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Vegetation units in the mountain areas of Scandinavia

By Rolf N o r d h a g e n , Oslo

(The following paper was read by the author before the Botanical Congress in Stockholm 1950. Photographical copies of the tables referred to below were then distributed to the audience. In the present paper the author has only had opportunity to publish the 3 first tables with some new additions from the last years field-work. Accordingly the reader has to seek out the remaining tables in my book «Sikilsdalen og Norges fjellbeiter» by means of their number and my references to the pages in the said book.)

About 35 years ago I started an investigation of the plant communities of the Norwegian mountains, from the subalpine belt up to the high-alpine belt. My intention was not only to study the vegetation units from a pure scientific point of view, but also with regard to their practical value. The pasture-land of our mountains has been used by farmers since the bronze-age, and to-day it is extremely important for the breeding and fattening of horses, sheep, young bulls and tame reindeer, and naturally for the grazing of dairy-cattle as cows and goats which are sent up to the mountains in summer, and for the wild reindeer.

Thanks to the deceased Norwegian ecologist Mrs. Hanna R e s - v o l l - H o l m s e n we had in 1920 some statistical knowledge concerning the constitution of the chief subalpine and alpine communities of Southern Norway, and the Swedish dissertations of Thore F r i e s (1913), T e n g w a l l (1920) and Harry S m i t h (1920) from the same decennium were also very important because the vegetation of Swedish Lapland and the Central Swedish Mountains is very similar to the Norwegian one. My first task was to procure statistical material from the plant-communities in question, and from as many mountain areas as possible.—Afterwards I tried to classify the lower units, and in the beginning (1928) I paid special attention to the life-forms of the dominating-physiognomic species, and operated with such higher units as f.i. thickets, dwarfshrub-heaths, grass and herb communities, mires etc. But very soon I found that such a grouping in many ways was unnatural, especially with regard to the ecological or causal side of the problems. Many distinct vegetation-units of great importance in the

landscape became separated in the system, in spite of obvious floristic and ecological conformity. The well known Scandinavian *Dryadetum octopetalae* on calcareous soils landed between the dwarfshrub communities, whereas the interesting *Kobresietum myosuroidis* had to be incorporated in the grass-herb-communities, in spite of the very great similarity between these two units in Scandinavia not only with regard to their constitution but also to their demands on soil, snow-cover, exposure, etc.

During excursions to North-Africa, the Alps and the Carpathian Mountains with professor J. Braun-Blanquet, professor W. Szafer and other prominent Middle-European ecologists, I had the opportunity to be introduced to the ideas of the so-called school of Zürich-Montpellier, to the floristic classification of vegetation units, the character species, the differential species, the fidelity and other concepts. When I came home again to my own mountains, I tried to apply these concepts to Norwegian vegetation. At first I met with numerous difficulties. The subalpine and alpine flora of Norway and Scandinavia as a whole is much poorer in vascular plant-species than f.i. the Alps. Enormous areas of our mountains are built up of hard, crystalline rocks of precambrian origin, very poor in lime and other basic minerals, and the vegetation of these extensive landscapes is composed of relatively few, easily contented phanerogams e. g. *Betula nana*, *Juniperus communis* var. *montana*, *Empetrum hermaphroditum*, *Vaccinium myrtillus*, *Vacc. vitis-idaea*, *Arctostaphylos uva-ursi*, *Juncus trifidus*, *Festuca ovina*, *Nardus stricta*, *Deschampsia flexuosa*, *Anthoxanthum alpinum*, *Alchemilla alpina*, *Carex Bigelowii*, *Salix herbacea*, *Cassiope hypnoides*, and a lot of lichens and mosses. The plant communities in these vast areas very often are dominated by one single or a few phanerogams, and it is difficult to point out so-called character-species. But the communities themselves are conspicuous and good enough. In this case the lower or basic vegetation units must be founded upon dominance alone, not only of phanerogams, but of lichens and mosses as well. These lower units are called *sociations* among Scandinavian ecologists. It is, however, possible to combine them

TABLE 1

Association: *Arctostaphyletum uvae-ursi alpicolum*

Alliance: *Loiseleurieto-Arctostaphylion*

Vi. = Örtterdal, Hardangervidda S.N. SKD. = Sikilsdal S.N. Trfj. = Tronfjell S.N. (after Du Rietz 1925). D. = Kongsvoll, Dovre S.N.
r = regional character species of the alliance. d = differential species
versus *Phyllodoco-Myrtillion*.

Sociations	Poor in cryptogams			<i>Alectoria ochr.</i> dominant			Transitory
Localities	Vi.	Skd.	Trfj.	Skd.	D.	Trfj.	Skd.
r <i>Arctostaphylos uva-ursi</i>	100 ⁵	100 ⁵ —	100 ⁵	100 ⁵	100 ⁵	100 ⁵	200 ⁴ —
<i>Vaccinium vitis-idaea</i>	100 ¹	92 ¹	82 ¹	100 ¹	100 ¹	100 ¹	70 ¹
— <i>uliginosum</i>	100 ²	100 ³	18 ¹	55 ¹	20 ¹	9 ¹	30 ³
<i>Empetrum hermaphroditum</i>	100 ¹	68 ¹	45 ¹	50 ¹	100 ³	9 ¹	—
<i>Festuca ovina</i>	100 ²	100 ²	91 ¹	100 ²	100 ²	100 ¹	100 ²
<i>Anthoxanthum alpinum</i>	—	40 ¹	—	5 ¹	—	—	97 ¹
<i>Euphrasia frigida</i>	—	100+	9 ¹	50+	—	—	67 ¹
<i>Campanula rotundifolia</i>	—	52 ¹	—	15+	50 ¹	—	83 ¹
d <i>Alectoria ochroleuca</i>	55 ¹	60 ¹	91 ¹	100 ⁴	100 ⁵	100 ⁵	—
d <i>Cetraria cucullata</i>	100 ¹	92 ¹	82 ¹	100 ¹	100 ¹	100 ¹	7 ¹
d — <i>nivalis</i>	95 ¹	76 ¹	64 ¹	100 ¹	60 ¹	100 ¹	10 ¹
— <i>islandica</i> coll.	55 ¹	64 ¹	54 ¹	95+	100 ¹	64 ¹	3 ¹
<i>Cladonia alpestris</i>	—	24 ¹	18 ¹	50+	60 ¹	100 ¹	10 ¹
— <i>gracilis</i> coll.	40 ¹	64 ¹	—	100 ¹	70 ¹	36 ¹	7 ¹
— <i>pyridata</i>	100 ¹	44+	18 ¹	100+	20 ¹	55 ¹	23 ¹
— <i>silvatica</i>	80 ¹	68 ¹	45 ¹	100 ¹	70 ¹	91 ¹	23 ¹
— <i>uncialis</i>	45 ¹	56+	9 ¹	100 ¹	60 ¹	36 ¹	7 ¹
<i>Peltigera malacea</i>	10 ¹	20 ¹	—	95 ¹	50 ¹	—	3 ¹
<i>Stereocaulon paschale</i>	—	68 ¹	18 ¹	100 ²	80 ¹	36 ¹	3 ¹
<i>Polytrichum piliferum</i>	35 ¹	48 ¹	—	100+	—	—	3 ¹
Medium vascular plant species pr. 1 m ²	5,8	10,4	4,7	5,8	7,2	4,1	17,6
Medium lichens and mosses species pr. 1 m ²	11,0	9,7	5,3	19,5	16,0	10,5	1,9
Number of quadrats and stands analysed	20 : 4	25 : 5	11 : 11	20 : 5	10 : 2	11 : 11	30 : 5

to units of a somewhat higher rank, associations, corresponding with the Middle-European associations (Nordhagen, 1943).

I should here like to call attention to table 1. It shows the results of statistical analyses of an association which I call *Arctostaphyletum uva-ursi alpicolum* and which is rather common on exposed moraines and more or less stable banks of soil formed by avalanchine materials in dry situation. I have as far seen 3 sociations belonging to this unit, one with unimportant cryptogams, one with a lot of *Alectoria ochroleuca* and some other very hardy lichens, and one pioneer-sociation on screes, which I call «transitory» (1943, p. 68—83). The different stands of the three sociations have been analysed by quadrats of 1 m², and in each quadrat the covering-degree of the different species has been estimated according to the 5 grades of Hult-Sernander. The columns marked Tronfjell I have compiled from a paper by Durietz printed in 1925. The stands very often are extremely homogenous. Usually *Empetrum hermaphroditum* plays a quite unimportant role in the stands, because *Arctostaphylos* is the stronger plant. But in certain districts, f.i. the Dovre-mountains (D.), *Empetrum* occurs as a subdominant. Next to the dwarf-shrubs only *Festuca ovina* is of some importance. The floristic «melody» of the sociations and the association as a whole is very monotonous. I have marked *Arctostaphylos uva-ursi* with the letter (r) because in the subalpine and lowalpine belt it is a regional character-species for this unit. The letter d, I'll explain in a moment. The association is xerophilous, acidophilous and chionophobic, it doesn't like a heavy or longlasting snow-cover in winter and spring, but an intermittent one. It becomes free of snow very early.

If we now proceed with table 2, one will there see the results of statistical investigations concerning another association which I have called *Loiseleurieto-Diapensietum* (1943, p. 64—68). In Norway this association consists of several rather feebly separable sociations. In districts where wild reindeer still exist or flocks of tame reindeer are kept by the peasants or lapps, these communities are grazed in winter because of the lichens, which accordingly decrease (cp. a in the table). In the most continental parts of Southern Norway, however, where reindeer

now are rare the lichens flourish, and *Loiseleuria procumbens* is here really handicapped. One only finds patches of the unit, either with dominating *Alectoria ochroleuca* or *Cetraria nivalis*. On wind-swept hills or moraines in suboceanic districts, however, the association is very widespread, and here *Empetrum hermaphroditum* increases in it. This is very evident in the Trollheimen district southwest of Trondheim.

One might call *Loiseleuria* a character species for this unit, *Arctostaphylos alpina* too, and this is also the case with *Diapensia lapponica* within the limits of its Scandinavian distribution. But their fidelity to the unit is not a very high one. They are not exclusive, but elective according to the nomenclature of Braun-Blanquet.

I must now refer to my book (1943). Its table No. 8 (p. 95) shows some very hardy *Betula nana*-*Empetrum* heaths from the continental areas of Southern Norway, extremely rich in lichens. Scattered in the stands one finds some individuals of *Loiseleuria*, *Arctostaphylos alpina* and *Arctostaphylos uva-ursi*.

In table 10 (p. 103) one finds the same monotonous floristic «melody», but here the dominating lichens are certain *Cladonia*-species, or the dominating cryptogam is *Dicranum fuscescens*. But a lot of the hardy lichens from table No. 8 are represented also in table No. 10. All these communities get rid of their snow-cover rather early in spring.

These low, creeping *Betula nana*-*Empetrum hermaphroditum*-sociations I have combined to a third association, *Empetretum*-*Betuletum nanae*. It very often occurs at rather high elevations, or in places where the *Arctostaphyletum uva-ursi* doesn't find optimal conditions, or where the *Loiseleurietum*-*Diapensietum* is out of the play because of the high vitality of the lichens.

In 1901—1902 the Swiss botanist Jaccard began to investigate the floristic interrelationship between certain types of alpine pastures. If an area A has 60 species of plants, and another area B has 50, but 30 of these species are common between A and B, Jaccard called the fraction

$$\frac{30}{60 + 50 - 30} = \frac{30}{80} = 37,5 \%$$

TABLE 2

Association: *Loiseleurieto-Diapsietum*

Alliance: *Loiseleurieto-Arctostaphylon*

Jd. = Skaiti, Junkerdal N.N. Skd. = Sikilsdal S.N. Trfj. = Tronfjell S.N. (after Du Rietz 1925). Vi. = Örterdal, Hardangervidda S.N. Syl. = Sylene S.N. FL. = Finnish Lapland (after Kalliola 1939). Th. = Trollheimen S.N. D = Kongsvoll, Dovre S.N. * = character species of the alliance. d = differential species versus *Phyllodoco-Myrtillion*.

Localities	Jd.	Skd.	Trfj.	Syl.	Vi.	FL.	Th.	D.
Sociations	a	d	c	b				
* <i>Loiseleuria procumbens</i>	100 ⁴	100 ³ +	100 ⁴ —	100 ⁵ —	100 ¹ +	100 ³	100 ⁵	100 ⁴ +
* <i>Diapensia lapponica</i>	100 ²	—	—	30 ²	—	89 ¹	100 ³	90 ²
* <i>Arctostaphylos alpina</i>	88 ¹	100 ²	9 ¹	75 ²	85 ²	89 ²	90 ²	90 ¹
<i>Empetrum hermaphroditum</i>	88 ¹	66 ¹	45 ¹	100 ³	100 ⁴	96 ³	100 ²	100 ²
<i>Vaccinium uliginosum</i>	100 ¹	100 ³	—	30 ¹	80 ¹	70 ¹	20 ¹	50 ¹
— <i>vitis-idaea</i>	—	25 ¹	100 ¹	95 ¹	45 ¹	93 ¹	80 ¹	100 ¹
<i>Betula nana</i> (prostrate)	75 ¹	—	45 ¹	85 ¹	70 ¹	85 ¹	50 ¹	90 ¹
<i>Festuca ovina</i>	—	42 ¹	—	10 ¹	15 ¹	15 ¹	—	50 ¹
d <i>Juncus trifidus</i>	100 ¹	66 ¹	—	55 ¹	—	89 ¹	100 ¹	70 ¹
<i>Carex Bigelowii</i>	38 ¹	17 +	45 ¹	80 ¹	35 ¹	33 ¹	80 ¹	30 ¹
d <i>Alectoria ochroleuca</i>	13 ¹	100 ⁵	100 ²	100 ²	100 ¹	67 ¹	100 ²	100 ³
d — <i>nigricans</i>	—	66 ¹	45 ¹	90 ¹	95 ¹	85 ¹	30 ¹	100 ¹
d <i>Cornicularia aculeata</i>	100 ¹	17 +	—	75 ¹	20 ¹	7 ¹	—	—
d — <i>divergens</i>	—	100 ¹	100 ¹	65 ¹	65 ¹	24 ¹	100 ¹	100 ¹
d <i>Cetraria cucullata</i>	—	100 ¹	100 ¹	85 ²	100 ¹	19 ¹	70 ¹	100 ¹
d — <i>nivalis</i>	100 ¹	100 ¹	100 ⁵	100 ³	100 ³	100 ²	100 ²	100 ⁴
— <i>islandica</i> coll.	100 ¹	100 ¹	100 ¹	100 ²	100 ¹	85 ¹	100 ¹	100 ¹
<i>Cladonia alpestris</i>	—	8 +	100 ²	—	5 ¹	4 ¹	—	20 ¹
— <i>rangiferina</i>	—	83 +	91 ¹	55 ¹	90 ¹	41 ¹	60 ¹	50 ¹
— <i>silvatica</i>	38 +	100 ¹	100 ²	100 ²	100 ²	52 ¹	90 ¹	100 ²
d — <i>alpicola</i>	—	8 ¹	9 ¹	20 ¹	50 ¹	—	—	—
— <i>coccifera</i>	38 +	42 ¹	73 ¹	95 ¹	85 ¹	15 ¹	50 ¹	40 ¹
— <i>gracilis</i> coll.	—	66 +	91 ¹	85 ¹	95 ¹	4 ¹	—	60 ¹
d <i>Ochrolechia frigida</i>	100 ³	17 +	18 ¹	100 ¹	100 ²	70 ¹	100 ²	100 ¹
<i>Solorina crocea</i>	50 ¹	42 ¹	—	60 ¹	25 ¹	37 ¹	90 ¹	—
d <i>Sphaerophorus globosus</i>	75 ¹	75 ¹	55 ¹	100 ¹	60 ¹	93 ¹	100 ¹	100 ¹
<i>Stereocaulon paschale</i>	75 ¹	100 ¹	64 ¹	95 ¹	20 ¹	41 ¹	90 ¹	70 ¹
d <i>Thamnotia vermicularis</i>	—	75 +	27 ¹	95 ¹	45 ¹	7 ¹	100 ¹	100 ¹
d <i>Gymnomitrium corallioides</i>	100 ⁵	17 ¹	—	25 ¹	5 ¹	37 ¹	100 ¹	70 ¹
<i>Anthelia Juratzkana</i>	100 ¹	8 +	—	—	—	37 ¹	20 ¹	—
<i>Dicranum fuscescens</i> coll.	—	75 +	—	40 ¹	85 ²	11 ¹	90 ¹	—
<i>Polytrichum juniperinum</i>	88 ¹	17 ¹	—	25 ¹	65 ¹	15 ¹	40 ¹	—
— <i>piliferum</i>	—	42 +	—	30 ¹	10 ¹	89 ¹	90 ¹	20 ¹
<i>Racomitrium hypnoides</i>	38 ¹	58 ¹	—	60 ¹	—	48 ¹	100 ¹	—
Medium vascular plant species pr. 1 m ² (4 m ²)	7,6	6,1	3,6	7,6	5,8	(10,3)	9,3	8,3
Number of quadrats and stands analysed	8 : 2	12 : 4	11 : 11	20 : 6	20 : 4	27 : 27	10 : 2	10 : 2

the Gemeinschaftskoeffizient, or the co-efficient of partnership. The computation of this co-efficient must, however, be based on exactly the same space from A and B because we now know that in all plant communities the total number of species increases with increasing space.

The quadrat-method which I have used, allows me to compute such co-efficients, f.i. for the hardy associations or sociations hitherto mentioned, and in my book (1943, p. 118—120) I have shown that they form an intimate chain of floristic interrelationship, with very high co-efficients.

This chain of subalpine and low-alpine dwarf-shrub communities I call an alliance (Verband), in accordance with the nomenclature of Braun-Blanquet. The character-species of the alliance are *Loiseleuria*, *Diapensia*, *Arctostaphylos alpina* and, regionally, *A. uva-ursi*. I call this alliance *Loiseleurieto-Arctostaphylion*, a name which was created by the Finnish ecologist Kalliola in 1939 in connection with his important investigations in Finnish Lapland. In 1936 I myself in the paper «Versuch einer neuen Einteilung der subalpinen-alpinen Vegetation Norwegens» used the name *Loisleurieto-Vaccinion*, but Kalliola's term is better, especially for practical purposes. In the tables mentioned so far, I have marked a great many plants with the letter *d*. This means that they are differential or distinguishing species between the said alliance and the next, very important one.

Let us now take a glance at the table 3, which contains in concentrated form the results of my extensive statistical analyses of the widespread *Vaccinium myrtillus*-heaths of the mountain districts of Southern Norway. Also in this case the floristic «melody» is very monotonous, but the number of species is greater, and the melody itself is a new one. Whereas the floristic setting of the alliance *Loiseleurieto-Arctostaphylion* is xerophilous, heliophilous and chionophobous, the *Vaccinium myrtillus*-heaths are distinctly more mesophilous and chionophilous. They require a solid and long-lasting snow-cover in winter and spring, and consequently occupy sheltered areas, either concavities in the landscape or the lee side of moraines and ridges. I have called this unit *Phyllo-*

TABLE 3

Association: *Phyllodoco-Vaccinietum myrtilli*

Alliance: *Phyllodoco-Myrtillion*

The localities are the same as in the preceding tables except M = Myrdal
(between Bergen and Finse).

Sociations	Continental <i>Myrtillus</i> -heath (without <i>Cornus suecica</i> ; very little <i>Hylocomium</i>)									Oceanic type (<i>Cornus</i> ; <i>Hylocom.</i>)		
Variants	<i>Phyllodoce</i> -variant	Main type					<i>Empetrum</i> -variant	<i>Dry-opt.</i> var.	<i>Clad.</i> var.	<i>Desch.</i> var.	<i>Phyl. lod.</i> var.	
Localities	D.	Vi.	Skd.	Syl.	Vi. N.	Vi. S.	Skd.	Vi.	Vi.	M.	M.	M.
d <i>Vaccinium myrtillus</i>	100 ⁴	100 ⁴	100 ⁵	100 ⁵	100 ⁵	100 ⁵	100 ¹	100 ⁴	100 ⁵	100 ⁵	100 ⁵	100 ⁴
* <i>Phyllodoce coerulea</i>	100 ⁴	100 ⁴	28 ³	27 ¹	—	—	70 ¹	—	—	20 ¹	60 ¹	100 ³
<i>Empetrum hermaphroditum</i>	100 ²	98 ²	76 ²	67 ¹	95 ²	70 ¹	100 ⁵	100 ⁵	80 ²	100 ⁴	100 ³	100 ³
<i>Vaccinium vitis-idaea</i>	30 ¹	50 ¹	76 ¹	52 ²	25 ¹	100 ²	100 ¹	100 ²	4 ¹	—	—	80 ²
— <i>uliginosum</i>	90 ²	45 ²	20 ¹	23 ¹	5 ¹	10 ¹	90 ²	30 ¹	64 ²	50 ¹	50 ²	100 ³
<i>Betula nana</i> (low)	30 ¹	53 ¹	44 ¹	35 ¹	23 ¹	—	100 ¹	—	16 ¹	—	—	—
d <i>Lycopodium alpinum</i>	60 ¹	43 ¹	20 ¹	67 ¹	5 ¹	—	—	30 ¹	—	—	—	—
<i>Salix herbacea</i>	20 ¹	100 ²	32 ¹	62 ²	85 ²	5 ¹	10 ¹	—	100 ³	50 ¹	100 ¹	60 ¹
d <i>Deschampsia flexuosa</i>	100 ²	100 ³	100 ²	100 ²	100 ²	100 ²	100 ¹	100 ²	100 ²	100 ²	100 ⁴	100 ³
<i>Carex Bigelowii</i>	30 ¹	80 ¹	84 ¹	100 ²	25 ¹	—	30 ¹	—	—	100 ²	—	—
<i>Festuca ovina</i>	10 ¹	20 ¹	28 ¹	—	45 ¹	100 ²	20 ¹	10 ¹	4 ¹	—	—	—
<i>Anthoxanthum alpinum</i>	—	25 ¹	40 ¹	—	—	15 ¹	—	—	68 ¹	—	80 ¹	50 ¹
d <i>Solidago virgaurea</i>	100 ¹	98 ¹	100 ¹	92 ¹	45 ¹	100 ¹	100 ¹	50 ¹	100 ¹	60 ¹	100 ¹	100 ¹
d <i>Trientalis europaea</i>	100 ¹	63 ¹	76 ¹	80 ¹	63 ¹	85 ¹	—	100 ¹	100 ²	30 ¹	—	40 ¹
<i>Pedicularis lapponica</i>	—	35 ¹	64 ¹	17 ¹	10 ¹	—	90 ¹	—	4 ¹	—	—	—
d <i>Hieracium alpinum</i> coll.	40 ¹	93 ¹	52 ¹	95 ¹	93 ¹	50 ¹	50 ¹	80 ¹	72 ¹	60 ¹	100 ¹	90 ¹
d <i>Melampyrum silvaticum</i>	10 ¹	—	16 ¹	—	—	—	—	—	32 ²	—	50 ¹	—
d <i>Dryopteris Linnaeana</i>	—	5 ¹	—	—	8 ¹	—	—	—	100 ²	—	50 ¹	—
d <i>Rumex acetosa</i>	70 ¹	5 ¹	85 ¹	12 ¹	18 ¹	20 ¹	10 ¹	40 ¹	84 ¹	—	—	10 ¹
d <i>Maianthemum bifolium</i>	—	—	—	—	—	—	—	—	20 ³	—	70 ¹	—
d <i>Pyrola minor</i>	40 ¹	3 ¹	28 ¹	12 ¹	5 ¹	—	—	—	40 ¹	—	40 ¹	10 ¹
d <i>Cornus suecica</i>	—	—	—	—	—	—	—	—	—	100 ¹	100 ³	100 ²
<i>Dicranum fuscescens</i>	}	100 ²	98 ²	100 ²	100 ²	100 ³	100 ²	100 ²	100 ⁴	100 ³	100 ²	100 ⁴
— <i>scoparium</i>		—	85 ¹	96 ¹	—	100 ¹	50 ¹	90 ¹	70 ¹	12 ¹	—	—
<i>Webera nutans</i>		—	38 ¹	32+	35 ¹	95 ¹	55 ²	40 ¹	20 ¹	12 ¹	—	100 ¹
<i>Polytrichum juniperinum</i>	—	—	12+	10 ¹	23 ²	10 ¹	—	—	—	100 ³	100 ¹	100 ³
<i>Pleurozium Schreberi</i>	—	—	40 ²	2 ¹	—	—	—	—	—	100 ²	50 ¹	100 ²
<i>Hylocomium splendens</i>	100 ³	58 ¹	84 ¹	75 ²	73 ²	65 ¹	50 ¹	90 ²	100 ²	} 100 ¹	100 ⁵	100 ³
d <i>Lophozia lycopodioides</i>	100 ¹	40 ¹	44 ¹	42 ¹	93 ¹	100 ¹	—	100 ¹	100 ²		100 ⁵	100 ³
— <i>Floerkei</i> + <i>Hatcheri</i>	—	30 ¹	15 ¹	—	5 ¹	35 ¹	—	10 ¹	—	10 ¹	70 ¹	100 ¹
<i>Ptilidium ciliare</i>	100 ¹	100 ³	100 ³	100 ³	100 ³	100 ³	100 ³	100 ³	96 ¹	100 ⁴	—	90 ¹
<i>Cladonia silvatica</i>	20 ¹	70 ¹	60 ¹	62 ¹	65 ¹	100 ¹	100 ¹	100 ²	32 ¹	100 ²	—	—
— <i>rangiferina</i>	—	60 ¹	60 ¹	100 ²	100 ¹	85 ¹	60 ¹	100 ¹	56 ¹	20 ¹	30 ¹	—
— <i>bellidiflora</i>	80 ¹	93 ¹	100 ¹	100 ¹	100 ¹	100 ¹	100 ¹	100 ¹	80 ¹	30 ¹	—	—
— <i>coccifera</i>	100 ¹	100 ¹	100 ¹	100 ³	100 ²	100 ²	100 ¹	100 ²	100 ¹	100 ¹	90 ¹	100 ¹
— <i>gracilis</i> coll.	40 ¹	73 ¹	88 ¹	97 ¹	100 ²	100 ¹	40 ¹	100 ¹	12 ¹	20 ¹	—	—
— <i>uncialis</i>	100 ¹	100 ²	100 ²	100 ²	100 ²	100 ¹	100 ¹	100 ¹	100 ¹	100 ²	100 ¹	100 ¹
<i>Cetraria islandica</i> coll.	—	10 ¹	32 ¹	2 ¹	20 ¹	—	100 ²	—	10 ¹	60 ²	—	80 ²
<i>Nephroma arcticum</i>	—	—	—	—	—	—	—	—	—	—	—	—
Medium vascular plant species pr. 1 m ²	13,3	12,9	16,0	10,2	7,8	10,2	12,5	7,7	13,2	7,8	12,5	12,1
Medium mosses and lichen species pr. 1 m ²	9,0	13,3	17,2	13,6	14,1	13,7	16,9	14,0	9,2	10,7	10,2	11,8
Number of quadrats and stands analysed	10:2	40:8	25:5	40:5	40:8	20:4	10:2	10:2	25:5	10:2	10:2	10:2

doco-Vaccinietum myrtilli. The association consists of several, but rather blurred sociations, however, with a distinct oceanic facies wherein *Cornus suecica* is represented on all quadrats. With the letter *d* I have marked a number of plants which are differential species versus the alliance Loiseleurieto-Arctostaphylion. The bulk of them are mesophilous herbs and grasses.

I must now again refer to my book from 1943. Table 18 (p. 145) shows a great many analyses of low thickets of *Betula nana* or *Juniperus communis* var. *montana* or both of them, with an undergrowth of a *Vaccinium myrtillus*-heath. These thickets occupy vast areas in the Norwegian low-alpine belt, occurring, however, in still more sheltered places than the pure *Myrtillus*-heaths, and often near the birch forest limit. I connect these communities under the association name Junipereto-Betuletum nanae myrtillosum. The floristic «melody» or the pattern is the same as in table No. 3 above, and it persists over very wide geographical areas. If one computes the co-efficient of partnership between these thickets and the pure *Myrtillus*-heaths on the basis of my statistical analyses one gets very high percentages (1943, p. 174). The lower units form again an intimate chain of interrelationship. This is indeed a good alliance. One might call *Vaccinium myrtillus* a regional character-species of the alliance, and according to my own experience, the beautiful *Phyllodoce coerulea* seems to be a real character-species of the alliance in so far as it never obtains such a vitality and such a density outside the alliance as inside it. But its ecological amplitude does not coincide with that of *Vaccinium myrtillus*, and it is only elective or preferent, not exclusive. I have called this alliance Phyllodoco-Vaccinion Myrtilli already in 1936, and I think the name is satisfactory.

In Sweden professor Du Rietz during the last decades has carried on the investigations inaugurated by Thore Fries, Tengwall and Smith. In two shorter papers published in 1942 Du Rietz has summarized his experience as to the classification of subalpine and alpine vegetation chiefly in Lapland, and the papers show that in many respects he has come to the same results as me in Norway. But as Du Rietz has not as yet

published statistics from the different units in Lapland, which is regrettable, it is difficult to discuss the interrelationship between these units and the South Scandinavian ones.

If we still concentrate our investigations on the mountains with hard crystalline rocks and their glacial or glacio-fluvial drift, we'll find that in depressions or grooves where the snow persists until, let us say, the end of June or in some years still later, the previously mentioned dwarf-shrubs disappear. The summer or rather the vegetation-period becomes too short for them. In such localities we are confronted with a series of interesting grass-communities. The most important units are exemplified in my book on table 40 (p. 256—257). They have been known very long. Already in 1902 the Swedish botanist Vestergrén thanks to his very important travels in Southern Lapland found out that these communities mirror the varied duration of the snow-cover. Later on statistical material has been collected not only by me, but also by Kalliola and Kalela in Finland, and Gjærevoll in Central Sweden. According to my opinion we have here a clearcut alliance Nardeto-Caricion Bigelowii (Nordhagen, 1936, p. 46) with at least 4, perhaps 5 associations. The physiognomically most important phanerogams are *Nardus stricta*, *Deschampsia flexuosa*, *Anthoxanthum alpinum*, *Alchemilla alpina* and *Carex Bigelowii*, sometimes *Lycopodium alpinum* and *Deschampsia atropurpurea*. According to my experience probably *Deschampsia atropurpurea* and perhaps *Carex brunnescens* are character-species of the alliance, at any rate elective or preferent. According to my opinion the name Nardeto-Caricion Bigelowii is absolutely satisfactory. A newer name, «Deschampsio-Anthoxanthion», proposed by Du Rietz, is an «empty» name because it doesn't tell us which *Deschampsia*-species are meant and because the *Anthoxanthum* in this case is not the low-land race of *odoratum*, but the *Anthoxanthum alpinum* Löve, with half the chromosome-number of *odoratum* proper. With the letter (h) I have marked hygrophilous species. The soil in these communities is rather wet during and after the disappearance of the snow-cover. But it usually dries up during July and August, the associations being only seasonal hygrophilous. With the letters (lo) I have

marked plant-species which have their ecological optimum in the real Schneetälchen communities. The interrelationship between the alliances Nardeto-Caricion Bigelowii and Cassiopeto-Salicion herbaceae is easily perceptible. The said alliance is of great importance as pasture for domestic animals; in fact the seeming dry *Carex Bigelowii* has turned out to be a first class pasture-plant if only it is grazed early in the season. The horses are extremely fond of it, the lemmings too. In the oceanic mountains of Southern Norway absolutely natural, low-alpine *Nardus*-grassheaths play a prominent role in the landscape. The line taxations which several Norwegian pasture advisers have performed in our mountains, following the vegetation system published by me in 1943, clearly show what a huge area these *Nardus*-communities are covering (cp. especially E. Vik, 1953). In contrast to the other associations of the alliance, the *Nardetum chionophilum* mihi gives a pasture fit for sheep only.

The time at my disposal forbids me to go into details in this case, but if one studies my book and the treatise published by O. Gjærevoll in *Acta Phytogeographica Suecica* 1949 (p. 42-55), one will get an impression of the composition, ecology and geographical distribution of this alliance, which forms one of the most striking features of the Scandinavian alpine vegetation. Its existence depends upon the undulating topography of our ice-eroded mountains, upon sufficient precipitation in winter, and the cool summer-climate which prevents strong evaporation. In stony localities it is replaced by interesting fern-communities with *Athyrium alpestre* or *Cryptogramma crispa* as the dominant species. They form an alliance of their own, *Cryptogrammo-Athyrium alpestris* (Nordhagen, 1936).

Between the Nardeto-Caricion Bigelowii and the alliance of Scandinavian Schneetälchen on soils poor in lime, the Cassiopeto-Salicion herbaceae (cp. table No. 46 in my book 1943, p. 285), plenty of intermediate stands are easily found in nature. In places where there is no afflux of running water our acidophilous Schneetälchen are very monotonous indeed, and it is rather difficult to separate sociations and associations. In the said table No. 46 I have delimited 3 units, *Salicetum*

herbaceae boreale, *Cassiopeetum hypnoidis* and *Luzuleto-Ranunculetum glacialis*, the last one being confined to very high levels. These communities are often difficult to analyse because of the many mosses, especially tiny liverworts, and crustaceous lichens which cover the ground between the low phanerogams. Without doubt important character and differential species are to be found among them, and I am glad to state the fact that my compatriot Mr. Olav Gjærevoll is working with a detailed treatise on this subject. There is only one way to follow here: to obtain statistical analyses from the whole range of the Scandinavian Mountain area, as I have tried to do myself until now.

Still more difficult to elucidate are the *Schneetälchen* communities influenced by running water, especially those on metamorphic cambro-silurian rocks, which dominate certain Scandinavian mountain areas. From table No. 48 in my book 1943 (p. 294—295) one will get an impression of the interesting floristic «melody» of these eutropheous communities, which are very important for wild and tame reindeer in the summer season, and for sheep. This group is separated from the *Cassiopeo-Salicion herbaceae* both by character-species and a lot of differential-species, but also united with the former by those species marked in the tables with the letters (lo). In 1936 I called the alliance *Ranunculeto-Oxyrion* and in 1943 divided it in two fractions (cp. table No. 48). In connection with the Stockholm Congress 1950 and the excursion to Lapland Mr. Gjærevoll has published a paper (guide) on the representatives of this intricate group in the Torne Träsk region. Instead of one alliance with 2 fractions, he operates with 6 groups. Time will show in how far this disunion is justified with regard to character- and differential-species and co-efficients of interrelationship.

The table No. 35 (1943, p. 223) gives a summary of my own investigations into the alliance *Juncion trifidiscaandinavicum*, the chief associations of which are the *Juncetum trifidi* and the *Festucetum ovinae alpicolum*. To get the right impression of the physiognomy and ecology of these dry looking units, one ought to take a trip to the high mountains of Southern and Central Norway. Here they are very important in

the middle alpine belt, above the realm of the dwarf-shrub-heaths. The xerophilous *Festucetum* is confined to high levels in our most continental districts, whereas the *Juncetum trifidi* is far more widespread. The character-species are few and rather doubtful, but a row of differential-species (d) enable us to draw a line between this alliance and f.i. the *Nardeto-Caricion Bigelowii*, respectively the *Cassiopeto-Salicion herbaceae*, which both occur in the middle-alpine belt, often forming intricate vegetation-complexes with the *Juncion trifidi*. This alliance is kept together by high co-efficients of interrelationship, which I have shown in my book. It is of great practical value as both horses and sheep feed on *Juncustrifidus* and *Festuca ovina*.

I must stop here. I could have spoken of the interesting calcicole communities of our mountains on dry, exposed ground, the alliance *Kobresieto-Dryadion* (1943, p. 573), or of the luxurious communities of tall herbs and grasses occurring on slopes with natural irrigation which I have called *Mulgedion alpini* (table No. 59, p. 383), and many other interesting features of Scandinavian Mountain vegetation. But I have here only tried to show that by means of statistical analyses, character-species, differential species, and co-efficients of interrelationship it is possible to arrange the lower units in chains of affinity. The higher units, the alliances, which have been established in this way, seem to me natural in as far as they clearly mirror the determining ecological factors e. g. the soil conditions, the exposure to wind, or the protection of the snow-cover, the shortening of the vegetation period in the Schneetälchen etc. In my book I have also tried to show that the higher units in Scandinavia clearly correspond with the chief higher units which f.i. Braun-Blanquet, Szafer and their collaborators have distinguished in Middle-Europe. The steeper topography and the stronger insolation in the Alps and the Carpathian Mountains, however, create a difference in as far as the hygrophilous and seasonal-hygrophilous groups are handicapped there, whereas they flourish in the Scandinavian mountains. The Schneetäl-

chen f. i. are far more important by us, and decidedly more difficult to elucidate.

In many cases the floristic similarity or relationship between the Middle-European and Scandinavian units of higher rank is very pronounced, which shows us that the alpine vegetation of Europe, in defiance of floristic diversity depending upon the different history of the local floras since the Tertiary, form an entirety in spite of all. Recent investigations by Danish ecologists in Greenland have shown that also the vegetation of this huge island link up with the Scandinavian. And according to letters which I recently have got from American ecologists at work in Canada and Alaska the regularity or lawfulness which has been ascertained within the subalpine and alpine vegetation of Scandinavia, seems to have its analogy or even homology in North American mountain districts.

I should like to conclude this fragmental lecture by expressing the hope that American ecologists in future will pay sufficient attention to the paramount role which the thickness of the snow-cover and its duration in spring and early summer play with regard to the local distribution and zonation of plant communities in alpine and arctic areas. Since the days of Kihlmann, J. M. Norman and Vestergrén, the influence of the snow-cover has been the leading motive in Fennoscandinavian ecological research within mountain areas. It was, however, first the deceased great Swedish ecologist Thore C. E. Fries, whom I regard as my teacher, who fully realized the importance of the snow-cover on all kinds of rocks and soils. Therefore I have dedicated my chief work (1943) to the memory of this outstanding personality who died in South Africa in 1936 only 44 years old.

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