia meadows, and mixed graminoid meadows of Bliss and Gold (1994) from Truelove Lowland, Devon Island; Alopecurus alpinus Community type and Carex aquatilis ssp. stans Community type of Kojima (1999) from Sverdrup Pass, Ellesmere Island.

5. Discussions

5.1. Environmental characteristics of the alliances

Table 4 summarizes characterizing features of the five syntaxonomical units of the alliance level. Figure 3 provides some aspects as to soil pH of the Canadian High Arctic in relation to the syntaxonomical units. Figure 4 shows a differentiation pattern of the units in relation to edaphic conditions based on the field observations and soil analysis.

The "polar desert complex" is generally recognized in excessively well-drained xeric habitats of exposed ridge tops, terraces and upper slopes. Because of the prevalent occurrence of calcareous geology in the High Arctic of Canada and slow process of soil leaching, soils are highly calcareous as soil pH is as high as 8.0 or more. Papaverion lapponici develops in fairly similar habitats to the "polar desert complex", but in a more wide range of habitat conditions. In this alliance soils are also calcareous as pH is usually more than 7.0. Dryado-Salicion arcticae represents mesic habitats of the moderately drained. Here, total vegetative cover is high and species diversity is moderate. It develops in soils slightly alkaline to circum-neutral as soil pH is about 7.0. This is the alliance to represent the mesic and mesotrophic habitats, hence, zonal phytogeocoenoses. A plant association "Dryado-Salicetum arcticae", as we may designate it provisionally, which belongs to this alliance may represent the zonal vegetation of the Canadian High Arctic. Cassiopion tetragonae develops in mesic habitats at slope base or slightly concave topography predominantly of north aspect, where snow tends to accumulate to form late snowbeds. In such a habitat, soils are more easily eluviated and leached due to the percolation of melting water. Consequence of this is an acidification of soil. In fact, most soils associated with this alliance are acidic as soil pH is less than 7.0 (Barrett, 1972; Kojima, 1999). In this alliance, vegetative cover is usually as high as 100%. Caricion stantis is a clearly distinguished type of vegetation

Table 4. General characteristics of the alliances including the polar desert complex.

		general geographical	corresponding	
Alliance	physiognomy	distribution in Canada	bioclimatic	habitat conditions
			zonation of CAVM	
1. "Polar desert complex"	polar desert	central Hihg Arctic	mainly Subzone A	well-drained habitats of ridges and terraces
	(IVD2)*		,	with highly calcareous substrates
2. Papaverion lapponici	polar desert	throughout entire area	Subzones A, B, C	well drained habitats of ridges, terraces and
	(IVD2)*			upper slopes with highly to moderately
				calcareous substrates
3. Dryado- Salicion arcticae	Polar semi-desert,	Polar semi-desert, throughout entire area	Subzones A, B, C	well to moderately drained mesic habitats
	mesic meadow			of highly to moderately calcareous
	(IVD2)*			substrates
4. Cassiopion tetragonae	Arctic heath,	eastern High Arctic	mainly Subzone C	moderately drained mesic habitats of slope
	mesic meadow			bases and concave topography associated
	(IVB3)*			with snowbeds, with neutral to weakly
				acidic substrates
5. Caricion stantis	sedge meadow	throughout entire area	Subzones A, B, C	poorly drained habitats of valley bottoms
	(VD1b)*			and flood plains with stagnant water, with
				circum-neutral to weakly acidic substrates

* Physiognomic ecological classification code of plant formations (Mueller-Dombois & Ellenberg, 1974)

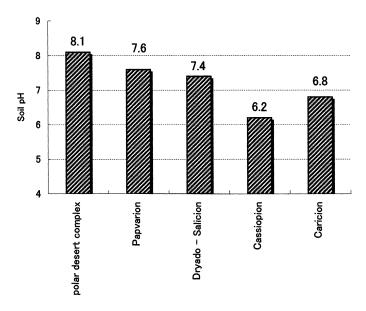


Fig. 3. Soil pH of the five syntaxonomical units at the alliance level. The numerals above the bars indicate averages of pH (source: Barrett, 1972; Batten and Svoboda, 1994; Kojima, 1999).

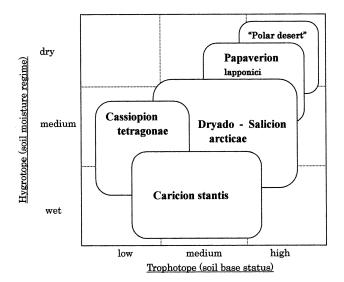


Fig. 4. An idealized scheme showing differentiation of the five syntaxonomical units in relation to edaphic conditions.

characterized by a distinct combination of characteristic species. It develops in poorly drained hygric habitats in valley bottoms, depressions, and alluvial sites. Soils are always saturated with water. Thickness of active layer ranges 30 to 50 cm approximately. Peat accumulation at the top of the solum is also characteristic. Vegetative cover is very high as it attains 100% in most instances.

Throughout the entire High Arctic of Canada, Papaverion lapponici, Dryado-Salicion arcticae, and Caricion stantis are the best representatives of the phytogeocoenoses of xeric, mesic and hygric habitats, respectively. Figure 5 illustrates biogeoclimatic processes to differentiate and establish the syntaxonomical units in the Canadian High Arctic.

The alliances of Papaverion lapponici, Dryado-Salicion arcticae and Cassiopion tetragonae described above may look like representing a successional trend from the initial to advanced, respectively. In fact, Okitsu *et al.* (2004), studying the vegetation development after deglaciation in Ellesmere Island, recognized that the *Cassiope tetragona* dominated communities would represent an advanced stage of vegetation succession there. However, I consider that, in the present study, the alliances in addition to the "polar desert complex" all represent more or less well-developed and stable stages of vegetation succession and reflect different moisture regime of the habitat as shown in Fig. 4. Yet, the matter of *Cassiope*-dominating communities in the Canadian High Arctic will be discussed thoroughly in the succeeding section.

5.2. Distribution pattern of the vegetation

In terms of geographical distribution of the syntaxonomical units, they are not necessarily distributed evenly throughout the High Arctic of Canada. Some alliances have a wide range of distribution whereas others are localized.

Edlund (1983) divided the Queen Elizabeth Islands into four bioclimatic zones based on life-forms, species diversity, and presence and abundance of indicator species. Zone 1 is the least diversified zone while zone 4 the most diversified in vascular species. Vegetative cover also follows the similar tendency as zone 1 shows the lowest cover and zone 4 highest. Edlund provided a map that showed an approximate geographical extent of the zones. She explained the differentiation of the zones primarily on the basis of thermal regime especially of warmth of growing season. Zone 1 is located in the harshest climatic environment and zone 4 in the mild environment comparatively. If we correlate the alliances of this article with Edlund's bioclimatic zones, alliances 1, 2 and 4 occur in the entire Queen Elizabeth Islands while "Polar desert complex" occurs primarily in the zones 1 and 2, and the alliance 3 in the zones 3 and 4 of the eastern High Arctic.

CAVM Team (2003) compiled and published a circumpolar arctic vegetation map. In the map, the entire Arctic of the world was classified into five subzones (A to E) in an order of environmental harshness from subzone A to E. In accordance with the system, "polar desert complex" of this study appears to be mainly associated with the Subzone A, and the alliance 3 with the Subzone C. Other alliances occur indiscriminately in any of the subzones recognized in the High Arctic of Canada.

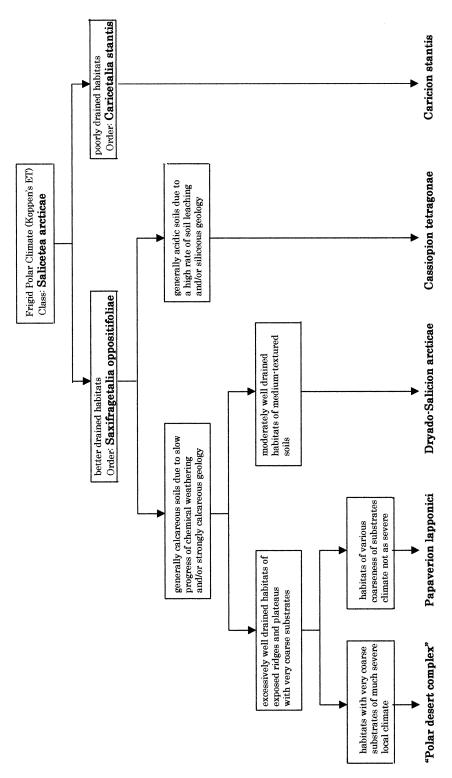


Fig. 5. A scheme of biogeoclimatic processes to differentiate and establish the syntaxonomical hierarchy in the Canadian High Arctic.

5.3. Problem of Cassiope tetragona

One of the interesting features of High Arctic vegetation of Canada is the problem of Cassiope tetragona. It is a species widely distributed in the circumpolar Arctic and northern high elevations (Hultén, 1968). It is known to be chionophilous and acidophilous. The Cassiope-dominating communities develop better in the Subarctic environment than in the High Arctic (Bliss and Matveyeva, 1992). In the High Arctic their occurrences are rather limited to such areas where climate is comparatively mild and humid with more precipitation that provides more snow. Indeed, the species is usually associated with snowbed habitats (Savile, 1972; Svoboda, 1977; Brooke and Kojima, 1985; Nams and Freedman, 1994). This seems to be the prime factor to get the Cassiopion tetragonae well established in the eastern part of the High Arctic of Canada, i.e., in Edlund's bioclimatic zones 3 and 4 and also in the Subzones B and C of CAVM. Those are the areas which enable the dwarf shrub communities to get established (Edlund, 1983).

Conrad (1946) proposed a method to assess continentality of climate based on temperature and latitude of the weather station. Figure 6 shows the geographical pattern of Conrad's continentality index and its isolines in the Arctic Canada. The east slopes of Ellesmere Island and Devon Island are characterized by relatively low continentality index, *i.e.*, less than 50. It becomes even further lowered down to less than 40 in the east coast of Baffin Island. These are the areas called "Arctic Cordillera"

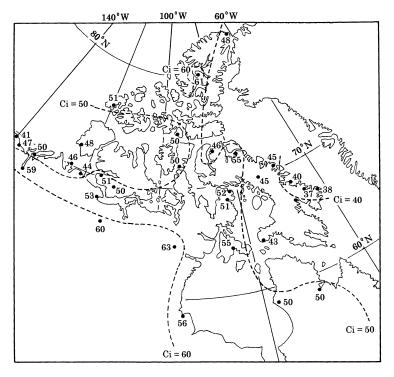


Fig. 6. Distribution of Conrad's continentality index (Ci) in the High Arctic of Canada with isolines of the index.

of Terrestrial Ecozone of Canada (Wiken, 1986) or "HAo: Oceanic High Arctic" of CCELC (1989) and these are where Cassiopion tetragonae is commonly recognized. Low continentality index implies relatively high amount of snow and a high rate of soil leaching to result in a formation of acidic soils. If parent material is siliceous rock, then soil acidification will be more pronounced. Interaction of the relatively mild and humid climate and siliceous substrates would generate acidic soil environment to a fair extent. Such soils are favorable to *Cassiope tetragona*. Indeed, soils associated with *Cassiope*-dominating communities are generally low in pH with averages of 5.2 (Muc et al., 1994) and 6.2 (Kojima, 1999). In such habitats, a possibility of a better supply of soil nitrogen is also suggested (Bowman et al., 2003).

In the areas of western part of Ellesmere Island, Axel Heiberg Island, and most of the Queen Elizabeth Islands, the continentality index is very high, *i.e.* more than 50 and up to 61 at Eureka. These areas are designated as "Northern Arctic" of Terrestrial Ecozone of Canada (Wiken, 1986) or "HA (incl. HAo at some areas)" of CCELC (1989). There climate is harshest and driest in the Canadian High Arctic. Such a high continentality and the extreme frigid climate appear to be the main reason that discourages the development of Cassiopion tetragonae.

5.4. Correlation of the Canadian High Arctic vegetation with that of Svalbard

Svalbard Archipelago is an excellent contrast to the High Arctic of Canada in vegetation and environment. It is located in the far north, off the northern Scandinavia in between Greenland and Novaya Zemlya. Latitudinally, it extends roughly from 76°30′N to 80°45′N. It is categorized as High Arctic (Bliss, 1979). Phytosociology of Svalbard has been thoroughly studied (see Thannheiser and Möller, 1992) and

Table 5. Major alliances of Svalbard and their habitat conditions (Hartmann, 1980; Elvebakk, 1994).

Habitat	Alliance
Polar desert	Papaverion dahliani Hoffman 1968, em Elvebakk 1985
Exposed ridges	Caricion nardinae Nordhagen 1935
	Luzulion arcuatae Elvebakk 1985
	Dryadion octopetalae Hartmann 1980
Mesic plains and slopes	Caricion nardinae Nordhagen 1935
Snowbeds	Luzulion nivalis Nordhagen 1936
	Luzulion arcuatae Elvebakk 1985
	Ranunculo—Oxyrion Nordhagen 1936
	Drepanoclado-Poion alpinae Hadac 1946
	Polytrichion norvegici Gjaerevoll 1949
Tundra mires	Eriophorion scheuchzeri Hadac 1939
	Ranuculo hyperborei-Drepanocladion revolventis Phillipi 1973
	Luzulion nivalis Nordhagen 1936
	Cardamino nymanii-Saxifragion foliolosae Hadac 1989
Bird cliff	Cerastio-Saxifragion cernuae Hartmann 1980
Sedimentation plain	Eriophorion scheuchzeri Hadac 1939
Strand habitat	Honkynyo peploides—Elymilion arenarii Galiano 1959
Anthropogenic habitats	Cochlerariopsion groenlandicae Hadac 1989

Region	Canada	Svalbard
Alliance	Dryado-Salicion arcticae	Caricion nardinae Nordhagen 1935
Association	Dryado-Salicetum arcticae	Cassiopo-Dryadetum octopetalae Ronning 1965
Major characterizing	* Saxifraga oppositifolia	Saxifraga oppositifolia
species	Carex misandra	Carex misandra
	Carex rupestris	Carex rupestris
	Oxyria digyna	Oxyria digyna
	Pedicularis hirsuta	Pedicularis hirsuta
	** Salix arctica	Salix polaris
	Dryas integrifolia	Dryas octopetala
	*** Stellaria longipes	Cassiope tetragona
	Carex nardina	Luzula arctica
Averaged soil pH of	7.7 (Barrett, 1972)	4.5 (Hartmann, 1980)
rhizosphere	7.7 (Walker and Peters, 1977)	5.8 (Kojima, 2004)
	6.4 (Muc et al., 1994)	
	7.6 (Kojima, 1999)	

Table 6. Species composition and soil pH aspects of the zonal phytogeocoenoses of the Canadian High Arctic and Svalbard.

syntaxonomical status has become known to a great extent, which is well summarized by Rønning (1969), Hartmann (1980) and Elvebakk (1985, 1994) (Table 5). A comprehensive treatise was published (Möller, 2000).

Out of many alliances, those developing in mesic habitats may be considered as the best representative, *i.e.*, zonal phytogeocoenoses. When we compare the structure of the zonal vegetation of Canada and Svalbard (Table 6), perhaps, the most striking difference is a presence/absence of *Cassiope tetragona*. The species is quite abundant and characterizing best the zonal vegetation in Svalbard (Hartmann, 1980; Elvebakk, 1985; Eberle *et al.*, 1993; Thannheiser, 1994, 1995; Kojima, 2004). However, it is practically missing in the zonal vegetation of the Canadian High Arctic, as I discussed.

This fact may be explained by the biogeoclimatic characteristics of the two regions. A fundamental environmental difference between the two regions is climatic characteristics. Climate of Svalbard is highly oceanic. Conrad's continentality index for Svalbard is, indeed, extremely low as it is 26, 21, and 15 for Ny-Ålesund, Longyearbyen and Barentsburg, respectively. On the other hand, it is substantially high in the Canadian Arctic (see Fig. 6). Such a high oceanicity of climate of Svalbard results in a higher rate of soil leaching. The consequence of this is a progress of soil acidification. If lithological characteristics are the same, soils in Svalbard should be lower in base status. This would be the prime factor of why *Cassiope tetragona* is so common in mesic habitats in Svalbard. Soils associated with the *Cassiope tetragona* communities in Svalbard are usually acidic as pH ranges from 4 to 6 (Hartmann, 1980; Kojima, 2004). At the same time, soils are kept fairly moistened most of the growing season. The species is designated as euryhygrotopic mesophyte (Kojima and Wada, 1999). In the Canadian High Arctic, occurrence of the species is generally restricted to the snow bed habitats where soils are well leached and low in base status. This would be the main

^{*} Common species to both regions, ** vicariant species, *** differential species.

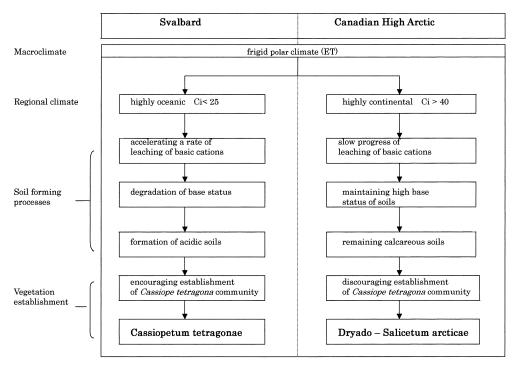


Fig. 7. A scheme of biogeoclimatic processes to substantiate the zonal phytogeocoenoses of the Canadian High Arctic and Svalbard (Ci: Conrad's continentality index).

reason why the *Cassiope tetragona* communities better develop in the eastern High Arctic where the climate is substantially oceanic. Figure 7 illustrates a summary of biogeoclimatic processes to differentiate and substantiate the zonal phytogeocoenoses in the Canadian High Arctic and Svalbard.

The relationship of *Dryas integrifolia* and *D. octopetala* may also be explained by the same fashion. In the High Arctic of Canada, *Dryas integrifolia* occurs exclusively while *D. octopetala* is the only *Dryas* in Svalbard. However, these two species occur widely together in northwestern North America mainly in the Subarctic and mountain regions. *Dryas integrifolia* is usually found in calcareous habitats and *D. octopetala* in noncalcareous acidic habitats. In the Subarctic, climate is milder and more humid. Snow accumulation is greater there than in the High Arctic. Such climate would promote acidification of soils by removing basic cations. *Dryas octopetala* seems to be well adapted to such an environment (Brooke and Kojima, 1985). In this respect, beside the historical background of evolution of the flora (Böcher, 1951), the environment of Svalbard seems to be better fitted to the ecological character of the species to get the species widely established.

Saxifraga oppositifolia is another intriguing species. It is one of the most ubiquitous species in the circumpolar Arctic including northern high mountain regions (Hultén, 1968). Although it tends to be associated with calcareous habitats (Acock, 1940; Brooke and Kojima, 1985), because of its extremely wide geographical range, it

should be well adapted to various environmental characteristics by differentiating ecotypes. It is known that there are two types of growth forms for this species, *i.e.*, cushion form and prostrate form (Rønning, 1996). From my field observations, majority of the Canadian High Arctic populations of the species seemingly exhibit a cushion form whereas those of Svalbard show more often prostrate form. Kume *et al.* (1999) studied the ecological significance of the two types of growth form and concluded that the cushion form is better adapted to drought condition and efficient in sexual reproduction, hence, well adapted to harsh environment especially in the early stage of succession. These traits of the cushion form plants are more advantageous in the Canadian High Arctic where climate is generally much harsher and habitats are more open than in Svalbard. This explains prevalent occurrences of cushion form in the Canadian High Arctic.

6. Concluding remarks

Fundamental environmental difference between the Canadian High Arctic and Svalbard may be the macroclimatic characteristics. Climate of the Canadian High Arctic is highly continental whereas that of Svalbard is strongly oceanic as shown by the Conrad's continentality index. Such climatic difference determines a course of soil development in the respective regions and subsequently promotes development of its own zonal soil and vegetation. In Svalbard, soils are generally moist and acidic in mesic habitats because of the higher rate of soil leaching under the oceanic climate. Accumulation of soil organic matter is higher here. Such a soil condition may be best manifested by the Caricion nardinae in which Cassiope tetragona is a dominant and characterizing species. On the contrary, in the Canadian High Arctic where climate is highly continental, soils are generally strongly calcareous even in the mesic habitats due to the lesser rate of soil leaching. There the zonal vegetation may be best represented by the Dryado-Salicion arcticae which is well fitted to the continental arctic climate and concomitant soils of high base status. In conclusion, it may be said that the aforementioned climate-soil-vegetation interactions regulate the course of zonal phytogeocoenoses development and to determine biogeoclimatic characteristics differently to the Canadian High Arctic and Svalbard. From the phytosociological point of view, the vegetation of the Canadian High Arctic is best represented by the Dryado-Salicion arcticae, more specifically by Dryado-Slicetum arcticae, whereas that of Svalbard by the Caricion nardinae, in particular by Cassiopo tetragonae-Dryadetum octopetalae.

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