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On the ecology and plant-sociology of "melur"-vegetation in Iceland*)

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ABSTRACT: The most common vegetation type in the desert-like landscapes of the Central Highlands of Iceland ("melur"-vegetation in Icelandic) is described by means of the BRAUN-BLANQUET plant-sociological method. Beside the association *Cardaminopsio-Armerietum maritimae* three sub-associations of the *Armerio-Silenetum acaulis* Hadac 1972 can be distinguished (*Thymus praecox-Galium normanii*-sub-association, *Stereocaulon*-sub-association, *Carex maritima*-sub-association). These very sparse phytocoena are connected with ecotopes the geo-ecological conditions of which are determined by the specific soil-arid properties as for instance a high infiltration and percolation rate and very low soil-water capacity. The relationship of the "melur"-associations and their position in a geo-ecological range are discussed, too.

INTRODUCTION

"Melur" (plural: "melar") is the Icelandic expression for a sandy, gravelly hill with very little vegetation cover. This term is the Icelandic common name for *Leymus arenarius* as well (LÖVE 1970, p.118). In the most important previous works on the vegetation of Iceland this word is used to describe the vegetation that "occurs at the top and on the ridges of the moraine walls" (MÖLHOLM HANSEN 1930, p. 102) or on gravel flats (STEINDÓRSSON 1945, p. 461). Whereas in those works the approach is essentially that of the Raunkiaer method (STEINDÓRSSON 1968, p.1) and therefore a comparison to Middle European vegetation classification is rather difficult, it is attempted in this paper to present this vegetation type that is very widespread in the Icelandic highlands by means of the BRAUN-BLANQUET method and by characterization of the specific geo-ecological conditions of its ecotopes.

First, however, the physio-geographical milieu of the region should be illustrated briefly.

PHYSIO-GEOGRAPHICAL MILIEU

The area where "melur"-vegetation is the most common vegetation type, and with which this paper is concerned, is situated in

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*) Nomenclature follows LÖVE (1970). - Determinations of mosses and lichens by herbarium material of the Museum of Natural History in Akureyri, North Iceland.

the Central Highlands of Iceland, generally higher than about 300 m above sea level. The substratum is of volcanic origin both of Holocene time, deposited as ash and eruptiva (tephra), and of Pleistocene time, built up by palagonite, palagonite breccia, and reworked as ground-moraine cover. In the shape of relief steep-walled table mountains alternate with more smoothened palagonite ridges that are orientated in the dominant tectonic lineaments, and with depressions in between filled up with glacial and fluvio-glacial sediments. Except for some glacier-fed rivers, the hydrological situation in the ecotopes and smaller ecotope sociations is determined by seasonal running rivulets and creeks fed by snow-melt water during a short period of the year.

The climatic conditions depend on the position of Iceland close to the polar circle in the North of the Atlantic Ocean and its circulations of water and air masses, and on the altitude of the central parts of the country. The transitional region between the peripheral lowlands and the highlands is characterized by the change from Cfc- to ET-climate (KÖPPEN's classification); most of the highlands have ET-, some even EF-climate conditions.

The annual precipitation decreases from the South-west and South (average about 1000 mm/year) to the North-east where due to the foehn effect north of Vatnajökull, only about 300 mm/year are reached. There, north of Vatnajökull, in "Ódáðahraun" an annual climatological water balance deficit occurs; potential evapotranspiration is 1.5 to 2 times higher than precipitation (EINARSSON 1972).

The annual temperature averages range between about +2.5°C in the transitional areas of the highlands and about -1°C in the central parts. Though the highlands are already more continental the annual temperature ranges of only 15-16°C still show the oceanic influence.

In the highlands the growing season (climatological definition: number of days with day mean temperature above +5°C) lasts only about two months, whereas this period is in the lowlands not far off two months longer. Beyond this the heat sum during the growing season is with about 130°C only one third to one fifth of the sum that is reached in lowlands (VENZKE 1982b, p. 44-46) and much more variable (VENZKE 1984, p. 329-331). The relation of temperature, precipitation, and potential evapotranspiration as well as the duration of the growing season are shown diagrammatically in fig. 1.

Referring to the frost climate this region can be characterized by more than 200 days with frost per year, and sums of negative degree days of less than -600°C x day in winter, less than -150°C x day in autumn, and less than -100°C x day in spring (LIEBRICHT 1983).

During historical time ecologically unsuitable range management with sheep has led to vegetation degradation and partly extinction, and soil erosion in many parts of the country (FRIDRIKSSON 1972, PREUSSER 1974, THORARINSSON 1962). These desert-like landscapes can be distinguished into deserts of natural origin (primary deserts) and of anthropo-zoogenic origin (secondary deserts) (VENZKE 1984a, 1984b); they are covered mostly by the very open and sparse "melur"-vegetation. In the Vegetation Map of Iceland (scale 1:40.000), however, these regions are declared as "Land without vegetation".

PEDO-ECOLOGICAL CONDITIONS OF "MELUR"-ECOTOPES.

The ecotopes of "melur"-vegetation as part of the landscape system of the Central Highlands of Iceland are mainly determined by their edaphic conditions. Briefly summarized the soil properties and their relevance for some other geo-ecological compartments of the system can be characterized as follows (ref. VENZKE 1982c):

In general the texture of the morainic or volcano-eolian substrata is middle sandy to sandy-gravelly, silty accumulations may occur here and there. This leads to a great saturated water conductivity that causes a high infiltration and percolation rate of the summer precipitation and the melting waters in spring. The conductivity co-efficient ranges between 0.30 and 8.00 x 10^{-2} cm/sec. Surface run-off and the associated fluvial morpho-dynamic processes therefore do not happen during the seasons of the year without frost in the soil.

The total porous volume is relatively low (50-60 vol.%), and the large pores (>50 µm pore diameter) make up more than 50% of the whole porous volume. These large pores do not keep any water at field capacity, the water storage of the soil is very low and amounts only 5-10% between pF 1.8 and 4.2. Very often the soil water of the upper 5-cm-layer of the substratum is evaporated during dry and windy weather conditions. Then the water content decreases to less than 2%, and the water tension below 4.2, so that seedlings and young plants with a shallow root system suffer extremely of insufficient soil water supply.

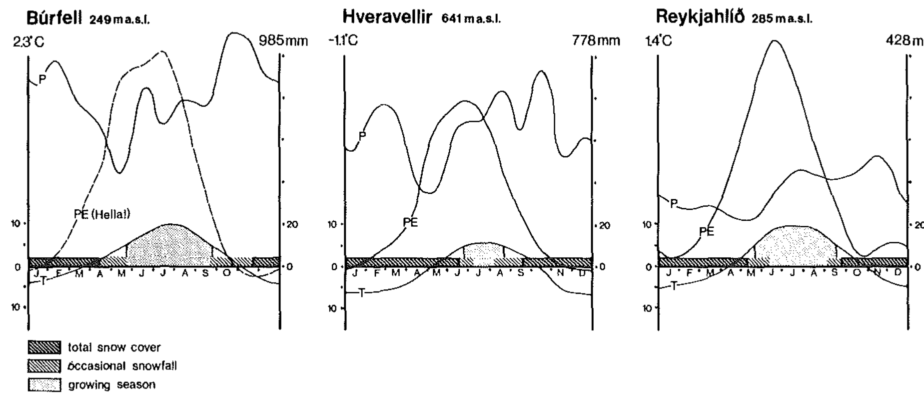

Fig. 1: Climatological diagrams of Búrfell (Southern transitional belt of the Central Highlands), Hveravellir (Central Highlands), and Reykjahlíð (Northern transitional belt).

These properties cause the phenomenon of soil aridity though the climate is generally rather humid. SCHWARZBACH (1963 and 1964) calls the landscapes characterized by soil aridity and related morpho-dynamic and vegetation conditions "edaphisch bedingte oder begünstigte Wüsten" (edaphically caused or favoured deserts).

Furthermore the soil shows a very little content of organic matter and very low rate of nitrogen net mineralization (0.9-4.7 mg NH_4^+/100 g soil and 3.1-9.3 mg NO_3^-/100 g soil; VENZKE 1982b, p. 33), too. As JÓHANNESSON (1960, p. 57) supposes and STREUBING & KNEIDING (1975) confirm the extremely little content of phosphorous restricts the life of edaphon very much. Because of the largely basaltic parent substratum the pH, in spite of the leaching soil water, is not too low and makes up about pH 5-6.

The dominant soil types are regosolic resp. lithosolic soils, here and there where some organic matter is accumulated a very small $A_{(h)}$-horizon may be developed. There the expression "råmark" can be used especially if there are traces of frost action like sorting of material or micro-solifluction.

THE "MELUR"-VEGETATION AS SUBJECT IN THE MAIN PREVIOUS WORKS*)

The habitats where "melur"-vegetation occurs are described by MÖLHOLM-HANSEN (1930, p. 102) as with a "slight or no snow-covering, solifluction, and bare gravelly or stony soil". Though the only vegetation analyses he had made on "melur" were taken near Úlfsvatn on Arnarvatnsheiði at about 500 m above sea level, the ecotopes seem to be similar to those this paper is dealing with and are described above. The floristic structure of MÖLHOLM-HANSEN's "melur", however, is quite different to what STEINDÓRSSON (1945) calls "melur" and this paper is going to call as well. MÖLHOLM-HANSENS's vegetation type is dominated by chamaephytes (52.5 cover %) and reminds with the most frequent species *Polygonum viviparum, Salix herbacea, Luzula spicata, Silene acaulis,* and *Juncus trifidus* of snow-patch vegetation, which indeed occurs very often together with "melur"-vegetation - mostly in a wind eroded and disturbed manner. Within the group of species some are missing, that are essential components of STEINDÓRSSON's and the author's definition of "melur", for example *Silene vulgaris.*

STEINDÓRSSON (1945, p. 461 ff.) gives another floristic definition of "melur" calling *Silene acaulis, Armeria maritima, Arabis petraea, Cerastium alpinum, Saxifraga oppositifolia, Salix herbacea,* and *Poa glauca* the most frequent phanerogams. He also refers to the fact that "melur" can be so poor in species and individuals, that it leads to "complete desert" (p. 462). STEINDÓRSSON has investigated and described within the "formation" of "melur" the (1) *Salix herbacea-Polygonum viviparum* - association, the (2) *Salix herbacea-Elyna Bellardi-Polygonum viviparum* - ass., the (3) *Salix herbacea-Dryas octopetala* - ass., the (4) *Salix herbacea-Saxifraga oppositifolia* - ass., the (5) *Salix herbacea-Poa glauca* - ass., and the (6) *Silene acaulis* - ass. In his last compilation of Icelandic plant-sociations (STEINDÓRSSON 1974) he divides the "melar"-vegetation into 26 "sociations" (most proba-

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*) Sometimes the cited floristic references follow another nomenclature than the author does.

bly in the DU RIETZ-sense), but, however, without any plant-sociological characterization. In this compilation only the *Armeria vulgaris-Cardaminopsis petraea* - sociation, the *Cardaminopsis petraea-Festuca rubra* - soc., and within the so-called "sandur"-formation - the *Silene maritima-Armeria vulgaris* - soc. seem to be close to what later on in this paper is called "melur"-vegetation.

Some other investigators have been occupied with smaller studies on the vegetation of the Icelandic highlands for example LAMPRECHT (1930), ANDERSON & FALK (1935), FALK (1940), and FRIDRIKSSON (1963). McVEAN (1955) and HADAC (1972) studied "melur"-vegetation in lowland regions.

ANDERSON & FALK (1935, p. 414) describe hilltop vegetation in the Kverkfjöll area as composed of *Cerastium alpinum, Silene acaulis, Saxifraga oppositifolia, S. decipiens, S. nivalis, Oxyria digyna, Salix herbacea, Poa alpina* and *Rhacomitrium canescens*.

FALK (1940, p. 23), investigating Mount Snæfell, compares the scree vegetation dominated by *Ranunculus glacialis* and with occasional abundance of *Oxyria digyna, Sedum roseum, S. villosum, Arabis petraea, Draba alpina, Saxifraga groenlandica,* and *S. nivalis* with the vegetation of moraines of Switzerland.

LAMBRECHT (1930, p. 120) itemizes *Salix herbacea, Cerastium alpinum, Silene maritima, S. acaulis, Viscaria alpina, Arabis petraea, Empetrum nigrum, Saxifraga oppositifolia, Armeria vulgaris, Thymus serpyllum, Galium silvestre,* and *Achillea millefolia* as characteristic for the vegetation of the deserted landscapes of Eastern Ódáðahraun.

McVEAN (1955) presents two relevés (p. 337) from lowland sites of Eastern Iceland on "melar" using the BRAUN-BLANQUET method. He calls the vegetation type "open *Dryas* heath". Though the vegetation covers there only 50 resp. 10%, which is very characteristic for "melur"-vegetation, several species are listed that - to the author's knowledge - are rather untypical for "melur" - sites, i.e. *Alchemilla alpina, Erigeron borealis, Leontodon autumnalis, Potentilla crantzii,* and most of the cryptogams. McVEAN's community is a typical heath vegetation but no "melur".

HADAC (1972) has investigated intensively the vegetation of the Reykjanes peninsula and describes "melar"-vegetation as part of the fell-field vegetation. He defines the association *Armerio-Silenetum acaulis* within the sub-alliance *Armerio-Juncion trifidi* by means of the BRAUN-BLANQUET method. The most constant species in his relevés are *Armeria maritima, Thymus praecox,* and *Silene acaulis* (V). *Cardaminopsis petraea* reaches only a constancy of IV, and *Silene maritima* only III. However, the list of species and their frequency resp. constancy corresponds very much with the author's relevés which are mostly taken in the Central Highlands where the landscape is much more dominated by "melur"-vegetation.

From this review on the use of the term "melur"-vegetation it might be clear that the cited authors partly define their "melur"-vegetation type quite different. In general "melur"-vegetation can only be a collective name for different associations of a plant-sociological system. The most important ones, especially in the Central Highlands, and their relationship to other vegetation types that may occur in "melur"-vegetation, are presented in the following chapters.

PLANT-SOCIOLOGICAL STRUCTURE OF "MELUR"-VEGETATION BY OWN RELEVÉS.

During the field seasons 1979, 1980, and 1983 about 280 relevés have been taken in different parts of the Central Highlands and other desert-like areas of Iceland using the BRAUN-BLANQUET method and estimating cover and sociability (BRAUN-BLANQUET 1964). In table 1 a collection of relevés are put together, the locations of which are shown in fig. 2.

Three species are so very frequent and constant and - beyond this - typical in their combination that they should get the function as character species. To my knowledge in no other vegetation type of Iceland *Cardaminopsis petraea, Armeria maritima,* and *Silene vulgaris* together have such a great frequency as in the "melur"-formation. *Cardaminopsis petraea* does nearly nowhere else occur but in this very sparse vegetation with more than 50-80% bare soil. The rosettes of this crucifer are often very hidden among the small stones of the stone pavement at the soil surface. *Armeria maritima* and *Silene vulgaris* are also to be found in some other vegetation types, especially in beach and sea shore

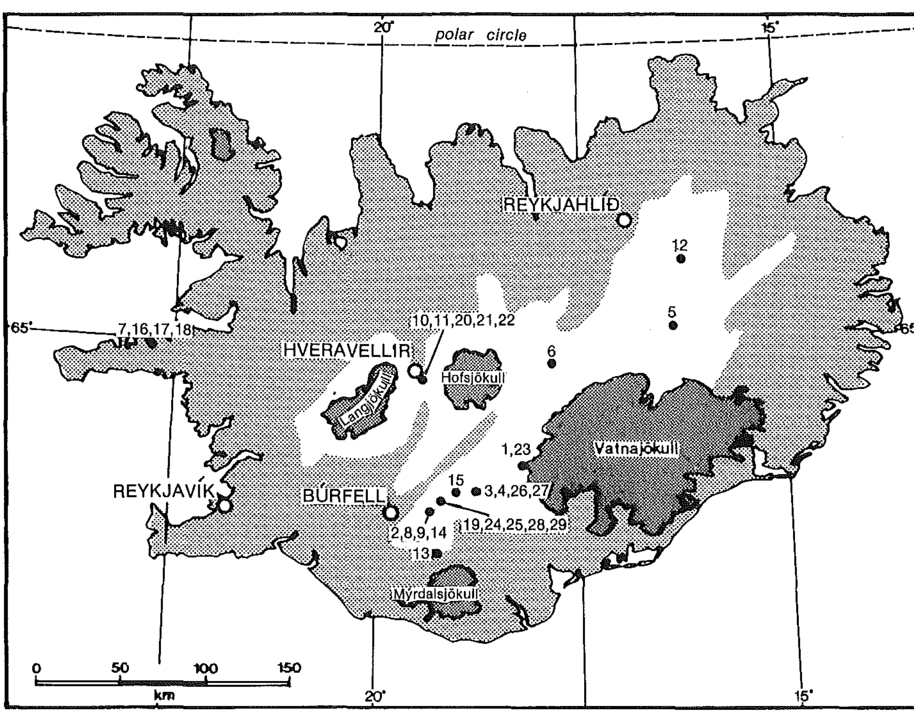

Fig. 2: Iceland. Black points with figures = locations of relevés of the plant-sociological table. Open circles (Reykjahlíð, Hveravellir, Búrfell) = locations of climatological stations (ref. fig.1). Dark grey = glaciers. White areas = areas of the Central Highlands showing more or less primarily deserted landscapes with "melur"-vegetation. However, all over the country, there are "melur"-sites, especially in secondarily deserted areas.

formations. *Armeria maritima*, for instance, is known to be salt tolerant. However, those formations are characterized distinctly by other species (FRIDRIKSSON, RICHTER & BJARNASON 1970 and HADAC 1970). *Silene vulgaris* is furthermore very characteristic for the vegetation of dunes, but there in combination with *Leymus arenarius* and *Festuca rubra* (TÜXEN 1970). Both occurrences in other vegetation types show already their ecological relationship to the "melur"-vegetation. Because of the high frequency and sociability of these three species characterizing the "melur" I should like to call the association *Cardaminopsio-Armerietum maritimae* (ref. relevés 1 to 6, table 1). The three named species - together with *Cerastium alpinum* and *Leymus arenarius* - seem to show the greatest resistance to the endangering morpho-dynamic processes, especially to wind erosion.

The association can be found without any other accompanying species (ref. relevés 1-4), sometimes at least one or two others, especially *Silene acaulis, Festuca rubra* or *Cerastium alpinum*, occur together with the character species, however. The table of relevés - compared with that one of HADAC's *Armerio-Silenetum acauli* (HADAC 1972, p. 351) - shows that there is great affinity to the described *Cardaminopsio-Armerietum maritimae*. Easily both associations could be put together to one association because they share the same character species except *Silene acaulis*. The author would propose to take *Cardaminopsis petraea, Armeria maritima,* and *Silene vulgaris* as character species for a joint association with four sub-associations. But, as the *Armerio-Silenetum acaulis* is already defined, this name has priority and will be used furthermore.

In the following the *Armerio-Silenetum acaulis* is divided into three sub-associations (*Thymus praecox-Galium Normanii* - sub-ass., *Stereocaulon* - sub-ass., *Carex maritima* - sub-ass.) which can be distinguished by means of differential species (ref. relevés 7 to 29, table 1).

The sub-association of *Thymus praecox, Galium Normanii*, and *Festuca vivipara* (ref. relevés 7 to 15) settles at the most favourable habitats within the generally harsh conditioned "melur"-ecotopes. The amount of silty material here is greater, and therefore the soil water supply is better than in the *Cardaminopsio-Armerietum maritimae* or in the two other sub-associations. This fact is documented, too, by the greater number of companions, especially grasses, that are using the uppermost layer of substratum for their root system. Here the competition pressure of grasses against the other herbs is greatest and the transition to grass-dominated associations is clearest.

The sub-association of lichens of the *Stereocaulon* family (most probably *St. arcticum* and *St. vesuvianum*) (ref. relevés 16 to 22) takes a place in the ecological ranges of *Armerio-Silenetum acaulis* that is characterized by a very stony and gravelly substratum surface. The lichens mostly colonize only the bigger stones and do not have any contact to the sandy or silty soil. They use - beside the air humidity - the moisture collected in the porous space inside the lava stones frozen up from sedimentated lava surfaces (VENZKE 1982b). It seems that this sub-association is absent from areas of heavy catabatic and foehn wind influence with dry air masses and intensive eolian morphodynamics, for example north of Vatnajökull. This corresponds to the humid and sandblast-free conditions that STEINDÓRSSON (1945,

p. 451) describes for the *Rhacomitrium* Heath; *Racomitrium canescens*, however, shows a very high resistance to desiccation (ABEL 1956).

The sub-association of Carex maritima occurs very rarely and is connected mostly with more sandy substratum within stone pavements areas. Beside the most frequent companions *Silene acaulis* and *Cerastium alpinum*, only *Leymus arenarius* may occur. This shows already the connection to the vegetation of larger sand accumulations and dunes which are dominated by grasses like *Leymus arenarius* and *Festuca rubra* (ref. vegetation relevés of Hans BÖTTCHER in TÜXEN 1970). From the eastern parts of the Central Highlands such sandy habitat phytocoenoses with *Festuca rubra* and *Calamagrostis neglecta* are described briefly by STEINDÓRSSON (1945). *Carex maritima*, however, is mostly known from coastal habitats where it may be associated with *Juncus balticus* (*Carici maritimae-Juncus baltici* VAN DEN BERGHEN 1969) (DIERSSEN 1977). The morpho-dynamic instability of the surface (deflation or oversanding), which is for instance tolerated by *Carex maritima* and *Leymus arenarius* quite well, is the reason for the absence of most of the accompanying species that can be found in the other sub-associations.

SOME VEGETATION ECOLOGICAL ASPECTS OF "MELUR"-VEGETATION

Most of the companions of the *Cardaminopsis petraea*-group (character species of *Cardaminopsio-Armerietum maritima* and *Armerio-Silenetum acaulis*) appear in tundra-like vegetation above the natural timberline, especially, however, in the so-called "*Rhacomitrium* Heath" (JÓNSDÓTTIR SVANE 1963) (*Cerastium alpinum, Luzula spicata, Saxifraga caespitosa*, and *Carex Bigelowii*). The connection to this kind of moss heath is demonstrated by the occasional occurrences of spots of *Racomitrium canescens*, too. Some grasses, for example *Poa glauca* and *Agrostis stolonifera*, do not have a special connection to any vegetation type; Festuca rubra, however, serves as character species of the *Molinio-Arrhenatheretea* (TÜXEN & BÖTTCHER 1969).

Pogonatum urnigerum, the other moss, is very hidden in the loose, gravelly surface and seems to get most of its needed moisture not from water in between the grains, but from the intragrain porous space of volcanic eruptiva.

Table 1. Locations and dates of relevés.

1, 23: Jökulheimar (Aug. 23, 1983). - 2: North of Sauðafell (Hekla pumice, Jul. 4, 1980). - 3: West of Þóristindur (stone pavement, Jul. 1, 1980). - 4: Northwest of Þóristindur (stone pavement, Jul. 1, 1980). - 5: 10 km south of Herðubreiðarlindir (pumice on lava, stone pavement, Jul. 27, 1979). - 6: Sandbúðir/Sprengisandur (Jul. 30, 1980). - 7, 16: South of Kothraunskúla/Northern Snæfellsnes (Jul. 13, 1979). - 8, 9, 14: Nýjahraun/northeast of Hekla (Jul. 4, 1980). - 10: South of Rjúpnafell/Hveravellir (Aug. 2, 1980). - 12: 12 km south of Hrossaborg (sserir-like stone pavement, Jul. 22, 1980). -13: Southwest of Álftavatn/south of Torfatindur (Aug. 30, 1980. - 15: Northeast of Sigalda (Jul. 1, 1980). - 17, 18: South of Kothraunskúla/Northern Snæfellsnes (Jun. 10, 1980). - 19, 24, 25, 28, 29: South of Sigalda fremri/north of Einbúi (Jul. 1, 1980. - 20, 21: North of Rjúpnafell/Hveravellir (Stone pavement, Aug. 2, 1980). - 26, 27: West of Þóristindur (Jul. 1, 1980).

Table 1. Plant-sociological table of *Cardaminopsio-Armerietum maritimae* and *Armerio-Silenetum acaulis* (so called "melur"-vegetation).

		Cardaminopsio-Armerietum maritimae						*Armerio-Silenetum acaulis*																						
								Thymus praecox - sub-ass.									*Stereocaulon* - sub-ass.							*Carex maritima* - sub-ass.						
	No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
	Area (m2)	100	200	250	50	100	25	100	80	50	50	100	25	10	100	100	50	50	50	5	100	100	100	100	50	60	5	300	25	10
	Altitude a.s.l. (m)	672	250	550	570	869	510	45	370	410	640	650	440	440	570	520	45	50	50	510	615	615	615	672	510	510	570	570	510	510
	Number of species	2	3	3	3	7	9	8	10	10	11	11	11	12	12	12	4	5	7	7	8	10	11	4	6	7	4	5	5	6
	Ch.Ass.																													
V	Cardaminopsis petraea	+.1	r	+.1	+.1	+.1	r	1.1	+.1	+.1	r	+.1	+.1	+.1	r	+.1	+.1	+.1	+.1	+.1	+.1	+.1	+.1	+.1	+.1	+.1	r	+.1	+.1	r
IV	Armeria maritima	r	r	+.1	+.2	+.1	r	r	+.1		r	1.2	+.1	r	+.1	+.1	r	r	r	+.1	+.1	+.1	+.2	+.1	+.1	+.1	+.2	+.1	+.1	r
IV	Silene vulgaris		r	+.1	r	r	r	+.1	+.1		+.1	+.1	+.1	+.1	+.2	+.1	r		r	+.1		r	r	r	r	r	r	r	r	+.1
IV	Silene acaulis						+.1	+.1	+.2	+.2	+.2	+.2	+.2	+.1	r	+.2		r		+.2	+.2	+.2	+.2		+.2	+.2			+.2	+.2
	D. Sub-ass.																													
II	Thymus praecox								+.2	+.1	+.2	r	r	r		+.2														
II	Galium normanii							r	r	r			+.1	+.2	r	+.1														
II	Festuca vivipara										+.1	r	r	r	r	r							r							
	D. Sub-ass.																													
II	Ste aocaulon spec.*)																1.1	2.2	+.1	+.2	1.2	+.2	+.1		+.2	+.2				
	D. Sub-ass.																													
II	Carex maritima																							+.2	+.2	+.2	1.3	+.2	1.2	+.2
	Companions																													
III	Cerastium alpinum					+.1	r		r	r	r	r	r	r	r	+.1				r	+.1	r	+.1			+.1		+.1		
II	Festuca rubra						r	+.1	+.1	+.1		+.2	+.1	+.1	+.1	+.1						+.1	+.1							
II	Luzula spicata						r	+.1		r			+.1	+.1	+.1	+.1					+.1	r	+.1							
II	Poa glauca								+.1	r			+.1		+.1	+.1				+.1		+.1								
II	Acetosa pratensis										r	+.1							r		+.1	+.1	+.1							
I	Poa alpina					r					+.1	+.2											r							
I	Saxifraga caespitosa									r				r	r	+.1														
I	Saxifraga oppositifolia					+.1	r			+.2																				
I	Arenaria norvegica					+.1					r	r																		
I	Pogonatum urnigerum						r		r										r											
I	Papaver relictum							+.1										r												
I	Racomitrium canescens																		r			+.1°								
I	Equisetum arvense										r																			
I	Carex bigelowii													r																
I	Agrostis stolonifera														r															
I	Leymus arenarius																													1.3

*) Most probably Stereocaulon arcticum and St. vesuvianum

Several plants put to "melur"-vegetation by MÖLHOLM-HANSEN, STEINDÓRSSON and McVEAN like *Salix herbacea, Polygonum viviparum,* and *Dryas octopetala* can not be verified by the own analyses. Most probably the often very close neighbourhood of eroded snow-patch vegetation and "real" "melur"-vegetation in secondary deserts leads to interferences of species in the surveys.

Three strategies for sufficient soil water supply can be distinguished:

(1) the very small hemi-cryptophytes like *Cardaminopsis petraea* are rooted in the shallow lenses of finer grain-sized (silty) material which is very often to be found below the stones of the stone pavement. These silts and fine sands are first blown onto the surface by the wind and afterwards washed in and accumulated below the stones, where they are protected against re-deflation, and provide a higher soil water content.

(2) The cushion plants or chamaephytes like *Silene acaulis* drive on their very long root system into greater depths to exploit the soil water which is not affected by evaporation. It may be pointed out that the cushion life form in open vegetation types is not only optimal because of the micro-climatic conditions it creates, but also because of the influence it exerts on the soil. SCHINNER (1982), investigating cushion plants of the alpine belt in the Austrian Alps (for example *Silene acaulis*), found that in the soil beneath cushion plants there are much more bacteria and a greater activity of cellulase, xylanase, and urease, which results in a higher litter mineralization rate, a greater CO_2-productivity, and a greater content of nitrate in the soil. These micro-biological conditions which are more favourable than in the bare soil near by, guarantee a much better nutrient supply for the single plants. Nevertheless, the amount of litter of the vegetation is low and mostly blown away by the strong winds, so that the organic matter that can be mineralized is extremely low. This cut-off of the nutrient cycle may be one reason for a stop of succession to higher developed vegetation types as for example SCHWARZENBACH (1960, p.57) suggests for the so-called "arctic steppe" of Northern Greenland's arid regions.

(3) Grasses like *Festuca rubra* or *Agrostis stolonifera* build up a root felt about 5-12 cm below the soil surface where it is not affected by evaporation, too. Here, however, the very quick percolating precipitation water can be used most efficiently. Whereas the seedlings of the non-grasses suffer very much from desiccation when they are rooted in the parching upper layer of the substratum during the first years, the grasses "conquer" this dangerous stratum from below by asexual young shoots.

Investigation on the productivity of "melur"-vegetation by means of determinations of phyto-mass per area in different regions (Þjórsárhraun, Sigalda, and Hverfjall) amount to 5-29 g dry phyto-mass/m² (resp. 0.05-0.29 t/ha) with up to 75% sub-surface parts (VENZKE 1982b, p.125-126). These very low figures reach the amount of above-surface phyto-mass that WIELGOLASKI (1972, p.302) cited for "polar semideserts" (40 g/m²) and "polar deserts" (6 g/m²); plant communities of sub-tropical deserts show such a low phyto-mass (0.5-0.75 t/ha) as well (GOUDIE & WILKINSON 1977, p.23).

The ecological characterization of the *Cardaminopsio-Armerietum maritimae* and, especially, the *Armerio-Silenetum acaulis* sites in general by means of the ecological values of the single species from Middle European and Alpine environments (ref. ELLENBERG 1979 and LANDOLT 1977) show that a lot of accompanying species have very low temperature figures (coldness indicators) (*Silene acaulis, Cerastium alpinum, Luzula spicata, Poa glauca, P. alpina, Saxifraga oppositifolia*). As well as this a very low nitrogen supply is indicated, too (*Silene vulgaris, S. acaulis, Cerastium alpinum, Luzula spicata, Poa glauca, Saxifraga oppositifolia*). Taking into account all the species that occur in the *Armerio-Silenetum acaulis* which have been investigated by LANDOLT and ELLENBERG in Central Europe the following indicator values for the *Thymus praecox*-sub-association (sub-association that is richest in species) can be calculated. The values are calculated by means of indicator values for the Swiss Alps (LANDOLT 1977, 5-value-scale), and in brackets the indicator values for Middle Europe (ELLENBERG 1979, 9-value-scale; there is no information on humus or aeration):

Humidity value	2.6 (4.4)	= dry-medium dry/damp soil
Temperature value	2.3 (2.7)	= subalpin/alpin and boreal
Reaction (pH) value	3.1 (6.3)	= weakly acid soils (pH 4.5-7.5)
Nutrient(esp. nitrogen) value	2.3 (2.8)	= poor soils
Light value	4.3 (7.8)	= full light conditions
Humus value	2.9	= average humus content (mull)
Dispersion (aeration) value	3.2	= permeable, gravelly, sandy soils

A comparison of these indicator values with the ecological behaviour of the species surveyed under Icelandic conditions does not show many important differences. Only the lack of humus in Icelandic sites is the main difference from the ecological conditions found in the alpine habitats of Switzerland. The *Cardaminopsio-Armerietum maritimae* and the *Armerio-Silenetum acaulis* thus can be described in general as plant-communities of extreme winter cold, often snow-free, summer dry, permeable, weakly acid biotopes poor in nutrients and humus. The Middle European and Swiss Alp ecological indicator values seem to be quite applicable for the use in this Icelandic plant-association as well.

ORIGIN OF THE *CARDAMINOPSIS-ARMERIETUM MARITIMAE* AND THE *ARMERIO-SILENETUM ACAULIS* AND RELATIONSHIPS TO OTHER PHYTOCOENA.

Some of the important plants of the "melur"-vegetation are also well-known from coastal sites. LINDROTH (1930/31, p.439) already points to the occurrence of *Silene vulgaris* and the salt tolerant *Armeria maritima* very high in the mountains and far away from the coasts. FRIDRIKSSON (1963) presumes that *Leymus arenarius* has followed the retreating glaciers from the coasts to the highlands already in Late Glacial times. These plants thus have passed a changing of biotope in the sense of the "geoökologisches Gesetz der relativen Standortkonstanz" (WALTER & WALTER 1953, 230).

In the highlands plants of coastal habitats have been associated with typical alpine plants like *Cardaminopsis petraea, Silene acaulis, Cerastium alpinum, Luzula spicata,* and *Saxifraga oppositifolia*. Most probably the amount of grasses has been much greater in former times. They have been extremely diminished by grazing sheep in historical times. Investigations on the preferences of range plants by sheep show that especially the gramineae and *Carex Bigelowii* are endangered by grazing (Gunnar ÓLAFSSON 1973). Fig. 3 shows the ecological ranges in between the *Cardaminopsio-Armerietum maritimae* and the sub-associations of *Armerio-Silenetum acaulis* ("melur"-vegetation). Furthermore the diagram may demonstrate that there are some close relations to other vegetation types in the ecological, floristic, and spatial neighbourhood.

The coarser the substratum becomes the more dominant the mosses (esp. *Racomitrium canescens*) are. Both vegetation types, "melur" and *Racomitrium* Heath, suffer from too little soil moisture; the moss cover on very coarse grained substratum and on lava as well, however, collects and stores precipitation, and thus can be a good inbedding for other flowering plants. These are very often from a *Salix herbacea-Bistorta vivipara-Juncus trifidus*-group that is characteristic for snow-patch vegetation, too. Very similar vegetation types - dominated by *Racomitrium canescens* and *Stereocaulon alpinum* - are described from just deglaciated habitats with dry soil in the Austrian Alps by JOCHIMSEN (1970 and 1975).

If the gravelly stone pavement surface turns to more rocky debris sites with sandy or silty matrix, there are shade, moist soil habitats settled by an *Oxyria digyna-Poa alpina*-association. Such a phytocoenose, that at least during the germination period is supplied by enough soil water, is also well known from young moraines in the Alps (JOCHIMSEN 1963, ELLENBERG 1978, p.585 ff.)

If the substratum turns to more sandy conditions where the *Carex maritima*-sub-association is favoured, the ecological affinity to "sandur"-vegetation is very close. This vegetation type is characterized especially by *Leymus arenarius* and the formation of dunes. STEINDÓRSSON (1945, p.458 ff.) distinguishes between two "sandur"-associations that are related to sandy and instable, mobile surface conditions with deep ground water table (*Elymus arenarius-Festuca rubra*-ass. and *Festuca rubra-Armeria vulgaris-Silene acaulis*-ass.). Similar plant-associations with *Festuca rubra, Agrostis stolonifera*, and *Equisetum arvense* are described by LÖTSCHERT (1974, p.17 ff.) from sand and pumice areas close to Mount Hekla in Southwest Iceland, formed by wind erosion and dust storms. TÜXEN (1970; see above) terms the dune vegetation rich in *Leymus arenarius*, he found in the Mödrudalur region in Northeast Iceland, the inland variant of a degenerated *Honckenya diffusae-Elymetum arenariae* lacking in typical coastal plants.

Thus, the Icelandic "melur"-vegetation with the *Cardaminopsio-Armerietum maritimae* and the sub-associations of *Armerio-Silenetum acaulis* includes floristic elements and settles biotopes that allots this special vegetation type to a plant-sociological and ecological position in between coastal dune and alpine resp. periglacial stone pavement, rock debris, and moraine vegetation.

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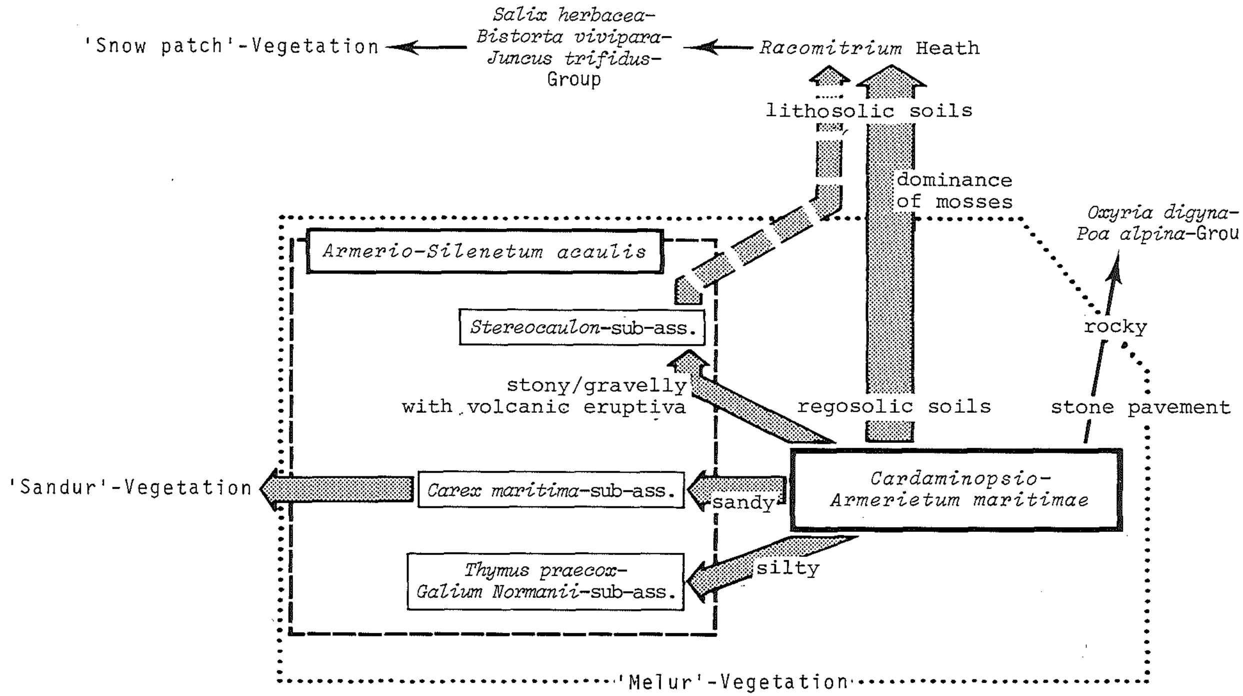

Fig. 3: Diagram of the ecological relationships between the *Cardaminopsio-Armerietum maritimae*, the sub-associations of the *Armerio-Silenetum acaulis*, and the vegetation types with spatial and ecological affinity.

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