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STUDIES ON THE PLANT GEOGRAPHY OF THE NORTH-ATLANTIC HEATH FORMATION

II. DANISH DWARF SHRUB COMMUNITIES IN RELATION TO THOSE OF NORTHERN EUROPE

BY

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CONTENTS

I. Introduction.

In the author's studies No. I (B. 1940), some of the most oceanic heaths (incl. moors) of north-western Europe, viz. those of the Faroes and western Norway, were described. Furthermore, heaths along the Atlantic coast of Europe were surveyed there. The present paper deals in particular with the heaths of Denmark; it contains some phytogeographical comparisons of the Danish with the alpine Scandinavian heaths as well as of the Danish heaths with the Dutch-German ones. Thus, studies I and II together tend to state a phytogeography of the dwarf shrub vegetation in the lowland of north-western Europe.

This work being especially phytogeographical, no great stress has been laid upon the ecology of the smallest vegetational units. In order to render the material amenable to ecologists and biologists, the paper is concluded by an index with references to those pages where the most important species or communities are mentioned in greater detail.

In the classification and division of the vegetation, similar principles to those advanced in B. 1940 are followed. On the basis of field studies (analysis of vegetation) and studies on the geographical ranges of the heath plants it is attempted to establish a number of geographical main heath types which may be further subdivided and collected into larger alliances and heath series also by means of distributional types. The series, the main types, and the different subtypes are held together by a number of guiding species (cf. MEUSEL's "Leitarten", 1939) belonging within each main type (series) to related distributional types.

The guiding species may be compared with, but must not be mistaken for, the character species employed by BRAUN-BLANQUET and others. A guiding species is used in a manner rather similar to the character species, however, it is based upon the range of the species as well as upon the degree of restriction ("fidelity") to a certain community or groups of communities[1].

It should be urged here that such geographical main types are not quite natural groups, since several ecologically related heath types belong to different main types. Thus, the dry alluvial *Empetrum*- or *Calluna-Empetrum* heaths belong to a northern type, while certain allied *Calluna* heaths from alluvial ground belong to a more

[1] Cf. the related conception of geographical "Differentialarten" (SCHWICKERATH 1940, 1942).

southern type. On the other hand, in most cases the geographical distribution of species may reflect some features of their ecology and, consequently, the main types are also to some extent ecological groups. Furthermore, it must be admitted that, as regards the ecology, none of the larger vegetational units defined by other scientists are much more uniform than our main types. With an increasing content of small units (sociations, societies, cf. DU RIETZ 1936) the larger units become less interesting from an ecological point of view. Moreover, it should be remembered that the main types constitute units of regional-geographical importance.

The use of guiding species and distributional types in the classification of the vegetation may often within the same large community be very important. The dry dwarf shrub heaths of Europe can thus be divided with the aid of distributional types, but it may not always be possible to separate woods from heaths nor dry heaths from wet heaths or bogs. The very Atlantic heaths of Europe contain a large number of oceanic species of dry as well as of wet heaths. Hence, it may be difficult to separate these communities by the distributional types. However, calculations performed e. g. on the basis of tables in LEMÉE's paper (1938) indicate that very oceanic wet and dry heaths also are different as regards their content of distributional types (cf. moreover, p. 119).

In the present paper, heath is defined as an Atlantic dwarf shrub formation and, thus, such dwarf shrub vegetations are generally excluded which are mainly characterized by continental or mediterranean species; on the other hand, heaths with a mixture of oceanic and continental species are included. The dwarf shrub vegetation is furthermore divided into two large groups, viz. the dry heath communities and the wet heath and bog communities.

II. Material and Methods.

The material used in the following was collected in the years 1933—1942 on journeys in Denmark and the Scandinavian peninsula. Only one large heath area (Randbøl Hede) was subjected to more detailed investigations (cf. B. 1941 a). On the other heath areas, most thorough attention was paid to such vegetations which are locally very characteristic or which show some interesting details.

The following journeys were undertaken[1]:

1) In 1933: Randbøl Hede, heaths at Ry in Jutland and at Rørvig on Sealand.
2) In 1934: Heaths at Gern, Viborg, Haderup, Flyndersø, Svinkløv, Bulbjerg, Hanstholm, Venø, Vind in Jutland, Dragsholm, Rørvig, and Gilleleje on Sealand.
3) In 1934: Heaths on Kullen and Halland Ås, at Torekov, on Tönnersjöhede and at Steninge in Halland. A very instructive excursion under the leadership of Professor

[1] Only longer journeys are mentioned.

E. du Rietz (Upsala). Furthermore, the heaths at Skanör were studied in collaboration with Fil. mag. Nils Dahlbeck, Stockholm.
4) In 1935: Heaths on the Faroes and in Norway (Bergen); cf. B. 1940.
5) In 1936: Heaths in Djursland-Mols (Jutland).
6) In 1936: Heaths in different areas of central and western Jutland. Experimental investigations on heath vegetation in relation to anthropogenic factors performed by Professor C. A. Jørgensen and the writer.
7) In 1937: Heaths as in 6). Moreover, Randbøl Hede was reinvestigated.
8) In 1937: Heaths in northern Jutland (Tolne, Gerum, etc., Skagens Odde).
9) In 1937: Heaths on Bornholm.
10) In 1938: Heaths as in 6). Reinvestigations on Randbøl Hede.
11) In 1938: Southern Norway, Sætesdalen, Haugesund, Karmöya, Mandal (cf. B. 1940).
12) In 1939: Danish dune heaths, Læsø; cf. B. 1941 b. Also Randbøl Hede and heaths mentioned in 6).
13) In 1940: As 6). Heaths on Sealand.
14) In 1941: Heaths on the peninsula Ulvshale on the Isle of Mön; cf. B. 1942.
15) In 1942: Heaths on Bornholm (Loc. 68) analyzed by members of an excursion arranged by the "Studenterraad" (Council of college members at the University of Copenhagen).

Journeys 1, 2, and 14 were rendered possible by grants from the Japetus Stenstrups Legat, and the journey to Læsø in 1939 by a grant from the Carlsberg Fund. The latter has also contributed to the costs of working up the material (determinations of lichens and bryophytes). I take the opportunity to express my sincere thanks to these two funds for their grants and to Mr. Aug. Hesselbo for the determination of many collections of mosses. Furthermore, my thanks are due to Professor C. A. Jørgensen for the permission to use some of the material collected in collaboration with him. Finally, I express my sincere thanks to Professor R. Tüxen (Hannover) for kindly lending me his card-index on heath literature.

The method used in the field work is mainly Raunkiær's method of frequency determination (cf. Raunkiær 1909—10, 1934 a) and, in particular, a modification of Raunkiær's method as described in B. 1935 and B. 1940, pp. 38—39. However, the figures thus obtained are published in a more concise form in the present treatise. In order to get narrower columns in the tables, the frequency is not indicated in per cent. When but ten sample areas are used, the calculations of percentage values are made by adding a zero, only. For the more frequent species (dominants and those from 60—90 %) two figures are given, the first one indicating the number of circular sample areas of 0.1 sq. m. and the second figure giving the number of such areas of 0.006 sq. m. which contain the species. A third figure indicating the minimum area (cf. earlier publications of B.) is omitted. The figures 10_3 mean that the species is constant (F % 100) within the large circles (0.1 sq. m.) and is found three times (F % 30) in the small circles (0.006 sq. m.). The average density of its shoots is determined by the chord$_3$ to the large circle (30.9 cm.). The shoots of a species denoted by the values 10_{10} are very much denser; in this case, the average shoot density is 7.7 cm. (k_3 to the small circle) or shorter.

According to Gram (1936, p. 360), the standard error of frequency percentages of 50 is 15.8 when only ten sample areas are used. The error is largest in values from 20—80 per cent and decreases rapidly to zero at F % 0 and 100. If two determinations of the frequency are performed (modification of Raunkiær's method), the figures support each other as regards the error. Thus, if two species obtain e. g. the percentages 70;50 (written 7_5) and 70;0

(7_0), the shoots of the first species are undoubtedly denser than those of the second one and, furthermore, the 70 % of the first species are much more probable than the 70 % of the second one. If a homogeneous distribution of shoots is assumed, a species obtaining the values 60;60 will most probably have got too low a value within the large circles. Practically, however, such figures as a rule indicate inhomogeneity, viz. they indicate that the species form tussocks or carpets of limited distribution within the respective vegetation.

In the tables, analyses made with the modified RAUNKIÆR method are marked S (shoots density), ordinary RAUNKIÆR analyses R, and determinations of the degree of covering D ("Deckung").

The modified RAUNKIÆR method is of greatest importance in the case of detailed ecological investigations or where the dominance conditions are difficult to survey (meadows with a large number of species). For more easily surveyed vegetations or in the case of plant-geographical descriptions of the vegetation (cf. e. g. B. 1942), the non-objective, more rapid method of covering-determination may be preferred. This view (cf. B. 1935) may be correct; it must, however, be emphasized that covering values and frequency values are generally encumbered with errors of almost the same magnitude.

An advantage of the frequency methods is the possibility of expressing the results in percentages, which can be directly applied to the calculation of life-form spectra (RAUNKIÆR 1934 a) or spectra of biological distributional types. It is a rather roundabout way of converting covering values into average percentages in order to make them better suited to be a basis for life-form spectra (cf. the calculations of "Gruppenmenge" in TÜXEN and ELLENBERG 1937).

Finally, it must be stressed once more that the use of the frequency methods leads to greater objectivity and thereby to greater conformity of the results; exact comparisons are made possible and the results are independent of vegetational aspects, since shoots only are considered during the field work.

Species groups. In the tables, the species are collected in groups composed of species which are more or less closely related with respect to their range and ecology. The species groups are numbered and the explanation of the numbers is found in the key to the tables.

Distributional types[1]. In the index, the distributional type is given for the heath species mentioned in the text. The following types and abbreviations are used:

a. Arctic alpine. (ah. high arctic; al. low arctic).

b. Boreal or northerly; the main area may include Denmark, but the frequency decreases rapidly in the lowlands south of Denmark or in southernmost Denmark. (ba. boreal-arctic; bs. boreal-rather southerly).

s. central European element. sb. reaching northern Scandinavia, s. northern limit in the neighbourhood of the *Quercus robur* limit in Scandinavia. sd. Southern; reaching South Sweden and Denmark (*Euonymus* limit); the main area south of these countries.

Me. Mediterranean (or submediterranean) with its main area in South Europe.

WMe. West-Mediterranean.

o_1. Oceanic; main area west of the *Erica-Ledum* boundary (p. 96) which is hardly exceeded.

o_2. Suboceanic; western and central European, exceeding the *Erica-Ledum* boundary, but rapidly decreasing in frequency towards the east.

[1] A more detailed treatment of this system of distributional types will be published in a special paper (B. 1943 b).

o_3. Widely ranging with oceanic tendencies. Frequent in oceanic Europe, rare and selective in the most continental eastern Europe.
c_1. Continental; lacking or very rare and selective in oceanic Europe, very frequent in the continental parts.
c_2. Subcontinental; rather rare and selective or locally absent in the oceanic tracts; decreasing in frequency towards west.
c_3. Widely ranging with continental tendencies; rare at the south-west coast of Norway, the Faroes, Ireland, and other extremely oceanic regions.
x. Indifferent, neither continental nor oceanic.
hy. hygric oceanic or hygric continental.
H. With central distribution, lacking in western as well as in eastern Europe.
└ Oceanic only in the northern part of the area.
┌ Oceanic only in the southern part of the area.
┘ Continental only in the northern part of the area.
┐ Continental only in the southern part of the area.
p. Polymorphic, containing several races with different areas and a different biology.

III. Distribution of the Heath in Scandinavia and Northern Germany.

Gams (1927, p. 11) reads as follows: "Die Unterschiede zwischen den atlantischen Heiden und den kontinentalen Steppen sind vor allem ökologischer Natur, sowohl klimatischer wie edaphischer." In Denmark and Germany, we find a gradual transition from heaths to steppe-like communities and, consequently, it may sometimes be difficult to decide whether some vegetation or other should most naturally be classified as a heath or as a steppe. As mentioned above, we shall here confine ourselves to the Atlantic-subatlantic heath (bog) dominated by dwarf shrubs. The grass-heath communities are mainly distributed east of the area of the true Atlantic heaths. The Danish grass-heath sociations will be mentioned in treatises to appear later.

The distribution of the dwarf shrub heath in South Scandinavia and North Germany appears from the map of Fig. 1. In a great many localities the map only shows the former area of the heath, thus indicating that since the middle of the last century the heath-covered land has to a great extent been replaced by cultivated land or conifer plantations. A map of the distribution of the heath in Jutland about the year 1800 was published by Hugo Matthiessen (1939, p. 13).

The occurrence of heath in the area shown in Fig. 1 is due to a complex of climatical, edaphical, and anthropogenic factors. In the Faroes, some of the most oceanic heaths of north-western Europe can be regarded as natural and may even be the climax in the lowland (B. 1940, p. 17). In western Norway, the *Calluna* heaths of Jæren may, according to Fægri (1940), primarily be governed by climatic factors. In Denmark, Sweden, and N.W. Germany, very few heaths are quite natural. Only near the sea, in the dunes or on raised stony beaches, some heath vegetations may have immigrated without influence of man. The vast inland heaths of Jutland, e. g. Alheden on the Karup heath plain south-west of Viborg and the Randbøl Hede west of Vejle must be considered to be destroyed woodlands (more particularly oak woods) or old fields invaded by the heather (cf. pollenstatistical investigations by JONASSEN (1935), JESSEN (1935), IVERSEN (1941, p. 52), and historical investigations by OPPERMANN (1932), MATTHIESSEN (1933 and 1939), and by the writer (1939, 1941 a)). Most Swedish heaths have also arisen after the destruction of woods or wasteful cultivation (literature, see in SCHOTTE (1921), SJÖBECK (1933), MALMSTRÖM (1937, 1939), ATLESTAM (1942)). For N.W. Germany, the investigations by OVERBECK and SCHMITZ (1931, p. 163) show that man has been the chief factor in the destruction of woods and the formation of heaths (cf., furthermore, ARNOLDT (1939) on the History of the East German Heaths). The same results were gained by historical (MAGER 1930—37) and botanical studies (TÜXEN 1938, 1939). According to OVERBECK and SCHMITZ, it seems probable that the age of the heaths decreases with the distance from the outer coast and that only the most exposed heaths at the coast are natural.

Thus, in the formation of heath, it is very probable that the role of the climate dominates as the climate becomes more oceanic. The present climate of the Faroes and of western Norway, where the heaths seem to be most natural[1], is more oceanic than that of Jutland, West Sweden and N.W. Germany, where heaths generally are at most semi-natural. The effect of the climate on the distribution of the heath is rather convincing in the case of North Germany. Here, pine forests replace the Atlantic heath on sandy, fluvioglacial soils as we pass from the oceanic westerly regions to more continental areas (GRÄBNER) and the isolated, easterly "Lausitzer Heide" is, according to SCHULTE (1936), not a true heath, but is dominated by pine woods rich in heather, bilberries, etc.

In Sweden, the eastern border of larger heaths runs parallel to the border of frequent occurrence of a number of oceanic plants (e. g. *Erica tetralix*), and the heath lies mainly in the regions with the heaviest precipitation. This would seem to indicate a marked climatic effect. SCHOTTE, however, concludes that the influence of man was the most important factor controlling the distribution of heath in Sweden. Not marked on the map Fig. 1 are many small heath patches which occur on skerries or small islands in the Baltic Sea. According to DU RIETZ, the partly heath-covered outmost zone in the Stockholm archipelago reaches a breadth of 15 km. Where the coast is not split up into islands, the heath zone (DU RIETZ' "maritime Kahlregion") is absent or very narrow. The heaths of the "maritime Kahlregion", where woods or scrubs are lacking, may in most cases be counted as natural climatic vegetations.

In Denmark, the distribution of the heath on a rather large scale is governed by edaphic conditions, the more oceanic climate of Jutland being probably of secondary importance. A number of species follow the areas of the heaths and raised bogs,

[1] TANSLEY (1939, p. 265) states that, in the British Islands, the heath on exposed coasts and on exposed mountain slopes can only be counted as a climatic formation.

Fig. 1. Distribution of the Atlantic dwarf shrub heath in South Scandinavia and North Germany. — Heath indicated by black areas and dots. Norway: mainly after a map "Norden" by Ehlin and Söderlund (1 : 1000000, P. A. Norstedt & Söner), where heaths (with the exception of alpine heaths) are indicated by a special signature. Sweden: according to Schotte (1921, Fig. 8). Denmark: after B. 1937 a (Fig. 3). Germany: hatching after H. Walter 1927 (cf., furthermore, a map after Werth in Hueck 1936).

i. e. the areas with sandy or peaty acid soil. The same seems to hold for the southernmost part of Sweden, where the heaths are almost restricted to acid soils on the low granite mountain ridges and to alluvial soils (e. g. Skanörs Ljung).

IV. Relation between the North Atlantic and the Arctic Alpine Heaths.

In many places in western Norway, on the Faroes, and in Great Britain, a gradual transition from Atlantic to alpine heaths is found. However, this is but rarely the case in central or eastern Norway and Sweden, as the lowlands here are occupied by woodland and cultivated land. Transitions from Atlantic to alpine heaths in central Scandinavia are sometimes found in the subalpine belt in glades of the birch scrub (Table 1, No. 19); furthermore, some of the alpine heaths, especially the snow-covered types belonging to *Myrtillion alpinum* (du Rietz 1942) or *Phyllodoco-Myrtillion* (Nordhagen 1936, 1943) contain a great number of southern heath plants and show some relationship to the lowland heaths mentioned in the following section of the present paper.

The heaths of the Scandinavian mountains have been studied by many scientists (Fries, Tengwall, du Rietz, Nordhagen, Lippmaa); a survey of the heath types and the literature on the subject may be found in du Rietz (1925 a) and Nordhagen (l. c.). In 1938, the present author had the opportunity of studying some alpine heaths of southern Norway. The studies were made in order to collect the material for a comparison with Danish heaths and, particularly, to investigate the heath plants when exposed to conditions different from those prevailing in Danish latitudes.

At the locality Bjåen north of the Sætesdalen (the valley north of Christianssand), the alpine heath vegetation was investigated along a profile through the uppermost peaks of Bjåenfjeldet. The profile shows a characteristic difference between northern and southern slopes or, more correctly, between heaths with long and with short snow-coverings, respectively.

Profile through the peaks of Bjåenfjeldet, South Norway.
(Cf. Fig. 2).

1. *Vaccinium myrtillus* soc. rich in mosses. Table 1, Nos. 9—10, cf. Fig. 3.
2. *Empetrum hermaphroditum-Arctostaphylos alpina* soc. Table 1, Nos. 3 and 5.
3. *Vaccinium myrtillus-* or *Vaccinium uliginosum* soc. with *Calluna*. Table 1, Nos. 6—7, and 11.
4. Birch scrub (*Betula pubescens* coll.).
5. *Empetrum hermaphroditum-Vaccinium myrtillus* soc. rich in mosses; scattered: *Juniperus communis* var. *montana, Salix herbacea, Geranium silvaticum* and *Gentiana purpurea.*
6. As No. 5, but with *Betula nana* as a dominant.
7. *Nardetum* with *Salix sp.*
8. *Carex rigida* moss soc. (snow patch) with *Salix herbacea, Viola palustris, Polygonum viviparum, Gnaphalium supinum, Sphagna,* and liver mosses.
9. Small watercourse. *Eriophorum polystachyum.*
10. *Carex rigida* moss[1] soc. (snow patch) with *Salix herbacea, Gnaphalium supinum, Sibbaldia procumbens*; scattered: *Betula nana.*

[1] *Dicranum starckei, Pohlia nutans, Hypnum uncinatum, Polytrichum alpinum, Jungermannia lycopodioides, J. ventricosa, Cephalozia bicuspidata, Haplozia sphaerocarpa.*

11. As No. 10, but also small patches with initial stages of *Vaccinium myrtillus* soc. and *Lycopodium alpinum.*
12. *Salix herbacea-Jungermannia alpestris* soc. (snow patch) with *Gnaphalium supinum, Cerastium cerastioides, Solorina crocea, Cladonia elongata, Cetraria islandica,* and *Crocynia neglecta.*
13. *Gnaphalium supinum-Solerina crocea*-moss soc.
14. *Vaccinium myrtillus*-moss soc. with *Phyllodoce coerulea, Lycopodium alpinum,* and on the rocky wall near No. 13, *Lycopodium selago.*
15. *Empetrum hermaphroditum-Vaccinium myrtillus*-moss soc. with *Salix herbacea.*
16. *Loiseleuria procumbens-Arctostaphylos alpina-Empetrum* soc. rich in lichens or without ground layer.
17. As No. 16, but also *Arctostaphylos uva ursi* and *Betula nana* (cf. Table 1, No. 4).
18. As Nos. 16—17, yet also *Juniperus communis* var. *montana.*
19. Birch scrub (cf. No. 4).

The most extreme snowpatch vegetations with very long periods of snow-covering are obviously Nos. 12—13 (cf. the position of the snow-drifts in Fig. 2). The *Carex rigida* snowpatches on both sides of the runnel are probably snow-bare somewhat earlier. Among the heaths, the *Vaccinium myrtillus* soc. thaws latest, the *Empetrum-Vaccinium myrtillus* soc. somewhat earlier, the *Empetrum-Arctostaphylos alpina* and the *Loiseleuria-Arctostaphilos alpina* soc. thaw very early or are more or less snow-free during the winter. The latter two belong to NORDHAGEN's Scandinavian *Loiselleurieto-Vaccinion uliginosi* (*Loiseleurieto-Arctostaphylion,* KALLIOLA 1939).

In the most typical *Vaccinium myrtillus* heaths, *Phyllodoce coerulea* is rather frequent (Table 1, Nos. 12—16). In certain places, this plant dominates, e. g. on slopes close to subalpine birch scrubs. In such localities (Table 1, No. 16), the *Phyllodoce* heath passes over into *Nardus* snowpatches and *Athyrium alpestre-* or *Polytrichum-Sibbaldia* soc. found at the bottom of the slope. *Phyllodoce* is mentioned by NORDHAGEN as the unique character species in the *Phyllodoco-Myrtillion* of Scandinavia. In East Greenland, it is mentioned together with *Lycopodium annotinum* and *alpinum* as character species for the relatively moist, snow-covered and frequently south-facing *Empetreto-Voccinietum uliginosi* (B. 1933, p. 61). This Greenland heath and the *Phyllodoco-Vaccinion* obviously belong to the same main type; in Greenland, however,

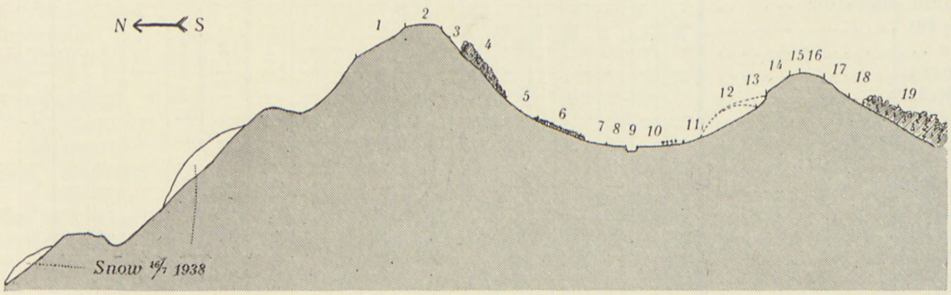

Fig. 2 Profile transect through the peaks of Bjåenfjeldet. Norway. (Alt. 1250 m. above the sea). Explanation of the figure in the text.

Table 1. Alpine Heaths of Southern Norway. Method: D, see p. 8.

	Alpine																		Subalpine				
Analysis No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Exposure	—	—	—	S	—	S	S	S	N	N	S	S	NW	NW	S	SW	—	—	N	—	N	S	S
Slope	—	—	—	45°	—	45°	40°	40°	35°	35°	40°	30°	35°	35°	40°	35°	—	—	25°	—	8°	10°	35°
1.																							
Arctostaphylos uva ursi	—	—	3	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
— alpina	2	—	4	—	3	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Loiseleuria procumbens	5	4	2	+	2	1+	—	2	—	—	—	1+	—	—	—	—	—	—	—	—	—	—	—
Juncus trifidus	+	—	—	—	—	—	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
Luzula spicata	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
2.																							
Melampyrum silvaticum	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	—	—	—	1+	—	3	1	—
Phyllodoce coerulea	—	—	—	—	—	—	—	—	—	—	—	2	2	3	3	5	—	—	—	—	—	1	—
Vaccinium myrtillus	—	—	—	—	1	1	2	1	5	5	4	5	4	4	4	1+	5	4	1+	1	5	5	3
Gentiana purpurea	—	—	—	—	—	—	—	—	—	—	1	—	—	1	1	+	1	—	—	—	—	—	—
Deschampsia flexuosa	—	—	—	+	1	2	1	—	1	1	3	1+	1	2	1+	—	1	—	1	—	1+	1	—
Solidago virga-aurea	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	+	—	—	—	—	—	—	—
Trientalis europæa	—	—	—	—	—	—	—	—	1	—	—	—	1	1	1	—	1	1	—	—	—	1	—
Luzula pilosa	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1	—	—	1	1
3.																							
Andromeda polifolia	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	1	—	—	—	—	—
Rubus chamaemorus	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—	2	—	—	—	—	—
Eriophorum vaginatum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1+	—	—	—	—	—
4.																							
Betula nana	—	—	—	1	—	—	—	2	—	—	—	—	—	—	1	—	3	3	—	3	—	—	—
Empetrum hermaphroditum	2	4	5	3+	4	1	1	4	5	5	1	1	5	4	2	—	1	2	1	2	1	2+	—
Vaccinium uliginosum var.	—	1	—	5	2	4	3+	1+	—	—	5	2	1	—	4	—	3	1+	2	1	1	1	—
— vitis idaea	1	1	—	1	1	2	—	—	1	1	1	—	1	1	1	—	—	—	—	1	1	1+	3
Calluna vulgaris	—	—	—	—	—	4	3	3	—	—	1	1	—	1	1	—	3	2	5	5	1+	1	—
Juniperus communis var.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1	—	—	—	—
Lycopodium alpinum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—
— annotinum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—
Salix herbacea	—	—	—	—	—	—	1	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—
— lapponum	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—
Linnæa borealis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2+	—	—	—	—
5.																							
Festuca ovina	—	—	1	1	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Anthoxanthum odoratum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1+	—	—	+	1	—	—	1	1
Nardus strictus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—
Carex rigida	—	—	—	—	—	—	—	—	—	—	—	—	1	2	1	—	1	—	—	—	—	—	—
— vaginata	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	1	—	—	—	—	—
Luzula multiflora	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1
Majanthemum bifolium	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	1	—	—
Polygonum viviparum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1+	—	—	—	1
Ranunculus acer	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—	1	1+
Alchemilla alpina	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1	—	—	—	—
— filicaulis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
Fragaria vesca	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Potentilla erecta	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	—	1	—	1	—	1
Oxalis acetosella	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Geranium silvaticum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	3
Cornus suecica	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	2	—	—
Pirola minor	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—	1
Prunella vulgaris	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1

Table 1 (continued).

	Alpine																		Subalpine				
Analysis No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Exposure	—	—	—	S	—	S	S	S	N	N	S	S	NW	NW	S	SW	—	—	N	—	N	S	S
Slope	—	—	—	45°	—	45°	40°	40°	35°	35°	40°	30°	35°	35°	40°	35°	—	—	25°	—	8°	10°	35°
Bartschia alpina	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	+	—
Melampyrum vulgatum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Veronica officinalis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Pinguicula vulgaris	—	—	—	—	—	+	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
Campanula rotundifolia	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	1
Gnaphalium norvegicum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—
Hieracium alpinum	—	—	—	—	1	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
6.																							
Alectoria ochroleuca	**5**	+	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cetraria nivalis	**3**	**3**	1	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
— cucullata	1+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cladonia alpestris	—	**4**	—	—	—	—	1	—	1	1	—	—	—	—	—	—	—	—	—	1	—	—	—
7.																							
Cladonia rangiferina	—	2	—	—	—	1	—	—	—	—	—	1	+	+	1	+	—	—	—	1	—	—	—
— mitis	—	**3**+	1	2	1	1	2	**3**+	1	1	**3**	**3**	**3**	2	1	+	—	1	—	1	—	—	—
— uncialis	—	—	1	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	1	—	—
— furcata	1	—	1	—	+	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—
— gracilis	1	—	—	—	+	—	—	—	1	1	—	1	—	—	—	—	—	—	—	—	—	—	—
— chlorophaea	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1	—	—	—	1	—	—	—
— bellidiflora	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—
— crispata	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	1	—	—	—	—	—	—	—
Stereocaulon paschale	—	—	1	1	1	1	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
— sp.	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cetraria islandica	1	1	1	—	—	—	1	1	1	1	—	1+	—	—	1	1	—	—	1	—	—	—	—
— crispa	—	1	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
— tenuissima	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Nephroma laevigatum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—
— arcticum	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—
Peltigera rufescens	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—
— malacea	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1+	—	—	—	—
Solorina crocea	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ochrolechia frigida	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Icmadophila aeruginosa	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—
8.																							
Rhacomitrium hypnoides	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Polytrichum juniperinum	—	—	1	—	**3**	1	2	—	1	—	—	1	—	—	1	—	—	—	—	—	—	—	—
Dicranum fuscescens	—	—	—	—	1	1	—	2	2	**3**	1	1+	**3**	—	2	—	—	—	—	2	—	—	—
— scoparium	—	—	—	—	—	—	—	—	—	—	—	1+	—	—	—	**4**	—	—	—	—	1	1	—
Pohlia nutans	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—
Hylocomium schreberi	—	—	—	—	—	—	—	**3**	1	2	—	—	—	—	—	—	1	2	2	**3**	—	—	—
— splendens	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	**3**	—	—
— squarrosum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—
Brachythecium velutinum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—
— reflexum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	**3**	—
Drepanocladus uncinatus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1+	—	1+	—
Pseudoleskea incurvata	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—
Rhodobryum roseum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
9.																							
Sphagnum rubellum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	**5**	**5**	—	—	—	—	—
Polytrichum commune	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	1	—	—	—	+	—
Dicranum bergeri	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—

Table 1 (continued).

	Alpine																		Subalpine				
Analysis No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Exposure	—	—	—	S	—	S	S	S	N	N	S	S	NW	NW	S	SW	—	—	N	—	N	S	S
Slope	—	—	—	45°	—	45°	40°	40°	35°	35°	40°	30°	35°	35°	40°	35°	—	—	25°	—	8°	10°	35°
10.																							
Jungermannia lycopodioides	—	—	—	—	—	—	—	1	4	2	—	1+	—	—	1	+	1	1+	—	—	2	1	—
— floerkei	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	1	—	—	—	—	—	—	—
— starckei	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1+	—	—	—	—	—	—	—
— ventricosa	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	1	1	—	1+	—	—	—
— gracilis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
— kunzeana	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—
— quinquedentata	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1+	—	—	—	—
Blepharozia ciliaris	—	—	—	—	1	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1	—	—
Cephalozia bicuspidata	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—
Kantia trichomanis	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—

Localities: Nos. 1, 2, 12: Bykle, Vaarstöl Bykleheia, altitude 1200 m. above the sea. Nos. 3—7, 9—11, 13—14, 16—18: Bjåen, altitude 1250 m. Nos. 8, 15: Haukelisæter, altitude 1100 m. Nos. 19—23: Bykle, altitude 6—900 m.
Vegetation: Nos. 1—4: heaths belonging to the *Loiseleurieto-Arctostaphylion* (*Empetrion emyrtillosum*). Nos. 5—8: transitions to the *Phyllodoco-Myrtillion*. Nos. 9—16: *Phyllodoco-Myrtillion*. Nos. 17—18: *Betula nana* bog. Nos. 19—20: subalpine *Calluna* heaths (No. 20: partially shaded by scattered trees (*Pinus*)). Nos. 21—23: subalpine birch scrub rich in bilberry.
Species groups: 1: *Loiseleurieto-Arctostaphylion* species. 2: *Phyllodoco-Myrtillion* species. 3: *Oxycocco-Empetrion* species. 4: dwarf shrubs. 5: herbs. 6: continental lichens of *Loiseleurieto-Arctostaphylion*. 7: other lichens. 8: bryophytes. 9: bryophytes of bogs. 10: bryophytes (*Jungermanniales*).

bilberry is lacking. The type is characterized by the occurrence of a great number of southern heath plants, viz. *Lycopodium annotinum, Dryopteris linnaeana, Cornus suecica, Deschampsia flexuosa, Nardus stricta, Scirpus caespitosus* var. and (only in Scandinavia) *Vaccinium myrtillus, Calluna, Solidago virga-aurea, Trientalis europæa, Luzula pilosa,* and *Melampyrum silvaticum.*

According to Nordhagen, the snowcovered bilberry heath is separated from the *Loiseleurieto-Arctostaphylion* by a great number of southern heath plants. Furthermore, *Geranium silvaticum* (in a sterile stage) and *Pedicularis lapponica* are much more frequent in this type. In southern Norway, *Gentiana purpurea* (sterile) also enters the snow-covered heath (Table 2). In the low alpine vegetation, it seems to be associated with the *Phyllodoco-Myrtillion* heaths. This heath type as a whole is characterized by species belonging to oceanic distributional types. The sole character species, *Phyllodoce coerulea,* has a low-arctic suboceanic range (B. 1938, p. 158). Subarctic or temperate and oceanic are *Cornus suecica, Alchemilla alpina, Scirpus caespitosus* var. *callosus,* and *Calluna vulgaris.* Furthermore, *Gentiana purpurea* may probably be classified as a hygric oceanic plant, however, its range is very disrupted and not easy to explain. Three species only, viz. the arctic *Betula nana, Pedicularis lapponica,* and the temperate *Melampyrum silvaticum* belong to subcontinental distributional types.

The *Calluna* occurrences in Table 1 are mostly found on southern slopes; on level ground, the heather enters the *Betula nana-Rubus chamaemorus-Sphagnum* soc. (Table 1, Nos. 17—18). In both habitats, *Calluna* is snow-covered during the winter.

In the Faroes, *Calluna* and several other oceanic species are snow-covered in the winter when growing in alpine situations (B. 1940, p. 56).

On the other hand, the more or less snow-bare *Loiseleurieto-Arctostaphylion* (the *Empetrion emyrtillosum* of DU RIETZ 1942) contains of southern flowering plants

Fig. 3. *Vaccinium myrtillus* heaths near the summit of Bjåenfjeldet. — To the left in the background subalpine *Betula* scrub. B. photo 1938.

only *Arctostaphylos uva ursi* (cf. p. 53) and it is, furthermore, dominated or characterized by a number of arctic-continental-subcontinental lichens, viz. *Cetraria nivalis* and *cucullata*, *Alectoria ochroleuca*, and *Cladonia alpestris*. Of suboceanic arctic plants, *Loiseleuria procumbens* and *Juncus trifidus* occur. The continental element in this heath type leads to NORDHAGEN's neutro-basiphilous *Elynion Bellardii* which is characterized by a great number of continental species and by almost complete absence of oceanic species (B. 1938). The name of this alliance has been altered to *Dryadion* (KALLIOLA 1939, DU RIETZ 1942) and recently (NORDHAGEN 1943) to

Kobresieto-Dryadion. It contains the continental arctic, more or less calciphilous *Rhododendron lapponicum*- and *Cassiope tetragona* heaths. Such heaths have almost no species in common with temperate heaths.

V. North Atlantic Dry Heath Communities.

This group includes heaths independent of ground water near the surface or a water-logged soil. The wet heaths are distinguished botanically by the occurrence of several oceanic plants frequently dominating the vegetation (e. g. *Myrica gale, Erica tetralix, Juncus squarrosus*). The dry heath is subdivided by means of distributional types. In the classification of the individual heath types, widely ranging heath plants, e. g. *Deschampsia flexuosa* and *Hylocomium schreberi*, are not used, nor is dominance for the guiding species definitely required.

1. The Scano-Danish heath series.

The conception of a Scano-Danish heath series is not only defined geographically by the range of the heath types belonging to the series, but furthermore and mainly by a number of heath species which reach their optimal development in Southwest-Scandinavia. The series is not restricted to this Scano-Danish area; in Scotland (cf. Tansley 1939, p. 752), very closely related types occur and, moreover, some North German heaths may be regarded as radiants of the Scano-Danish (Scotch) heath series. In the same manner, the Dutch-German heath series radiates to Denmark and southern Sweden. Some heath sociations must be considered transitions between the Scano-Danish and the Dutch-German heath series.

The species occurring in the heaths of Southwest-Scandinavia which, however, are more or less rare towards the south, are *Empetrum nigrum, Arctostaphylos uva ursi, Vaccinium vitis idaea, Vaccinium uliginosum, Cornus suecica, Trientalis europaea*, and *Arnica montana*. *Lycopodium annotinum* which has only a scattered occurrence in Danish heaths, seems also to be less frequent towards the south (cf. Hård 1935). These species are applied as guiding species in the demarcation of the Scano-Danish series. *Vaccinium myrtillus* has a large distribution south of Denmark; in Britain, it is, according to Matthews, a northern species, and it is absent or rare in the greater part of the lowland heaths of Germany. Hence, it may most naturally be included among the guiding species of the Scano-Danish series.

From the arctic alpine heath series, the Scano-Danish series is bordered by a number of arctic species, e. g. *Phyllodoce coerulea, Loiseleuria procumbens*, and *Arctostaphylos alpina* (cf. above, Table 1).

Not all Danish heaths contain the northern distributional types. Consequently, a number of heaths, particularly of south-eastern Denmark, do not belong to the

Fig. 4. Position of localities where the heath vegetation has been studied and to which reference is made in the text and in the tables. — The broken line indicates that position of the ice-edge which has been of the greatest importance for the development of the topographical features.

Scano-Danish series. They are collected in the main types of the Baltic submontane heath series. For the distinction of the Scano-Danish from the Baltic series, the absence in the latter of northern heath plants is used as a test.

Before going into further details, a list of localities investigated in Denmark and Sweden is given (cf. Fig. 4).

Localities in Denmark.

1. Skagens Odde, cf. Raunkiær 1934a VIII.
2. Raabjerg Mile, Bunken.
3. Tværsted.
4. Pikkerbakken near Frederikshavn.
5. Tolne Bakker.

6. Flade Bakker and Gerum Hede[1].
7. Solsbæk Strand.
8. Læsø near Vesterøhavn.
9. Læsø near Østerby, cf. B. 1941b.
10. Hammer Bakker, cf. also GRØNTVED 1926.
11. Svinkløv.
12. Bulbjerg region.
13. Heaths between the lake Nors Sø and the North Sea.
14. Heaths at Østerild and Tovsig.
15. Skyum Bjerge.
16. Fur, island in the Limfjord.
17. Heaths at Skörping and Madum Sø (Ræbild and Knebel Bakker).
18. Bramslev Bakker at Hobro.
19. Heath between Fjeldsted and Hem.
20. Heaths at the lake Skörsø.
21. Heaths at the lake Flyndersø.
22. Heaths between Mønsted and Ravnstrup.
23. Dollerup Bakker.
24. Kaas in Salling.
25. Venø island in the Limfjord.
26. Klosterhede[1] near Risbæk and Vilhelmsborg.
27. Heaths at Vind.
28. Store Sande.
29. Bregning Krat.
30. Heaths at Haderup.
31. Alheden at Søndre Feldborg Plantage.
32. Heath at Studsgaard.
33. Hessel Hede at Grenaa.
34. Heath at the lake Øjesø.
35. Helgenæs south of Dragsmur.
36. Gern Bakker.
37. Heaths at Ry.
38. Heaths at Hem, lake Mossø.
39. Vrads and Bryrup Langsø.
40. Heath between Kristianshede and Hjöllund St.
41. Borris Hede, cf. also GALLØE and JENSEN.
42. Knude Hede and Tinghede, cf. RAUNKIÆR 1934a.
43. Holmslands Klit, cf. RAUNKIÆR 1934b.
44. Randbøl Hede[1], Bindeballe, cf. B. 1941a.
45. Randbøl Hede[1] between Frederikshaab and Vorbasse, cf. B. 1941a.
46. Utoft Hede[1], cf. BØRGESEN and JENSEN.
47. Nørholm Hede[1], cf. also MØLHOLM HANSEN 1932.
48. Skallingen at Esbjerg.
49. Heaths on the island of Fanø, cf. RAUNKIÆR 1934a.
50. Heaths on the island of Rømø.
51. Heaths in the vicinity of Gram.
52. Heaths at the lake Hostrup Sø.
53. Nordby Hede, island of Samsø.
54. Hals Odde, cf. WIINSTED 1940.
55. Horneby Fælled.
56. Slopes at Nakkehoved.
57. Heaths at Raageleje.
58. Melby Overdrev and Sandet (Kassemose Overdrev.)
59. Heaths at Hundested and Lynæs.
60. Kregme at the Roskilde Fjord.
61. Heaths north of Rørvig.
62. Heaths near Hovvig.
63. Dragsholm Hede.
64. Osen, cf. WIINSTEDT 1938.
65. Kastrup Overdrev.
66. Ulvshale on the island of Møn, cf. B. 1942.
67. Møns Klint; Jydelejet.
68. Hammeren and Slotslyngen, cf. also WARMING 1914.
69. Kleven and Højlyngen, cf. also WARMING 1914.
70. Paradisbakkerne, cf. HAMMER PEDERSEN 1938.
71. Heaths at Boderne.

Localities in Sweden.

72. Steninge in Halland.
73. Haverdal.
74. Tönnersjö Hede, cf. also MALMSTRÖM 1937.
75. Hovshallar, Scania.
76. Torekov.
77. Hallands Väderö.
78. Kullen.
79. Hallands Ås at Tosjö.
80. Skanörs Ljung.

[1] Hede = heath.

A. Heaths characterized by northern and oceanic species and rich in hygrophytic mosses. (*Myrtillion boreale*) (Tables 2—4).

Heaths abundant in hygrophytic mosses are most frequent on slopes with a northern exposure; sometimes, they are also found on western or eastern slopes

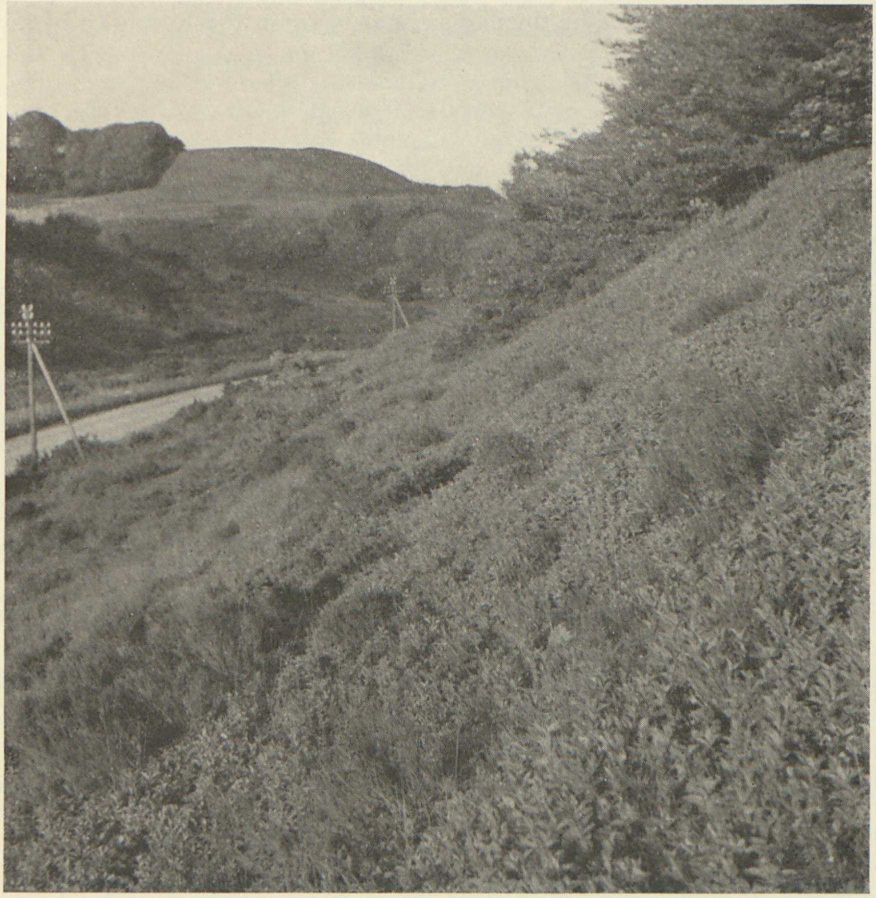

Fig. 5. *Myrtillus-Cornus suecica-Hylocomium* soc. (Table 2, No. 13) on northern slope in the large valley of the National Park Ræbild Bakker in Jutland (Loc. 17). B. photo 1943.

and, in certain areas, they may even grow on level ground. They are absent on the large level areas of the heath plaines or old moraine sands of western Jutland; they occur, however, on slopes formed by the glacial rivers (cf. B. 1941 a, pp. 46, 149). On the other hand, large areas of the hilly districts are covered with this type.

In these late-glaciated parts, the soil is generally more fertile. The same is the case with the heaths in Halland (Loc. 74) described by Malmström (1937). Here, podsolation is not marked and the ground layer is dominated by *Hylocomium splen-*

dens and *schreberi*. Furthermore, *Ctenium crista castrensis* and *Plagiothecium denticulatum*, which seem to be absent in Danish heaths, occur scattered. According to MALMSTRÖM, the rare occurrence of lichens may be a result of the heavy precipitation, and the same may possibly apply to the heaths of Jæren in Norway where, according to FÆGRI, lichens do not play any considerable part in the vegetation. In Denmark, however, there seems to be no direct connection between precipitation and the heaths rich in bryophytes; these heaths depend primarily upon the humidity of the air (cf.

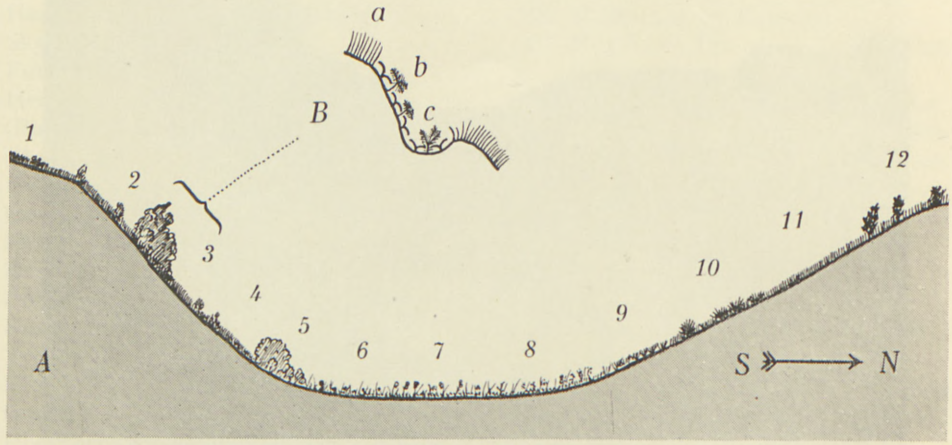

Fig. 6 A. Profile transect through a valley in Gerum Hede (North Jutland). Explanation of the numbers in the text.

Fig. 6 B. Profile through a small depression in the northern slope near the vegetation No. 3.

evaporation data in B. 1941 a, p. 158), yet the richest development of such heaths may probably also originate from the better soil.

Before going into further details, we shall describe two profile transects showing the position of the mossy heaths and the transition from such heaths to other types.

I. Gerum Hede (Denmark). Loc. 6 (cf. Figs. 6 A—B).

Hill slopes covered with heath, *Juniperus communis* scattered in the dwarf shrubs.

1. *Calluna-Vacc. vitis idaea-Empetrum* soc. rich in *Cladina*, *Hylocomium schreberi*, *Hypnum cupressiforme*; more scattered *Deschampsia flexuosa*, *Lycopodium clavatum*, *Erica tetralix*, and *Vacc. uliginosum*.
2. As No. 1, but only very few *Cladoniae* and plenty of *Vacc. myrtillus* (in patches, *Vacc. myrtillus-uliginosum-Polypodium* soc.). Dense and low *Fagus* scrub with *Vacc. myrtillus* soc. in the ground (here, *Blechnum* and *Dryopteris linnaeana*).
3. A number of different heaths with *Calluna*, *Empetrum*, *Vacc. myrtillus*, and *Hylocomium schreberi* dominating. In patches (Table 3, No. 31—32), *Lycopodium annotinum* as a dominant. Where the inclination is great (near elongated depressions, see Fig. 6 B), we have
   a. *Calluna-Vacc.-Hylocomium* soc. (*Vacc. myrtillus, uliginosum, vitis idaea, Empetrum, Juniperus, Dryopteris linnaeana, Plagiothecium undulatum*).

b. *Blechnum-Dryopteris linnaeana* soc. with *Vaccinia, Athyrium filix femina,* but only very little moss owing to almost complete shade near the ground.
c. *Blechnum* soc. very dense, occasionally *Dryopteris oreopteris.*
4. Mostly as No. 3, but, near the edge of the heath, *Calluna-Empetrum-Cornus suecica* soc. or *Vacc. uliginosum-Hylocomium* soc. (Table 3, Nos. 6—10). Close to the vegetation No. 5, *Dryopteris oreopteris* locally common, further *Dryopteris linnaeana* soc., *Juniperus, Circium palustre,* and *Viburnum opulus* scattered in the heath.
5. Transition between heath and meadow (bog). *Salix pentandra, Salix cinerea* (× *aurita*) scrub, *Sphagnum* bogs with *Drosera rotundifolia, Oxycoccus,* and locally *Anemone nemorosa.*
6. *Comarum palustre-Sphagnum* soc. (*Gymnocybe palustre, Oxycoccus, Drosera*).
7. *Menyanthes trifoliata* soc. with *Acrocladium cuspidatum, Philonotis fontana, Eriophorum latifolium*; furthermore, *Carex dioeca,* and *flava, Crepis paludosa, Pedicularis palustris.*
8. *Comarum-Sphagnum* soc. (*Agrostis canina, Carex echinata* and *hostiana, Viola palustris*).
9. *Nardus* soc. with *Erica tetralix* and *Empetrum.*
10. *Scirpus caespitosus-Erica-Calluna* soc. with *Orchis maculatus.*
11. *Calluna-(Erica)* soc. with mosses and *Cladonia.*
12. *Calluna* soc. with mosses and *Cladina*; scattered *Platanthera bifolia.*

II. Tönnersjöhede, Halland (Sweden), Loc. 74.

Profile through a low heath-covered ridge ("Ås").

1. *Calluna-Arctostaphylos uva ursi-Cladina* soc. (southern slope).
2. *Calluna-Arctostaphylos* soc. with *Empetrum, Vacc. vitis idaea, Cladonia impexa* and *Hylocomium schreberi.* (Level ground on top of the ridge).
3. *Calluna-Vacc. vitis idaea-Hylocomium schreberi* soc. with *Vacc. myrtillus, uliginosum, Deschampsia flexuosa, Trientalis, Potentilla erecta,* and *Hylocomium splendens.* (Upper part of northern slope).
4. As No. 3, but also *Empetrum, Salix repens, Lycopodium annotinum, Dicranum rugosum* and, very scattered, *Arctostaphylos.* (Lower part of northern slope).
5. *Myrica-Calluna-Sphagnum imbricatum* soc. with *Erica, Carex echinata, panicea, Scirpus caespitosus, Narthecium, Viola palustris, Potentilla erecta, Nardus, Agrostis canina, Drosera rotundifolia, Juncus conglomeratus,* and *Lycopodium selago.* (Bottom of northern slope).
6. *Carex lasiocarpa-Sphagnum papillosum-magellanicum* soc., locally with *Calla palustris.*

In profile I, the mossy heath type is typically developed in Nos. 2—4, and in profile II, in Nos. 3—4. Further below as well as in the papers by Hammer Pedersen and B. (1941 a), other examples of heaths rich in bryophytes mostly with a northerly exposure may be found.

Tables 2—3 contain a number of analyses of the heath type in question (main type A). The list of species is very interesting. Some of the typical species, e. g. *Vacc. myrtillus, Trientalis, Dryopteris linnaeana,* and *Luzula pilosa* are also characteristic of the alpine *Myrtillion.* Consequently, the Scano-Danish heaths of northern slopes belong to a type closely related to this alpine-subalpine alliance. Both types contain a large number of boreal wood plants. In Denmark, some of them are very probably present exclusively as remains of the destroyed woods.

Lippmaa (1939) proposed to work especially with unistratal communities. This synusiological view (cf. Gams and du Rietz) is of importance also for the study of the heath which is mostly a two-layered vegetation (cf. du Rietz 1930, Table 2).

Table 2. Scrubs and heaths of the *Myrtillion boreale* (A main type). Method: S, see p. 8.

Analysis No.	Distributional type	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	Constancy pCt. Nos. 6—14 and 16
Locality No.		36	5	21	21	25	75	75	75	75	78	78	78	17	4	56	56	56	
Exposure		—	NE	W	N	NW	N	NE	N	NW	N	N	NW	N	NW	N	N	N	
Slope		—	20°	15°	40°	40°	40°	40°	40°	40°	40°	30°	35°	30°	30°	5°	15°	30°	
1.																			
*Vaccinium myrtillus	b(al)sx	10_8	10_8	+	—	—	10_{10}	10_6	2	1	—	1	3	10_7	8_3	—	10_{10}	10_{10}	**90**
— vitis idaea	bs(┐)	10_7	4	—	—	—	6_2	10_9	—	—	—	—	—	10_7	1	10_6	9_4	—	50
— uliginosum	bs┌p	10_7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Empetrum nigrum	bs┌	1	—	—	1	1	2	—	10_{10}	8_2	—	3	—	9_6	—	—	—	—	50
*Cornus suecica	bso$_2$	—	8_3	—	—	—	—	—	—	—	—	—	4	10_9	—	—	—	—	20
Ligusticum scoticum	bso$_2$	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	10
*Blechnum spicant	bso$_2$hy	—	—	—	10_{10}	10_{10}	—	—	—	—	—	—	—	—	—	—	—	—	—
*Trientalis europaea	b(al)sx	1	5	8_2	3	6_0	—	—	—	—	—	—	1	5	—	—	—	—	20
*Majanthemum bifolium	bsc$_3$	—	—	5	4	—	—	—	—	—	—	—	—	5	—	—	—	—	10
*Melampyrum vulgatum	bsx	—	7_2	2	4	—	—	—	—	—	—	—	—	1	—	—	—	—	10
Antennaria dioeca	bsx	—	—	—	—	—	—	—	—	—	—	—	—	—	5	—	—	—	10
*Dryopteris phegopteris	bsx	—	—	—	—	—	8_2	—	—	—	—	—	—	—	—	—	—	—	10
* — linnaeana	bsx	—	—	—	—	—	+	+	—	—	—	—	—	—	—	—	—	—	20
2.																			
*Lonicera periclymenum	so$_2$	+	—	—	—	—	—	—	—	—	6_2	9_3	3	—	—	—	—	—	30
*Lathyrus montanus	so$_3$	—	1	—	—	1	2	7_1	1	—	—	—	—	+	6_2	—	—	—	50
Calluna vulgaris	sbo$_3$	2	—	—	—	+	—	—	1	10_9	10_{10}	10_{10}	10_9	3	10_{10}	10_8	10_7	2	**80**
Galium saxatile	sbo$_2$	—	—	—	—	—	2	7_2	4	—	—	—	—	1	1	4	8_2	7_1	60
Sieglingia decumbens	sbo$_3$	—	—	—	—	—	1	—	1	—	—	—	—	—	1	—	—	—	30
Carex pilulifera	sbo$_3$	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	10
— arenaria	so$_2$	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	10
Holcus mollis	so$_3$	—	—	—	7_2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
3.																			
*Rumex acetosa	sbxp	—	—	2	—	—	—	—	—	—	—	—	—	—	—	1	6_2	2	10
Juniperus communis[1]	sbx	—	3	—	—	—	1	—	1	2	+	—	—	1	—	—	—	—	50
Deschampsia flexuosa	sbax	3	4	9_3	2	—	10_6	10_9	10_6	6_4	5	10_6	10_6	10_8	6_3	10_7	10_9	10_7	**100**
Anthoxanthum odoratum	sbxp	—	—	—	1	—	—	—	—	—	—	—	+	—	—	2	7_2	5	20
Agrostis tenuis	sbx	—	1	+	—	—	—	4	4	—	—	—	—	—	—	—	—	—	20
Festuca ovina	sbxp	—	—	—	—	—	—	—	—	—	1	—	—	—	—	5	6_1	2	20
— rubra	sbxp	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	4	4	20
Luzula multiflora	sbxp	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	10
— campestris	sbxp	—	—	—	—	—	—	—	—	—	—	—	—	—	1	3	10_4	3	20
Campanula rotundifolia	sbaxp	—	—	2	—	—	1	—	—	2	—	—	1	—	1	2	5	5	50
Potentilla erecta	sbxp	—	—	—	3	1	+	8_2	—	+	—	+	+	1	5	—	—	—	70
Viola canina	sbxp	—	—	—	—	—	—	—	—	—	—	—	3	—	—	—	—	—	10
Equisetum arvense	sbaxp	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	9_2	10
4.																			
*Polypodium vulgare	sbx	—	—	10_9	+	—	—	—	—	2	5	6_1	4	—	—	—	—	4	40
*Luzula pilosa	sbx	—	—	5	1	—	—	—	—	—	—	—	5	4	—	—	—	—	20
*Convallaria majalis	sbx(?c$_3$)	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	10
*Solidago virga aurea	sbxp	—	—	—	—	—	—	—	—	—	—	—	1	+	—	—	—	—	20
Dryopteris spinulosa	sbxp	—	—	—	—	—	—	—	—	—	1	—	3	—	—	—	—	—	20
— filix mas	sbx	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	10
Hieracium vulgatum	sx?	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	10
Fragaria vesca	sbx	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—
Stellaria holostea	sx	—	—	—	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Anemone nemorosa	sbxp	—	—	1	3	—	—	—	—	—	—	—	—	1	—	—	—	—	10
Oxalis acetosella	sbx	—	—	—	3	—	5	4	1	1	—	—	1	—	—	—	—	—	50

[1] In the scrub layer.

Table 2 (continued).

Analysis No. / Locality No. / Exposure / Slope	Distributional type	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	Constancy pCt. Nos. 6—14 and 16
Analysis No.		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	
Locality No.		36	5	21	21	25	75	75	75	75	78	78	78	17	4	56	56	56	
Exposure		—	NE	W	N	NW	N	NE	N	NW	N	N	NW	N	NW	N	N	N	
Slope		—	20°	15°	40°	40°	40°	40°	40°	40°	40°	30°	35°	30°	30°	5°	15°	30°	
5.																			
Hylocomium loreum	ohy	—	—	—	—	—	10_9	10_6	10_{10}	9_6	2	—	—	+	—	—	—	—	60
Dicranum majus	ohy	—	—	—	—	—	6_1	2	4	7_5	—	—	1	—	—	—	—	—	50
Thuidium tamariscifolium	ohy	—	—	—	—	—	2	+	—	—	—	—	2	—	—	—	—	—	30
Frullania tamarisci	ohy	—	—	—	—	—	1	+	—	—	—	—	—	—	1	—	—	—	30
Bazzania trilobata	ohy	—	—	—	—	—	2	2	1	—	—	—	—	—	—	—	—	—	30
6.																			
Hylocomium schreberi	—	6_4	—	3	1	—	7_3	9_3	1	2	—	2	6_3	10_8	6_4	10_8	8_4	8_6	**90**
— splendens	—	2	1	—	1	—	1	6_2	1	5	—	1	+	10_9	1	10_6	10_{10}	9_7	**90**
— triquetrum	—	—	10_7	—	1	—	9_3	—	7_3	2	—	—	2	1	—	—	2	10_{10}	60
— squarrosum	—	—	—	—	2	—	—	6_2	—	—	—	—	1	—	—	1	10_5	6_2	30
Hypnum cupressiforme	—	8_3	—	2	1	—	—	3	1	8_3	2	10_5	8_4	—	10_9	—	—	—	70
Dicranum scoparium	—	—	—	—	+	—	1	—	—	2	3	1	6_2	1	1	2	—	—	70
— rugosum	—	—	3	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—	10
Plagiochila asplenioides	—	—	—	—	—	—	—	—	—	—	—	—	3	—	—	—	—	—	10

Vegetation: Nos. 1—5 ground vegetation in scrubs (1—2 of *Populus tremula*, 3—4 *Quercus robur-petraea*, 5 *Salix cinerea* × *aurita*) Nos. 6—17 heaths (6—12 on screes of gneiss, 13—17 on sandy slopes). pH in No. 1 3.4, No. 3 5.1, No. 13 4.1. No. 15 not typical.
Species groups: 1: Boreal (and montane) species, 2: southern suboceanic species, 3: southern widely ranging heath or grassland species, 4: southern widely distributed wood plants, 5: hygric oceanic bryophytes, 6: other important bryophytes. * characteristic A-type species. Such species are lacking in No. 15 which occurs near the top of the slope and belongs to main type B.
Species not mentioned in the table: No. 1: *Molinia coerulea* 1, No. 2: *Rubus saxatilis* (bsx) 3, No. 3: *Populus tremula* +, No. 4: *Carex stolonifera* 1, *Viola palustris* ($sbalo_2$) 1, *Lophocolea bidentata* 1, No. 6: *Avena pratensis* (sbc_2) 1, No. 8: *Hypericum montanum* (s_H) 1, No. 9 *Clad. impexa* 2, No. 10: *Rubus idaeus* 1, No. 11: *Calamagrostis epigeios* (sbc_3), 1, No. 12: *Blepharozia ciliaris* 2, *Rhodobryum roseum* 2, No. 13: *Calamagrostis arundinacea* (sbc_1) +, *Hierac. umbellatum* 1, *Peltigera canina* +, No. 14: *Veronica officinalis* +, *Thymus serpyllum* 1, *Pimpinella saxifraga* 1, No. 16: *Trifolium medium* 2, *Veronica chamaedrys* 1, No. 17: *Achillea millefolia* 1, *Peltigera canina* 1.

Many sociations in our main type A are largely held together by the ground layer where two related bryophyte unions are present. The occurrence of hygrophytic mosses is of fundamental significance, since these plants are indicators of a microclimate with high air humidity. Hence, the heaths rich in these mosses form a group of ecologically related sociations. Some vascular plants also require high air humidity; a species like *Blechnum spicant* is restricted to damp places and, where it grows, it suppresses the mosses. In fact, it may sometimes belong to one of the ground layer unions. On the other hand, *Luzula pilosa* or *Cornus suecica* also require dampness, but they belong to a stratum above. If such plants occurred in a heath without ground layer, they would probably justify the classification of such a heath into the main type.

The main type, however, is not only an ecological group defined by the occurrence of mesophytic-hygrophytic life forms (cf. Iversen 1936); it is also, and perhaps to a greater extent, a group of geographically related sociations. The main type is characterized by northern and oceanic species; southern oceanic and continental species are almost absent. This is why the *Callunetum* rich in a mesophyte-like bracken (p. 78) does not belong to the *Myrtillion boreale*.

In the sequel, the individual sociations which are collected in the tables will

Table 3. Heaths of the *Myrtillion boreale* (A main type). Method D. In Nos. 1—30, the first value is the constancy (5 = 100 %), the second is the degree of covering.

	Distributional type									
Analysis No.		1—5	6—10	11—15	16—20	21—25	26—30	31 32	33	34 35
Locality No.		5	6, 10, 17	24	6, 36, 39	4	4, 6	6	10	8
Exposure		N	N	N	N	NW	N	N	NE	N
Slope		20—25°	5—20°	10—15°	5—20°	25—35°	15—25°	30°	5°	15°
1.										
*Vaccinium myrtillus	b(al)sx	5. +–3	5. 1–4	—	4. +–2	5. 2–4	5. 2–4	1 1+	1	—
— vitis idaea	bs(┐)	4. 1–2	4. 1–2	—	2. 1–2	3. 1	3. 1–2	2 2	2	—
— uliginosum	bsΓp	—	1. 3	5. 1–2	—	—	—	—	1	—
Empetrum nigrum	bsΓ	5. 1–2	5. 1–3	4. 2–3	2. 1	—	2. 1–3	2 4	3	4 3
*Cornus suecica	bso_2	5. 3–5	5. 3–5	5. 3–5	1. 4	—	—	—	—	—
*Blechnum spicant	bso_2hy	—	1. 1–2	—	5. 3–5	—	—	—	—	—
*Trientalis europaea	b(al)sx	4. +–2	1. 1	2. 1	3. 1	—	2. 1	1 1	1	—
*Lycopodium annotinum	b(al)sx	—	1. 2	—	—	—	—	4 4	—	—
*Majanthemum bifolium	bsc_3	2. +	—	—	2. 1–2	1. 1	—	—	—	—
*Melampyrum vulgatum	bsx		—	—	2. 1	—	1. 1	—	—	—
*Dryopteris linnaeana	bsx	—	—	—	1. 3	—	—	—	—	—
Myrica gale	bso_2(Γ)	—	—	2. 1	—	—	—	—	—	—
Arnica montana	so_2(H)Mo	—	—	—	—	—	1. 1	—	—	—
2.										
*Luzula silvatica	sbo_2	—	—	—	—	5. 2–3	—	—	—	—
*Lonicera periclymenum	so_2	—	—	—	1. 2	—	—	—	—	—
*Lathyrus montanus	so_3	—	—	—	—	3. 1	1. 1	—	—	—
Calluna vulgaris	sbo_3	5. 4–5	5. 1–5	1. 2	2. 2–3	5. 2–5	5. 5	4 2	4	5 4
Galium saxatile	sbo_2		—	1. 1–2	—	2. 2	1. 1	—	—	—
Sieglingia decumbens	sbo_3	—	—	—	—	—	1. 1	—	—	—
Carex pilulifera	sbo_3	—	—	—	—	2. 1	1. 1	—	—	—
— arenaria	so_2	—	—	5. +–2		—	—	—	—	1 1
3.										
Juniperus communis[1]	sbx	1. 2	—	—	—	5. 2–4	1. 1	—	—	—
Deschampsia flexuosa	sbax	5. +–2	4. 1	5. 1–3	5. 1–2	5. 1–2	5. +–2	1 1	1	—
Anthoxanthum odoratum	sbxp	—	—	—	1. 1	—	—	—	—	—
Festuca ovina	sbxp	1. 1	—	—	—	1. 1	—	—	—	—
Nardus stricta	sbx(L)	—	—	—	1. 1	—	1. 1	—	—	—
Luzula multiflora	sbxp	—	—	—	—	—	2. 1	—	—	—
Hieracium umbellatum	sbxp	1. 1	—	—	—	2. 1	2. 1	—	—	—
Campanula rotundifolia	sbaxp	—	—	—	—	—	1. 1	—	—	—
Potentilla erecta	sbxp	—	1. 1	3. +–1	4. 1–2	1. 1	3. +–1	1 1	—	—
4.										
*Luzula pilosa	sbx	2. +	2. 1	5. 1	5. 1	—	2. 1	—	—	—
*Polypodium vulgare	sbx	1. 2	—	1. 2	—	—	—	– 2	—	—
*Solidago virga-aurea	sbxp	—	—	—	—	—	2. 1	—	—	—
Pteridium aquilinum	sbx(cosm)	—	—	3. 1–5	—	—	—	—	—	+ 2
Pirola minor	sbx(L)	—	—	—	—	—	—	—	—	—
Anemone nemorosa	sbxp	1. +	—	—	—	—	—	—	—	—
5.										
Hylocomium loreum	ohy	1. 1	—	—	—	—	—	1 –	—	—
Plagiothecium undulatum	ohy	1. 2	—	—	1. 1	—	1. +	—	—	—
Frullaria tamarisci	ohy	1. 1	—	1. +	—	2. 1	—	—	—	—

[1] In the scrub layer.

Table 3 (continued).

Analysis No.	Distributional type	1–5	6–10	11–15	16–20	21–25	26–30	31 32	33	34 35
Locality No.		5	6, 10, 17	24	6, 36, 30	4	4, 6	6	10	8
Exposure		N	N	N	N	NW	N	N	NE	N
Slope		20–25°	5–20°	10–15°	5–20°	25–35°	15–25°	30°	5°	15°
6.										
Hylocomium schreberi	—	5. 2–5	3. 1–4	5. 2–3	2. 4	5. 1–4	5. 2–4	3 3	4	2 3
— splendens	—	5. 2–5	4. 2–5	—	2. 4	4. 1–2	5. 1–5	4 5	—	2 3
— triquetrum	—	4. 1	1. 1	5. 2–5	2. 1+	4. 1–4	3. 1–3	1 1	—	5 –
— squarrosum	—	1. 1	—	—	—	—	3. 1–2	—	—	—
Hypnum cupressiforme	—	2. 1–2	2. 1–2	4. 1–2	1. 1	5. 1–3	4. 1	—	1	1 1
Dicranum scoparium	—	—	1. 1	—	—	2. 1	2. 1	—	—	—
— rugosum	—	—	—	—	—	—	—	—	1	—
Lophocolea cuspidata	—	—	—	—	—	4. 1–2	—	—	—	—
— bidentata	—	—	1. 1	—	—	—	—	—	1	—

Vegetation: Nos. 1—15: patches with *Cornus suecica*. Nos. 16—20: patches with *Blechnum spicant* in the heath or at the edge of the scrubs. Nos. 12—25: patches with *Luzula silvatica*.
Nos. 1—33: Diluvial sandy heath slopes. Nos. 34—35: Alluvial brink at Vesteröhavn. The vegetation not typical, but rather a poor dune variety of the main type. One of the analyses of the *Blechnum*-soc. is from Norway; cf. Fig. 8. Two of the analyses, 26—30, are from level ground between scrubs of beech and juniper. No. 33. On the western side of a beech scrub on the top of a hill. pH-measurements of the soil: Nos. 1—5: 4.4, 4.5. Nos. 11—15: 3.8, 3.9. Nos. 21—25: 4.1.
Species groups: See Table 2.
Species not mentioned in the table: Nos. 1—5: *Clad. impexa* 1.1. Nos. 11—15: *Erica tetralix* 1.1. Nos. 16—20: *Athyrium filix femina* and *Scorzonera humilis* 1.1. Nos. 21—25: *Clad. impexa, sylvatica* and *rangiformis* 1.1. Nos. 26—30: *Platanthera bifolia* 2.1, *Leucobryum glaucum* 1.2, *Porella platyphylla, Jungermannia barbata, Holcus mollis, Carex panicea* 1.1. No. 33: *Clad. sylvatica* 1. No. 34: *Plantago maritima* 1, *Peltigera canina* 2. No. 35: *Salix repens* 4, *Lotus corn.* and *Festuca rubra* 1.

not be dealt with separately. Mention is made only of the more significant units. Details will appear from the keys to the tables and from the treatment of the guiding species.

In the ground layer, two bryophyte unions are to be found, viz. the union of hygric oceanic mosses, and the union of widely ranging hygrophytic mosses.

In the field layer, the dominance fluctuates between *Calluna, Empetrum, Vacc. myrtillus*, and *vitis idaea;* frequently, two of the dwarf shrubs reach almost the same abundancy (cf. the shoot density values). As *Calluna, Empetrum*, and *Vacc. vitis idaea* are widely distributed within the Scano-Danish heath series and common to different main types, it seems useless to divide the field layer in accordance with the dominance of these specie.. On the other hand, we find a number of subdominants or rather frequent species which are useful for a classification of the layer. These species are the following: *Vaccinium myrtillus, Dryopteris linnaeana, D. phegopteris, Lycopodium annotinum, Cornus suecica, Luzula silvatica, Lathyrus montanus*, and a few more.

a. Ground layer.

1. Hygric oceanic mosses. In common with the heaths of the island of Jungfrun (du Rietz 1925a, p. 335) and Håøya (Størmer 1938, p. 43), where *Hylocomium loreum, Bazzania trilobata* and others are abundant, the heaths of Hovs Hallar (Loc. 75, cf. Fig. 4, Table 2, Nos. 6—9), are obviously very closely related to the oceanic heath of the Faroes and West Norway, where the same bryophyte union is developed in the ground layer of the *Callunetum* and the *Empetreto-Vaccinietum* (more rarely in the *Calluna-Erica-cinerea* heath).

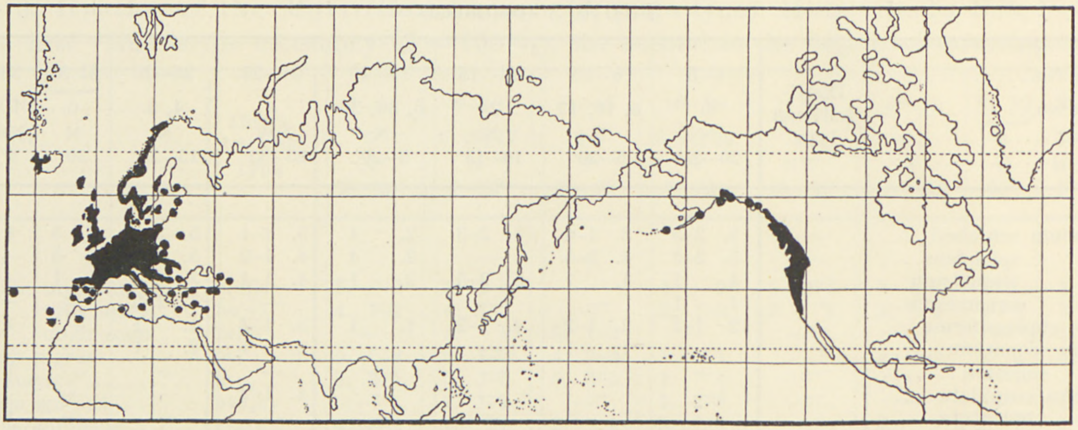

Fig. 7. Total range of *Blechnum spicant*. For further details, cf. ANDERSSON and BIRGER 1912, FERNALD 1929, PALMGREN 1932, HERMANN 1936, RECHINGER 1938 (Fedde Repert. Beih., Vol. 98), HULTÉN 1941, GRÖNTVED 1942, WEIMARCK 1942, and floristic manuals.

The union of hygric oceanic mosses occurs, moreover, in different European conifer woods (GAMS 1941, p. 228). In Denmark, the union occurs in the scree near Jons Kapel (Loc. 68, WARMING 1914, p. 293) and on northern slopes in conifer woods (Gels-Skov, Sealand) or in beech woods (cf. p. 29). In Danish heaths, the union is not typical; only mixtures of unions 1 and 2 being found (HAMMER PEDERSEN 1938, p. 343 and Table 3).

2. Widely ranging hygrophytic mosses. This union dominates the ground layer in most Danish heaths on northern slopes. Characteristic species are *Holycomium splendens*, *triquetrum*, and species otherwise almost restricted to woods. *Hylocomium schreberi* is often very abundant, yet this species is not hygrophytic, but rather mesophytic and is sometimes solely dominant in level heaths (e. g. Ulvshale, B. 1942) and occurs, though mostly scattered and very sparse, in the driest heaths (Table 9). In the same manner, *Hypnum cupressiforme* and *Dicranum scoparium*, which are able to grow in dry habitats, do not characterize the present main type nor other main types. The union also occurs in the closely related heaths of northern slopes described on p. 66.

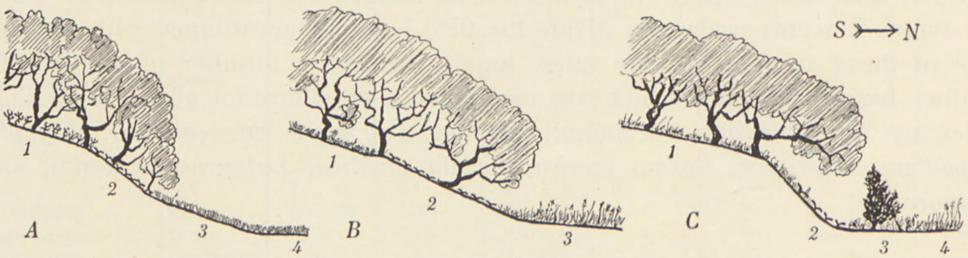

Fig. 8. Three profile transects showing characteristic occurrences of *Blechnum spicant*.
A. Norway, Bykle. Subalpine birch scrub. 1. *Vacc. myrtillus* soc., 2. *Blechnum* soc., 3. *Nardus* soc. (snow-patch).
B. Jutland (Loc. 29). Oak scrub (*G. petraea and robur*); 1. *Polypodium vulgare* soc., 2. *Blechnum* soc. (with *Polypodium* and *Lonicera pericl.*), 3. Wet acidic grassland.
C. Oak scrub in the valley at the lake Flyndersö (Loc. 21, cf. Fig. 4). 1. *Holcus mollis-Deschampsia flexuosa* soc. with *Majanthemum*; 2. *Blechnum* soc. (Table 4, No. 2); 3. *Juniperus*; mixture of heath and meadow; 4. meadow wery rich in species near river.

Blechnum spicant is a boreal oceanic-montane species (see map, Fig. 7). In the Faroes, it occurs in lowland heaths as well as in subalpine *Nardeta* and alpine snow-patches (B. 1937b, Fig. 8(4), Tables 10, 13, and 14). In Norway, it is found in the *Cornus suecica* type of the subalpine birch scrubs (NORDHAGEN 1928, Fig. 19). Near the Atlantic, it may be completely dominating on northern heath slopes in Karmöya. Its occurrence especially at the edge of subalpine birch scrub close to open *Nardus* snow-patches (Fig. 8 A) corresponds entirely to its occurrence in Danish oak scrubs (Fig. 8, B, C). In the heath outside northern slopes *Blechnum* is only found in the shade in *Calluna-Pteridium* soc. (Table 19) or very low *Salix cinerea* scrub (Table 7, Fig. 15). The *Blechnum* society occurs, furthermore, in patches in Danish beech woods (Velling Skov near Loc. 39) or conifer plantations. Thus, the occurrence in northern Europe does not show any close connection between *Blechnum* and conifer woods (cf. GAMS 1941, p. 228).

As compared with *Cornus suecica*, *Blechnum* tolerates deeper shade and seems to be more dependent on slowly oozing soilwater (cf. Fig. 8 C and B. 1941a, p. 46; furthermore, cf. WEIMARCK 1942, p. 402). The occurrence in damp woods and northern slopes suggests a hygric oceanic plant.

Owing to the rather reduced variability, *Blechnum* is particularly valuable as a guiding species. On the possibility of the occurrence of northern and southern races, see WEIMARCK, l. c.

b. Field layer.

Dryopteris phegopteris, *linnaeana* and *oreopteris* are boreal montane species. The two first mentioned species are widely ranging, while *Dryopteris oreopteris* is suboceanic. In Denmark, this species is very rare in the heath. Outside acidic beech woods, *Dryopteris linnaeana* and *phegopteris* may be very characteristic of damp northern heath slopes in areas where the heath vegetation is generally young.

Lycopodium annotinum has also a boreal-montane distribution. In the heath, it was only found to be frequent in northern slopes (Table 3).

Luzula silvatica (*L. maxima*). According to WIINSTEDT (1937, p. 94), it is mediterranean-atlantic, not continental, as proposed by MATTHEWS. In southern Europe it is montane-alpine. In north-Atlantic regions, it is an important plant in different types of grassland (e. g. OSTENFELD 1908, pp. 966, 983). In the British Islands, it is abundant in damp woods and may dominate in oak scrub, but is also found in the *Callunetum* of the wicklow mountains (TANSLEY, PRAEGER). In Denmark, it is very characteristic in certain beech woods of eastern Jutland. Here, it forms dense societies on slopes (e. g. Munkebjerg at Vejle) in damp woods with frequent occurrence of a number of oceanic species (*Ilex*). At Aabenraa, the *Luzula silvatica* vegetation contains *Deschampsia flexuosa* and *Hylocomium triquetrum*, *loreum*, *schreberi*, *Dicranum majus*, and *Thuidium tamariscifolium*. In the heaths of Denmark, *Luzula silvatica* is very local. At Kilen (near Loc. 25), it grows on slopes with *Vaccinium myrtillus*, *Blechnum*, *Anemone nemorosa*, and *Trientalis* (WIINSTEDT) and on the Pikkerbakker (Table 3, Nos. 21—25) in a similar habitat most frequently near junipers and temporarily shaded. Its occurrence in heath soils (pH 4.1) and calcareous soils (Alps, BROCKMANN JEROSCH, Skarreklint in North Jutland, WIINSTEDT) suggests a large pH domain; according to LUZZATTO (1935, 27 samples), it occurs on soils from pH 4.2 to 7.4.

Cornus suecica has a pronounced subarctic-oceanic range (for further details, cf. B. 1938). In southern Sweden and in Denmark, it keeps to light woods (e. g. *Populus tremula* wood, Table 2, No. 2) or northern heath slopes, but occurs moreover very rarely in dune heaths (cf. p. 88, Table 22). Already HORNEMANN (1821, p. 180)[1], in his attempt to study the flo-

[1] J. W. HORNEMANN, 1821, Bemærkninger angaaende Forskelligheden af Vegetationen i de danske Provindser. Det Kgl. Danske Vidensk. Selsk. phys. Skrifter, Første Deel, 1. Hæfte.

ristic differences within Denmark, points out that northernmost Jutland has a more boreal vegetation, as is indicated through the frequent occurrence of *Cornus suecica*. In Northwest Germany it is very rare, being found near the sea only (GRÄBNER 1925, p. 31).

HELMS and JÖRGENSEN (1924, Fig. 1 and p. 179) mention that *Cornus* in the *Sphagnum* bog Maglemose is restricted to a very small area north of and close to a wood situated on a small island in the bog. The cold microclimate of the spot must, according to these authors, be well suited for this northern species. Almost the same type of occurrence was observed in the heaths of Jutland in Loc. 10 and 17 (Figs. 5, 9 A and B), where *Cornus* is beautifully developed in the shade of low beech scrub, but cannot penetrate into the darkness of the scrub.

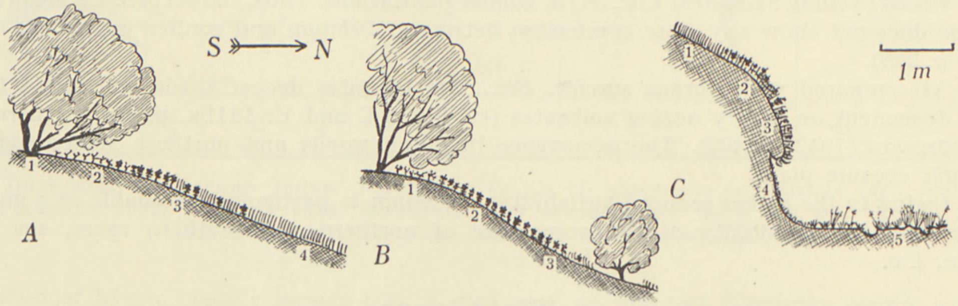

Fig. 9. Profile transects showing typical occurrences of *Cornus suecica* in Denmark.
Profile A. Beech scrub and heath in Hammer Bakker (Loc. 10). 1. *Trientalis europaea* very scattered in deep shade. 2. *Vaccinium myrtillus* soc. 3. *Calluna-Cornus* soc., *Cornus* scattered north of point 3. 4. *Calluna-Hylocomium* soc., without *Cornus*.
Profile B. Beech scrub at Rold Skov (Loc. 17). 1. *Vaccinium myrtillus-Hylocomium splendens* soc. Scattered *Vaccinium vitis idaea* and *Cornus*. 2. *Cornus-Vaccinium myrtillus* soc. 3. *Cornus-Vaccinium uliginosum* soc.
Profile C. Heathslope near small road in Tolne Bakker (Loc. 5). 1. *Calluna-Hylocomium* soc. with *Vaccinium myrtillus*. pH. 4.5. 2. Heath rich in *Cornus suecica*; cf. Table 3 No. 1—5 pH. 4.7. 3. As No. 2, but also *Erica tetralix*. 4. Mosses on moist, somewhat clayey sand: *Nardia scalaris!*, *Haplozia crenulata!*, *Cephalozia bicuspidata!*, *Pellia epiphylla!*, *Hylocomium squarrosum* and *H. loreum*, *Polytrichum juniperinum*, *Plagiothecium undulatum*, *Sphagnum palustre*, scattered *Mnium hornum*, *Dicranella heteromalla*, *Hylocomium splendens* and *schreberi*. Phanerogams: *Pinguicula*, *Pedicularis silvatica*, *Viola palustris*, *Blechnum*, *Agrostis tenuis*, *Anthoxanthum*. pH 5.3. 5. Road with *Juncus effusus*, *squarrosus*, *lampocarpus*, *Anthoxanthum*, *Prunella vulgaris*, etc.

In the profile (Fig. 6 A), *Cornus* is abundant near the luxuriant meadow and in the profile Fig. 9 C, it is dominating near a spot where water oozes out of the soil; both localities are characterized by very slowly flowing soil water and, hence, they may be relatively good from an edaphic point of view. Measurements of soil-acidity from spots with abundant *Cornus* (pH 3.8, 4.1, 4.1, 4.5, 4.7) and its occurrence in raised bogs, however, indicate that the pH domain of the species is rather large, including very acid and moderately acid soils.

The variability is slight and its value as a guiding species is considerable.

Vaccinium myrtillus[1] forms alpine heaths particularly in those parts of Scandinavia where the snowfall is heavy (DU RIETZ). The plant is weakened when the snow cover is incomplete or of short duration (NORDHAGEN 1928, p. 224). In Iceland, the Faroes (B. 1937b, p. 176) and the Alps (GAMS 1940, p. 15), its occurrence reminds us of that of the Scandinavian mountains. In England, on the other hand, bilberry may be the dominant species on the exposed, wind-swept ridges and summits (LEACH 1925, p. 89), and in Oberharz, it seems to be constant and rather frequent in the wind-swept heaths (TÜXEN 1937, p. 122). The mode of occurrence mentioned by LEACH may be a local behaviour due to the high humidity of the air. In Den-

[1] On biology, structure, and range, cf. GREVILLIUS and KIRCHNER, and B. 1937 a.

mark, bilberry is only of common occurrence in acid woods and northern heath slopes and we may also explain this fact by the air humidity and low summer temperatures of the spot.

Possibly, the alpine British plants belong to a special dwarfish race (*f. pygmaea* Ostf.). Alpine dwarfs of this species are mentioned in Tansley's work (1939) and a single observation made by the writer points in the direction that *f. pygmaea* is not a modification[1]. He has cultivated a dwarf individual from the Faroes mountains and a Danish individual which originally was of the same size as that from the Faroes. The plants have been kept in pots with acid soil for five years. The alpine plant has reached a height of 3.4 cm. and the largest leaves are 1.06 × 0.9 cm.; the corresponding measures of the Danish plant are 7.5 and 1.6 × 1.0 cm. Unfortunately, the cultivation was difficult owing to the special soil requirements of the plants.

The frequency of bilberry in relation to the exposure of the slope is beautifully shown in the figures of Hammer Pedersen (1938, p. 345: F $^0/_0$ N.N.E.-slopes 69, W.N.W.-slopes 28, E.S.E.-slopes 1 and S.S.W.-slopes 0)[2]. The *Calluna-Vaccinium myrtillus* heath is the most important heath within our main type; it has been described by Hammer Pedersen, B. 1941 a, and is moreover mentioned in Table 2. In No. 1, an example of a scrub rich in *Vaccinia* is given.

Trientalis europaea is a northern species in Denmark (cf. Sørensen's map) associated with acid woods and heaths, especially the types rich in hygrophytic mosses. In level heath areas, it is sometimes rather common on deep acid peat, e. g. in heath vegetation developed on very old fields (B. 1941 a, Table 34, pp. 158, 226; cf., furthermore, Mølholm Hansen 1932, Table 4 a). The highest frequency is reached in places with abundant *Cornus suecica* (Table 3, Nos. 1—5). *Melampyrum vulgatum* is also a boreal plant af acid woods.

Lathyrus montanus has a suboceanic, montane-mediterranean range (Hård 1935, p. 368, Hermann 1936, p. 35). Outside woods, it is most frequent in our main type, but occurs also, though very scattered, in level heaths on raised, stony beaches (Loc. 61). At Pikkerbakke (Loc. 4, Table 2, No. 13) and Tolne (Loc. 5, Table 3), it is abundant in the *Callunetum*, and the same is the case on the western slope of the tumulus Maglehøj near Loc. 60 (Table 4, No. 11).

Lonicera periclymenum is suboceanic (map in Czeczott 1926, p. 387; notes in Hermann 1936, p. 36), not continental (cf. Matthews l. c., p. 46). In Denmark, it is sometimes dominant in the field layer (and as a woody climber) in oak scrub. In the heath, it is only met with near scrub or woods (Gern Bakker, Loc. 36; Kullen, Loc. 78, Table 2, Nos. 10—12).

The following species are widely distributed and not northern. As in the case of *Hylocomium splendens* and *triquetrum* they are, with the exception of *Polypodium*, characteristic of the main type A, the northern variety of *Callunion balticum* (main type G) as well as the *Myrtillion alpinum*.

Rumex acetosa is valuable as a "Differentialart" in the separation of A- and related G-heaths from other heath types.

Solidago virga-aurea has some predilection for northern heath slopes (B. 1941 a, Table 50, No. 4) but is otherwise found in oak scrubs or woods and on northern grassy slopes on neutral-alkaline soils. In the level heaths, it is occasionally frequent in successional stages after cultivation and burning (B. 1941 a, Table 26). Owing to the great variability (cf. Turesson's works), the value of *Solidago virga-aurea* s. l. as a guiding species is very limited.

Luzula pilosa has a wide range in Europe (Wiinstedt) and Asia (eastwards to Lake Baikal). In southern Europe it is montane. Outside woods, it is found only in the main heath type in question and the related *Phyllodoco-Myrtillion*. Hence, it is a valuable character

[1] On true modifications, see Grevillius and Kirchner (1923, p. 107), and Firbas (1931, p. 516).

[2] *Vaccinium myrtillus* occurs sometimes also on level ground or even on southern slopes. On the summits of Kullen a *Calluna-Vaccinium myrtillus* (*Deschampsia*) soc. was found on an almost level area which had probably been burnt formerly.

species. Plants from alpine heaths (Table 1, No. 15) and from temperate beech woods are genetically different. The alpine plants are 7—10 days earlier as compared with the wood plants (Fig. 10).

Polypodium vulgare. Owing to the great content of different races, the distributional type is difficult to establish. The maps in FERNALD (1929) and HULTÉN (1941) suggest a sub-oceanic range. On the other hand, the wide range in Asia (map in FOMIN 1930) suggests a widely distributed type. *Polypodium* covers the soil in many oak scrubs. This *Polypodium* society may occur on slopes above the *Blechnum* societies (Fig. 8 in B.) or on western slopes exposed to wind (Table 2, No. 3). Outside woods, *Polypodium* may be abundant on northern slopes with heath or acidic grassland. At Gilleleje (Loc. 56), it forms dense patches of a *Polypodium-Vaccinium myrtillus* soc. On the Island of Bornholm, it is very frequent in northern slopes of old blow-outs (Table 15, No. 4) or, as in the case of the heaths of Kullen (Table 2), in *Calluna-Hylocomium* heaths on rocky ground (Table 15, No. 3). At any rate, *Polypodium* is useless as a guiding species; however, it may be of some importance for the separation of the A- and related G-heaths from other heath types.

Fig. 10. Transplant individuals of *Luzula pilosa* from the alpine heaths at Haukelisæter, Norway (to the right) and from a *Deschampsia* soc. in Geel Skov (beech wood) near Copenhagen (to the left). B. photo, April 7th, 1941.

Among the 16 vascular plants mentioned above, 6 are oceanic-suboceanic, 10 montane or northern, and 4 widely distributed. True continental species are lacking in the tables, but in the keys to the tables *Scorzonera humilis* and *Pimpinella saxifraga* are mentioned. Furthermore, *Majanthemum* may be classified as a subcontinental species (cf. MATTHEWS who terms it "northern-continental")[1]. A few other plants occasionally entering northern slope heaths are also slightly continental (*Carex montana, Primula veris,* B. 1941 a, p. 60), subcontinental or continental (*Lycopodium complanatum, Calamagrostis arundinacea,* see later). Heaths with abundance of some northern continental species and with hygrophytic bryophytes in the ground layer belong to a transition type between the main types A and C.

In addition to the numerous wood plants among the guiding species or other characteristic species, a number of other, more widely ranging wood plants may be particularly frequent in main type A. Thus, *Deschampsia flexuosa,* which is an important character species in the alpine *Myrtillion,* gets higher F $^0/_0$ values on northern slopes as compared with southern ones (HAMMER PEDERSEN, Table 5; B. 1941 a, Table 50). The same is the case with *Pteridium aquilinum* (see later, p. 77). *Anemone*

[1] It is widely distributed (map in LIPPMAA 1938, p. 53), but is lacking in Ireland, rare in Great Britain and West France, lacking in the Faroes, Rundöy, Froöene, Utsire and the westernmost parts of the Sogn district in Norway.

Table 4. Heaths related to *Myrtillion boreale*. Method: D.

Analysis No.	Distributional type	1	2	3	4	5	6	7	8	9	10	11
Locality No.		6	6	6	6	6	6	74	74	5	5	60
Exposure		—	—	—	—	—	—	—	—	—	W	W
Slope		—	—	—	—	—	—	—	—	—	15°	25°
1.												
*Vaccinium myrtillus	b(al)sx	1	1	1	1	1	3+	—	—	1	—	—
— vitis idaea	bs(┐)	3	3	3	2	3	4	2	2	1	—	—
*Trientalis europaea	b(al)sx	—	1	—	—	1	—	1	1	—	—	—
Antennaria dioeca	bsx	—	—	—	—	—	—	3	1	—	2	—
Habenaria albida	bo_2Mo	1	1	2	—	—	—	—	—	—	—	—
Arnica montana	$so_2(H)Mo$	1	2	3	—	—	2	1	—	—	—	—
Carex ericetorum	bsc_1	1	—	—	—	—	—	—	—	—	—	—
— montana	sc_3Mo	2	—	—	—	—	+	—	—	—	—	—
2.												
*Lathyrus montanus	so_3	1	—	1	—	+	—	—	—	—	3	3
Calluna vulgaris	sbo_3	5	4	4	5	5	+	5	5	5	5	5
Galium saxatile	sbo_2	1	—	—	—	—	1	—	—	—	—	—
Sieglingia decumbens	sbo_3	1	1	—	—	—	1+	—	—	—	1	—
Carex pilulifera	sbo_3	1	—	1	—	—	—	—	—	—	—	—
— arenaria	so_2	—	—	—	—	—	—	—	—	1	—	—
Erica tetralix	so_1	—	—	—	—	—	—	—	—	1+	—	—
Euphrasia gracilis	so_2	—	—	—	—	—	—	—	1	—	—	—
3—4.												
*Solidago virga-aurea	sbxp	—	1	—	—	—	—	—	—	—	—	—
*Rumex acetosa	sbxp	—	—	—	—	—	—	—	—	—	—	1
Lycopodium clavatum	sbx	2	2	1	2	1	4	4	3	—	—	—
Deschampsia flexuosa	sbax	1	1	2	1	—	2	—	—	1	1	2
Festuca ovina	sbxp	1	—	2	—	—	1	1	2	—	—	—
Potentilla erecta	sbxp	1	—	—	—	1	1	1	1	1	—	—
Hieracium umbellatum	sbxp	1	—	—	—	1	1	—	—	—	—	1
Campanula rotundifolia	sbaxp	—	—	1	—	—	—	—	—	—	—	1
Platanthera bifolia	sbx	—	—	—	+	—	—	—	—	1	—	—
Anemone nemorosa	sbxp	—	—	—	—	1	—	—	—	—	—	+
5—6.												
Hylocomium schreberi	—	4	1	1	3	2	1	1	3	5	5	—
— splendens	—	—	—	—	2	2	—	—	—	3	+	—
Pseudoscleropodium purum	—	—	—	—	—	—	—	—	—	—	—	1
Hypnum cupressiforme	—	1	+	+	1	—	1	—	—	2	2	—
7.												
Cladonia silvatica	—	—	4	—	2	—	2	—	—	—	2	—
— impexa	—	1	—	—	—	—	4	—	—	1+	1	—
— rangiferina	—	—	—	—	—	—	1	—	—	—	—	—
Cetraria islandica	—	2	—	—	—	—	—	—	—	—	—	—

*) characteristic A-type species.

Vegetation: Nos. 1—3: patches with *Habenaria albida*, in No. 3: 9 specimens in 1 square metre. Nos. 4—8: patches with *Lycopodium clavatum*, cf. text, p. 76. No. 9: somewhat moist variety with *Erica* and *Platanthera bifolia*, cf. text, p. 92. Nos. 10—11: patches with *Lathyrus montanus*, in No. 11: var. *tenuifolia* Raf.

Species groups: As in Table 2; however, 7: lichens.

Species not mentioned in the table: No. 1: *Hierac. pilosella* 1. No. 3: *Agrostis canina*, *Anthoxanthum*, *Luz. multifl.*, *Blephar. ciliaris* 1. No. 5: *Majanthemum* 1, *Lophocolea bidentata* +. No. 6: *Hypochoeris maculata* (sbc_3), *Dicran. rugosum* 1. Nos. 7—8: *Lotus corn.*, *Agrostis stolonif.* 1. No. 9: *Molinia*, *Succisa* 1. No. 10: *Viola canina* 1. No. 11: *Luzula campestris*, *Fissidens adianthoides* 1.

nemerosa is sometimes rather frequent on northern heath slopes (Loc. 6, 19, 44, 70). In the Randbøl area (B. 1941 a, p. 179) and on the Halland ridge (Loc. 79), *Equisetum silvaticum* occurs on northern slopes or in depressions of the hills where water oozes out.

Before leaving the A-type, we may mention three species which belong to distributional types closely related to the A-guiding species and which sometimes occur in heaths belonging to the A-type or related types. Some of these heaths (cf. Table 4) form a transition between the A-main type and the Dutch *Calluna Genistetum* subass. with *Orchis maculatus* (cf. Tüxen 1937, pp. 120—121).

Fig. 11. Burdus hall, Hovs Hallar, Sweden (Loc. 75). Northern exposed gneiss rocks. In the foreground, maritime *Empetrum* heath with *Ligusticum* exposed to wind and spray. In the background, *Callunetum* in old shingle at the bottom of the scree. B. photo 1934.

Habenaria albida is a montane, suboceanic species ranging from East-America-Greenland (var. *straminea*) to Scandinavia and the mountains in Central Europe. The writer has observed it in the heath of northern Jutland (Loc. 6) growing at the bottom of a small valley in a *Calluna* heath very rich in species. Obviously, this heath (Table 4, Nos. 1—3) is closely related to the A-type and the heath patches rich in *Arnica* or *Lyc. clavatum* (Table 4). As regards the occurrence in dune heaths, see later (p. 86).

Arnica montana. The distribution of this species is somewhat problematic. It is clearly montane, but not subarctic or boreal. According to Hård (1935, p. 185), its northern limit in Sweden is not conditioned by the lower temperatures. The limit reminds us of that of true suboceanic species and of the boreal-montane-suboceanic *Ajuga pyramidalis*. In Norway and Denmark, its distribution corresponds to that of many oceanic species. In northern Germany, it decreases in frequency from west to east, reaching, however, Poland and Lithuania. The total range includes western Europe (excluding the British Islands), Scandinavia, Central European mountains, and mountains of the northern parts of the three south-European peninsulas and of Portugal. Thus, it seems to be montane and suboceanic, and its absence from Britain may perhaps be due to historical factors.

In Denmark, *Arnica* is found mainly in heaths, more rarely in acidic grassland. It is most frequent in heaths with richer soils and is sometimes dominant in successional stages after cultivation or burning (B. 1941, pp. 120—121). In patches, it dominates northern slopes where water oozes out (B. 1941 a, Table 57 and Fig. 52,4). In Norway, Sweden (see STERNER 1921, p. 342) and more rarely in Jutland, it occurs abundantly in woodland meadows or acidic grassy slopes.

In northern Germany, it is rare in heaths (JONAS 1935, LANGERFELDT 1939, p. 19, LIBBERT 1940, p. 124). In the vicinity of Giessen in central Germany, it is rare, occurring in low mountains (altitude 330 m.) in heathlike communities very rich in species, mostly clothing northern slopes or temporarily shaded ground (SCHNELL 1935). In the low mountains south of Waldenburg, *Arnica* occurs abundantly in a similar, although more meadowlike heath (LIBBERT 1939, pp. 83—84; cf. below p. 104).

Ligusticum scoticum is a north-Atlantic species. According to ROSENVINGE it grows in Greenland on the beach and higher up in heathlike vegetation. In Sweden, it occurs, though not frequently, in the maritime heaths of Kullen and Hovs Hallar where also *Silene maritima*, *Armeria*, and *Plantago maritima* enter the heath from the more saline vegetation below. Single individuals of *Ligusticum* are found in typical A-heaths (Table 2); but when this plant increases in frequency, the heath vegetation is very deviating and shows a close relationship to *Festuca rubra* salt marshes (Fig. 11).

B. Heaths characterized by northern species; oceanic or continental elements reduced (*Empetrum-Vaccinium vitis idaea*-group of *Empetrion boreale*).

The main type B comprises a number of heaths which are phytogeographically situated between the preceding and the succeeding main types. In Denmark, the heaths in question cover the largest areas. The inland heaths of Jutland are to a large extent covered with *Calluna*, *Empetrum*, and *Vaccinium vitis idaea* and the many dry coastal dune heaths contain *Calluna* and *Empetrum*. In some localities, however, the southern heath dwarf shrubs, *Genista anglica* and *pilosa*, are rather frequent and such heaths form transitions to the German-Dutch heath series.

With respect to their ecology, the B-heaths are rather different, due mainly to the soil conditions. We may subdivide the B-type in an inland type on more or less heavy podsolated soils derived from glacial sands and a coast type on alluvial soils generally almost without podsolation. Such a subdivision may perhaps be rather valuable, but it does not lead to a plant-geographical classification. Moreover, it became apparent that no distinct limitation could be obtained between the subclimax *Calluna-Empetrum* heaths of coast and inland. It is first of all the successional stages, the young dune heaths, which differ from the typical *Calluna-Empetrum* heaths by their content of a number of dune species and the moderately acid soils. In the sequel, these successional stages are considered separately, and the subclimax heaths are divided into two subtypes which seem to be of regional plant-geographical importance.

The *Calluna-Vaccinium vitis idaea-Empetrum* heath. This heath was described by B. (1941 a, pp. 142—150, Table 53, No. 1, Table 58 and p. 185—187). On the Randbøl heath, it is mostly developed on very old inland dunes and in such localities *Empetrum* tends to occur with the greatest shoot-density (Table 5, No. 8).

Table 5. Heaths of the *Empetrion boreale* (B main type). Method: S.

Analysis No.	Distri-butional type	1	2	3	4	5	6	7	8	9	10	Con-stancy pCt.
Locality No.		31	31	31	40	40	41	41	45	32	32	
pH		3.3	3.3	3.2	3.5	3.4	3.5	3.3	4.2	4.2	4.2	
1.												
Empetrum nigrum	bsΓ	8_7	10_6	9_9	4	8_5	1	+	10_{10}	6	7_3	**100**
Vaccinium vitis idaea	bs(˥)	10_8	10_5	10_7	10_8	10_5	10_1	7_3	10_9	3	5	**100**
Arctostaphylos uva ursi	bsc_3 (Γ)	+	+	+	—	—	3	+	+	+	+	**80**
Vaccinium uliginosum	bsΓp	—	—	—	+	+	—	—	—	—	—	20
Trientalis europaea	b(al)sx	—	—	—	—	—	—	—	—	1	1	20
Arnica montana	so_2(H)Mo	—	—	—	—	—	—	—	—	+	+	20
2.												
Calluna vulgaris	sbo_3	10_8	7_7	8_5	10_7	10_7	10_{10}	10_9	6	10_{10}	10_{10}	**100**
Genista anglica	sdo_1	—	—	+	—	—	+	—	—	+	+	40
— pilosa	sdo_2(H)	—	—	—	—	—	—	—	—	+	+	20
Scirpus caespitosus	sbo_3	+	+	+	—	—	—	—	2	+	+	60
Juncus squarrosus	sbo_2	—	+	+	—	—	+	1	—	—	—	40
Sieglingia decumbens	sbo_3	—	—	—	—	—	—	—	—	+	+	20
Carex pilulifera	sbo_3	—	—	—	—	—	—	—	—	+	+	20
3.												
Deschampsia flexuosa	sbax	1	4	5	1	1	—	1	2	1	3	**90**
Carex stolonifera	sbx	8_5	+	+	1	+	+	+	—	—	—	70
— panicea	sbx	+	1	1	1	+	—	—	—	3	2	70
Molinia coerulea	sbxp	+	+	+	—	—	—	—	—	+	+	50
Agrostis stolonifera	sbxp	—	—	—	—	—	—	—	—	1	2	20
Populus tremula	sbx	1	+	+	—	—	—	—	—	1	2	50
4.												
Cladonia impexa	—	6	9_8	10_9	10_9	10_8	10_8	10_{10}	10_6	10_8	9_3	**100**
— silvatica	—	8_8	8_5	5	5	6	3	2	—	4	3	**90**
— rangiferina	—	+	+	3	+	+	—	—	1	8_0	2	**80**
— uncialis	—	4	1	+	+	+	+	+	—	3	2	**90**
— chlorophaea	—	4	3	1	4	1	4	1	1	—	—	**80**
— squamosa	—	+	+	+	1	+	+	+	—	—	—	70
— crispata	—	1	—	—	—	—	+	+	—	—	—	30
— gracilis	—	—	1	+	—	+	+	—	—	—	—	30
Cetraria tenuissima	—	3	+	1	+	+	+	1	—	—	—	70
— glauca	—	—	—	+	1	+	1	—	—	—	—	40
Parmelia physodes	—	3	2	4	6	4	8_2	9_1	—	—	—	70
— tubulosa	—	—	—	—	—	—	3	1	—	—	—	20
5.												
Hypnum cupressiforme	—	7_3	5	6	8_1	3	7_0	5	10_8	9_7	10_9	**100**
Hylocomium schreberi	—	1	2	1	4	3	1	+	10_7	—	5	**90**
Dicranum scoparium	—	1	+	+	1	1	6	2	—	2	1	**90**
Blepharozia ciliaris	—	+	+	+	1	+	—	—	7_4	5	3	**80**
Polytrichum piliferum	—	—	—	—	3	1	—	—	—	—	—	20
Jungermannia ventricosa	—	—	—	—	1	+	—	—	—	—	—	20

Species groups: 1: northern (montane) species. 2: suboceanic (oceanic) species. 3: widely distributed species. 4: lichens. 5: bryophytes.

Species not mentioned in the table: No. 9: *Scorzonera humilis* (sc_2) +. Nos. 2, 3, 4: *Cladonia cornuto-radiata* +—1. Nos. 3, 5, 6: *Cladonia glauca* +—1. No. 5: *Cladonia furcata* +, *Cladonia floerkeana* +. No. 6: *Cetraria juniperina* 1. No. 9: *Dicranum rugosum* 1. No. 10: *Dicranum spurium* 1. Nos. 1, 2, 3, 5: *Marasmius androsaceus* +—3.

In those heaths which clothe the infertile plains or the heavy podsolated areas of the old "hill islands", *Vaccinium vitis idaea* is generally more frequent than *Empetrum* or even, together with *Calluna*, the only dominant among the flowering plants. On the other hand, *Empetrum* is lacking in the relatively rich *Calluna-Vaccinium vitis idaea* heaths in Sweden (Loc. 74, see Malmström 1937).

The soils of this heath type are very acid (Randbøl heath pH 3.4—4.4, Table 5, pH 3.2—4.2; Grindsted heath, according to Weis, pH 3.6—3.7). The thickness of the raw humus layer varies between 3 and 11 cm. Concerning soil profiles, see Weis and B. 1941 a, for chemical analyses, see Weis.

As in the case of the *Arctostaphylos* heath (p. 50), the number of phanerogams is very low. This must probably be due to the soil reaction. From Table 5, which shows an analysis of typical *Calluna-Vaccinium vitis idaea-Empetrum* heaths, it is evident that the heath from hill islands (Loc. 32) and the old inland dunes (Loc. 45), where the pH values are relatively high, houses the largest number of species or deviates by the high F percentage for *Empetrum*. In the table, only heaths rich in *Cladina* are given. In somewhat moister localities, bryophytes dominate the ground layer and *Cladina* species are less frequent. This is the case on slopes, cf. Table 6 No. 7 (Hjerl Hede) and B. 1941 a (Tables 45 and 53, No. 1). In such heath with dominating mosses, *Deschampsia flexuosa* may be co-dominant or shows great shoot density and *Orchis maculata* gets F percentages up to 60. Simultaneously, the number of phanerogames increases. In the Randbøl Hede, *Orchis maculata* is only abundant in slopes with slowly oozing soil water. From an edaphic point of view, such habitats are relatively rich and such heaths may be related to the *Calluna-Genista* heath with *Orchis maculata* which has been reported from NE Holland on relatively rich soils. The Swedish heaths mentioned by Malmström are also rich in bryophytes and phanerogams and here, too, the soil is relatively fertile. Where the slopes incline in a northerly direction, the B- and A-main types merge into each other.

Apart from *Calluna*, oceanic or suboceanic plants play no considerable part in the vegetation. In very old heaths, *Calluna* is frequently scattered, probably because the plants die out and conditions are bad for the germination of seeds and the growing of seedlings. Thus, in the sublimax heath of Jutland, the heather is not always the most prominent plant; the complete dominance of *Calluna* is mostly obtained in heaths on burnt areas, on old fields which have been colonized by the heather, or on areas otherwise influenced by man (cf. p. 51).

The plant-geographical relations of the *Calluna-Empetrum-Vaccinium vitis idaea* heath are easily ascertained. To the south, there are clear relations to the *Calluna-Genistetum*, which may occur already in Denmark, but which is the dominating heath type in North Germany. In the German mountains, closely related *Calluna-Vaccinium-Empetrum* heaths occur (see Tüxen 1937, Schwickerath 1933, p. 112 "nordisch montane Subassoziation"). To the north, the relations are equally distinct. Here, a number of alpine heaths occur which, in respect of their ecology (snow covering) are situated between the *Loiseleuria*- and the *Phyllodoce* heaths. According to Nord-

Table 6. Heaths of the *Empetrion boreale* (B main type) and profile transect through Hjerl Heath. Method: S (R in No. 5). In No. 5 the first value is the constancy (5 = 100 %), the second one is the average frequency in percent.

Analysis No.	Distri-butional type	1	2	3	4	5	6	7	8	9	Constancy % Nos. 1—6
Locality No.		24	24	24	24	47	21	21	21	21	
pH		3.4	3.7	3.3	3.5	—	4.3	4.2	3.8	4.0	
1.											
Empetrum nigrum	bs⌈	10_{10}	10_8	10_9	9_7	5; 96	10_8	8_7	—	—	**100**
Vaccinium vitis idaea	bs(⌉)	—	—	—	—	—	—	10_7	3	—	—
2.											
Calluna vulgaris	sbo_3	8_4	4	5	9_8	5; 90	10_4	10_7	1	—	**100**
Scirpus caespitosus	sbo_3	+	+	+	+	5; 5	+	—	—	—	**100**
Erica tetralix	so_1	—	—	—	—	2; 2	—	2	+	—	20
Galium saxatile	sbo_2	—	—	—	—	—	—	—	2	1	—
Carex pilulifera	sbo_3	—	—	—	—	1; 2	—	—	—	—	10
— arenaria	so_2	3	2	2	3	—	5	6	1	—	50
3.											
Deschampsia flexuosa	sbax	2	1	1	2	3; 5	—	7_3	10_9	1	70
Carex stolonifera	sbx	—	—	—	—	1; 1	—	—	8_3	10_{10}	10
— panicea	sbx	+	1	2	+	5; 20	+	2	2	—	**100**
Molinia coerulea	sbxp	—	—	—	—	1; 2	—	+	—	—	10
Agrostis canina	sbxp	—	—	—	—	—	—	—	—	1	—
Festuca ovina	sbxp	—	—	—	—	—	—	—	—	1	—
Luzula multiflora	sbxp	—	—	—	—	—	—	—	1	—	—
Potentilla erecta	sbxp	—	—	—	—	—	—	—	3	—	—
4.											
Cladonia impexa	—	8_3	8_6	8_5	10_5	5; 100					**100**
— silvatica	—	6	10_4	10_5	8_6	5; 97	10_{10}	2	—	—	**100**
— rangiferina	—	1	3	2	3	5; 88					**100**
— uncialis	—	+	1	2	1	5; 91	—	—	—	—	**90**
— chlorophaea	—	2	1	1	1	5; 68	—	—	—	—	**90**
— squamosa	—	+	—	+	1	5; 51	—	—	—	—	**80**
— crispata	—	—	—	—	—	5; 47	—	—	—	—	50
— gracilis	—	—	—	—	—	1; 2	—	—	—	—	10
Cetraria tenuissima	—	1	2	5	3	5; 59	—	—	—	—	**90**
— islandica	—	1	1	3	2	—	—	—	—	—	40
Parmelia physodes	—	1	+	2	1	—	—	—	—	—	40
5.											
Hypnum cupressiforme	—	10_5	10_2	10_2	10_4	5; 98	10_3	10_4	10_8	6	**100**
Hylocomium schreberi	—	9_6	9_5	10_3	7_3	5; 30	7_2	2	4	7_3	**100**
Dicranum scoparium	—	4	6	7_1	6	4; 7	1	—	2	—	**90**
Blepharozia ciliaris	—	7_1	7_2	6	7_2	5; 49	1	3	9_5	—	**100**
Leucobryum glaucum	—	—	—	—	—	3; 11	—	—	—	—	30

Vegetation: Nos. 1—6: *Calluna-Empetrum-Cladina* heath. (No. 5 is taken from Mølholm Hansen's work, Table 3a Nos. 1, 2, 4, 5, 6). Nos. 6—9: profile transection of one of the large depressions in Hjerl Heath near the lake Skallesø. No. 6: near the top of the slope, inclination 10° (Exp. N). No. 7: at the bottom of the slope, inclination 5° (Exp. N.). No. 8: *Deschampsia* margin vegetation forming a circular zone outside the central *Carex stolonifera* meadow (No. 9) which clothes the bottom of the depression.

Species groups: As in Table 5.

Species not mentioned in the table: No. 4: *Cetraria glauca* and *Parmelia sulcata* +. No. 5: *Cladonia destricta* 4; 19, *Cl. floerkeana* 4; 10, *Cl. pleurota* 2; 4, *Rhacomitrium hypnoides* 3; 4, *Cephaloziella divaricato* 2;4, *C. elachista*, *Jungerm. porphyroleuca*, *J. excetiformis* and *Hypnum imponens* 1; 1. No. 7: *Lophocolea cuspidata* 1. No. 9: *Hylocomium squarrosum* 1.

HAGEN (1928, p. 210), such heaths cover large areas in the Sylene mountains. *Empetrum (hermaphroditum), Vaccinium vitis idaea, Carex rigida, Cladonia silvatica* coll., *rangiferma, gracilis,* and *Dicranum scoparium* are dominants or very constant. In other places, a *Calluna-Cladina* heath with *Hylocomium schreberi* occurs.

The *Calluna-Empetrum* heath.. First RAUNKIÆR (1909, 1934, p. 269), later MØLHOLM HANSEN (1932, pp. 131—132) and, finally, the writer (1941 a, Table 37, Nos.

Fig. 12. Hjerl heath (Loc. 21). In the foreground, *Calluna-Empetrum* heath. In the background, a number of pot-shaped depressions (Jordfaldshuller) which have arisen after the melting of isolated small parts of the inland ice. WM. BERTHELSEN photo.

5—6, Table 45, No. 1) have published analyses of this heath. In the Nørholm heath, it is a very important type and the same may be the case in the Knude-Ting heath. In Randbøl heath, dry vegetations without dominating *Vaccinium vitis idaea* are rather rare and the same applies to a large number of inland heaths which were analyzed by C. A. JØRGENSEN and the writer (Table 5). In the Randbøl region, the *Calluna-Empetrum* heaths are generally found in places where the vegetation is rather young and where sometimes the raw humus layer is comparatively thin. Thus, the *Calluna-Empetrum* heath appears to be developed on drier soils (with lower water capacity) than the heath with *Vaccinium vitis idaea.* A profile transection through one of the depressions in Hjerl Hede (cf. Fig. 12) points in the same direction. Here (Table 6), a *Calluna-Empetrum* heath is gradually succeeded downwards by a *Calluna-Empetrum Vaccinium vitis idaea* heath which near the bottom of the depression (with *Carex stolonifera* soc.) is followed by a narrow zone with a *Deschampsia flexuosa* soc. This fact, however, does not explain vegetation why the heath with *Vaccinium vitis idaea* seems to be absent or rare in the areas investigated by RAUNKIÆR and MØLHOLM

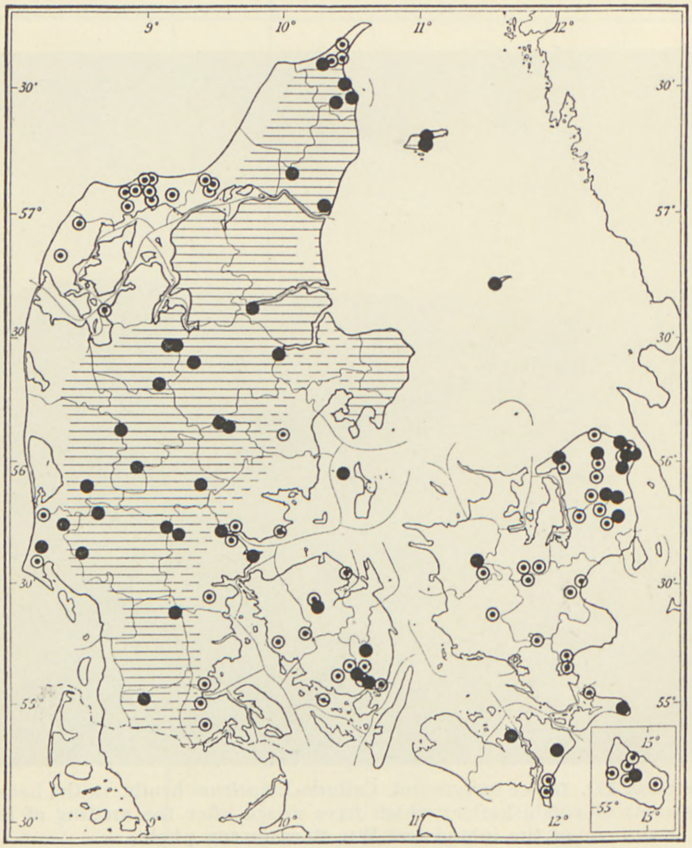

Fig. 13. *Vaccinium vitis idaea* in Denmark. After B. 1937 a.

HANSEN: A glance at the map, Fig. 13, showing the Danish area of *Vaccinium vitis idaea* may give the explanation. From this map, it is evident that the red whortleberry is very rare in West Jutland; the heath localities investigated by RAUNKIÆR and MØLHOLM HANSEN (Loc. 42, 47) are situated near the frequency limit of the species. The range of *Vaccinium vitis idaea* in Denmark was discussed in B. 1937 a (pp. 24—25). The absence in West Jutland, it was suggested, was a result of edaphic differences, historical factors (formerly the species was probably frequent in pine woods in Central Jutland), or anthropogenic factors (effects of fire). Keeping in mind the fact that the two heath areas in question as well as Hjerl Hede (Loc. 21) and Klosterhede

(Loc. 26), where the plant also is more scattered or rare, have been exposed to the same anthropogenic influences as Randbøl Hede and Karup Hede, the question arises whether its sporadic occurrence in West Jutland should be a function of the climate (mild winters). In the Faroes, *Vaccinium vitis idaea* is extremely rare and, according to Ostenfeld, it may be taken for granted that it does not bear fruit on the

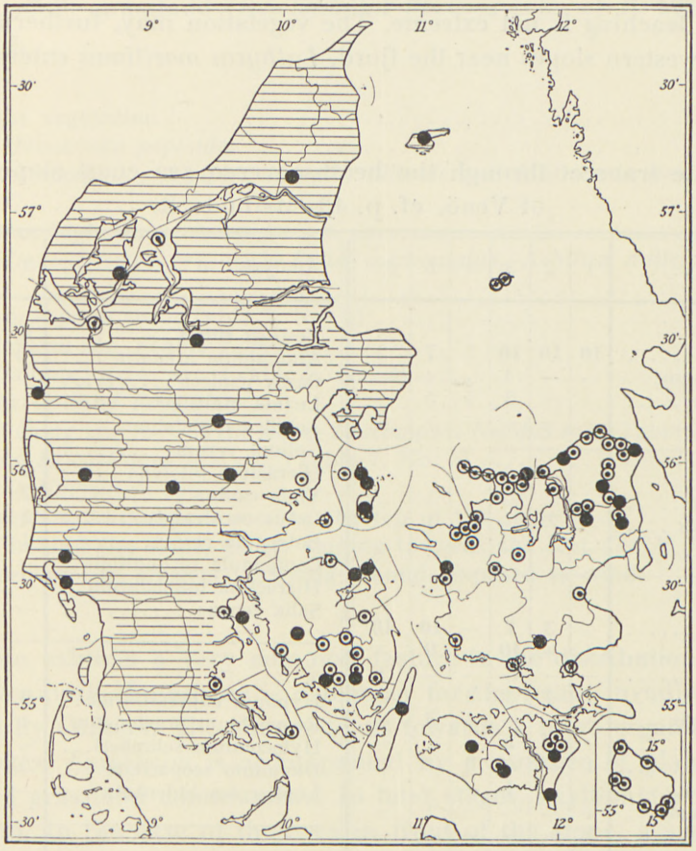

Fig. 14. *Empetrum nigrum* in Denmark. After B. 1937 a.

islands. In Iceland too it is very rare. This fact and the continental behaviour of *Vaccinium vitis idaea* var. *minus* in Greenland (B. 1938, p. 162) indicate that *Vaccinium vitis idaea* may have some predilection for continental boreal climates. In the southern part of the range, it seems to avoid coast areas, while *Empetrum* near the southern frequency limit to some extent keeps to coast areas (e. g. North Germany, Bornholm, see Fig. 14 (right corner)).

Hence, the heaths rich in *Vaccinium vitis idaea* may, plant-geographically, be rather closely related to the *Arctostaphylos* heaths. In Sweden, the *Calluna* heaths rich in *Vaccinium vitis idaea* are frequent (see, e. g. Malmström 1937) while *Calluna-Empe-*

trum heaths may be very local. They were observed at Torekov and Haverdal near the sea (Loc. 73 and 76) and occurred frequently on rather wet soils.

A large area covered with *Calluna-Empetrum* heath is found near the manor seat Kaas at the Limfjord (Loc. 24). This heath (Table 6, 1—4) is very exposed to the wind and forms in every respect a transition to the dune heaths. The heath at Kaas occupies level- or somewhat hilly ground; the soils are of glacial or alluvial origin, and the leaching is not extreme. The vegetation may, furthermore, be rather young. On the western slopes near the fjord, *Lathyrus maritimus* enters the *Empetrum* heaths.

Table 7. Profile transect through the heath-covered sea coast slopes of the island of Venö, cf. p. 43. Method: R.

Analysis No.	1	2	3	4	5	6
1.						
Empetrum nigrum	**10**	**10**	**10**	5	**7**	2
Vaccinium uliginosum	—	—	4	—	+	—
Trientalis europaea	—	—	3	5	5	—
Blechnum spicant	—	—	—	—	+	—
2.						
Polypodium vulgare	—	—	—	—	+	—
Solidago virga-aurea	—	—	—	—	1	—
Rumex acetosa	—	—	—	5	—	—
3.						
Calluna vulgaris	+	3	**7**	—	**10**	**10**
Erica tetralix	+	+	**10**	—	**9**	—
Genista anglica	—	—	—	—	—	1
Carex arenaria	1	4	3	2	1	—
Sieglingia decumbens	—	—	—	4	3	—
Juncus squarrosus	—	—	2	—	—	—
Galium saxatile	1	—	—	**9**	—	—
Pedicularis silvatica	—	—	1	—	—	—
Hypericum pulchrum	—	—	—	—	1	—
Armeria maritima	2	—	—	—	—	—
4.						
Deschampsia flexuosa	—	—	+	**10**	6	1
Agrostis tenuis	—	—	—	**8**	5	—
Nardus stricta	—	—	—	**7**	—	—
Festuca ovina	—	—	1	3	—	—
Festuca rubra	**9**	—	—	—	—	—
Ammophila arenaria	**10**	—	—	—	—	—
Carex panicea	—	—	4	—	—	—
Luzula multiflora	1	—	1	5	2	—
Achillea millefolium	**8**	—	—	—	—	—
Galium verum	4	—	—	—	—	—
Hieracium pilosella	2	—	—	—	—	—
Viola canina	2	—	—	—	—	—
Lotus corniculatus	1	+	+	—	—	—
Potentilla erecta	1	—	2	6	6	—
Campanula rotundifolia	—	—	—	4	1	—
Hieracium umbellatum	—	—	—	—	2	—
Salix repens	—	—	—	—	+	1
5.						
Hypnum cupressiforme	**9**	**8**	**10**	3	**7**	**9**
Eurynchium praelongum	4	—	—	—	—	—
Hylocomium schreberi	—	1	4	**10**	3	1
Dicranum scoparium	—	—	—	1	3	1
Lophocolea bidentata	—	—	—	2	1	—
6.						
Cladonia impexa + silvat.	1	**10**	**7**	1	1	**8**
— rangiferina	—	2	—	—	—	—
— chlorophaea	—	—	2	—	—	—
Cetraria tenuissima	+	+	—	—	—	—
Peltigera canina	—	—	—	1	—	—

Species groups: 1: northern species. 2: species belonging to main type A. 3: oceanic-suboceanic species. 4: widely distributed species. 5: bryophytes. 6: lichens.

The *Empetrum* heath. As an introduction, we may examine a profile running from the beach to the heaths behind the exposed western slopes of the Isle of Venö in the Limfjord (Loc. 25, Fig. 15). From the profile and the corresponding analysis (Tab. 7) it is evident that *Empetrum* is able to dominate heaths placed close to dune grassland. Moreover, it is co-dominant in the exposed *Callunetum* of the slope and, finally, it is co-dominant in the moist *Erica* dune heath (Table 7, No. 3).

The *Callunetum* near the bottom of the slope (No. 5) has also *Erica* as a co-dominant, however, this vegetation belongs, if anything, to the A main type (*Trientalis, Solidago, Hypericum pulchrum, Blechnum, Polypodium*). As in the profile p. 39, Table 6, Nos. 6—9, the dwarf shrub heath disappears at the bottom of the slope and is replaced by acidic grassland (*Deschampsia flexuosa* soc., cf. B. 1941 a, Tables 41, 60 and Fig. 53).

		Distance in m.
1.	Beach without vegetation	14
2.	Beach with *Honckenya peploides*	3
3.	Beach with *Ammophila, Atriplex hastata, littorale* and *Matricaria inodora* var. *maritima*	1.5
4.	Brink Abt. 1 m high. *Armeria vulgaris*	1
5.	*Ammophila-Festuca rubra* soc. with *Lotus corniculatus, Achillea millefolia, and Armeria*	1.5
6.	*Empetrum-Ammophila* soc. (Table 7, No. 1)	5
7.	*Empetrum-Cladina* soc. (Table 7, No. 2)	12
8.	*Empetrum-(Calluna)-Erica* soc. (Table 7, No. 3)	6
9.	As No. 8, but *Calluna* F $^0/_0$ 100	7.5
10.	Narrow zone along the foot of the slope. *Descampsia-Nardus* soc. (Table 7, No. 4)	2
11.	Slope. *Calluna-Erica-Empetrum* soc. (Table 7, No. 5)	10
12.	Slope. *Calluna-Empetrum* soc.	7
13.	*Calluna-Empetrum-Salix repens* soc. on the top of the slope	1.5
14.	*Calluna* soc. behind the slope, gently sloping towards the east (Table 7, No. 6)	6
15.	*Calluna-Empetrum* soc. on gently sloping ground, exposed to wind.	

The profile exhibits a very common feature in the distribution of dune heath sociations in Denmark. *Empetrum* is a pioneer for the heath invading a dune area. It is succeeded by *Calluna*. The change tends towards a more organic and acid soil. In the first stages, *Empetrum* is accompanied by a number of plants belonging to moderately acid grassland communities. In later stages, oxylophytes (e. g. *Cladinae*) are co-dominant. In the case of the area in front of the slope, a succession of this kind is probable for some earlier time; now, however, it may largely have ceased and the zonation in the vegetation may be caused by differences in the supply of basic particles from the sea-shore. The profile contains two important *Empetrum* dune heaths, viz. that developed in dune grassland and that developed in grey, more acid dunes rich in lichens.

On the peninsula of Skallingen (Loc. 48) *Empetrum* colonizes in the fixed dune vegetation. It forms circular patches in the *Thymus-Hypnum cupressiforme* soc. on moderately acid soil or even in the *Festuca rubra-Galium verum-Tortula ruralis* soc. on neutralbasic soils. The pH values found in the *Empetrum* patches are 5.3, 6.7 (*Thymus* soc.) and 6.7, 7.3 (*Festuca* soc.). The most prominent plants in the patches are *Thymus serpyllum, Festuca rubra, Vicia cracca* var., *Hierac. umbellatum, Galium verum, Am-*

mophila, Lotus corniculatus, Anthyllis, Poa pratensis var. *humilis, Trifolium arvense,* and *Hypnum cupressiforme.* The same type of pioneer *Empetrum* dune heaths was observed in numerous localities at the North Sea, Skagerrak, and Kattegat coasts.

In later stages, the patches fuse and large *Empetrum* dune heaths are formed. This type may be exemplified by an investigation of the dunes at Bulbjerg (Loc. 12). The vegetation (Table 8 a, No. 13) was found on a northern dune slope (inclina-

Fig. 15. Heath slopes on the Isle of Venö near the profile transect p. 43. In the background, the Limfjord and alluvial heaths, in the foreground, exposed *Calluna-Empetrum* heath on the slope and very low *Salix cinerea* (× *aurita*) scrub with *Blechnum* dominating in the ground layer (cf. Table 2, No. 5). B. photo 1934.

tion 20°). In still later stages, *Rosa spinosissima* is sometimes dominant (see Table 8 a, No. 12 which is also from a northern slope (inclination 10°) cf. the content of plants from main type A).

The *Empetrum* pioneer heath described by B. 1941 a (Table 16, Nos. 6—9) from Randbøl Hede is devoid of mosses, lichens being very scattered. The development of this type is due to accumulation of sand on the lee side of large inland dunes or in places east of blow outs. The same is sometimes the case in coast dune areas as, e. g., at Loc. 2 and in the dunes at Haverdal in Sweden (Loc. 73) where mosses or lichens are completely absent. Here, *Salix repens* (*arenaria*) and *Empetrum* are able to stand the greatest supply of sand and basic particles (Table 8, No. 14); at some distance from the dunes, *Calluna* and, on moister ground, *Erica tetralix* are co-dominant (Table 8 a, Nos. 15—16).

Where the leaching of the soil advances, *Empetrum* colonizes *Corynephorus* sociations. However, the soil may frequently be too dry for the establishment of a

Table 8a. Heaths of the *Empetrion boreale* (B main type) and heaths related to this type. Method: S.

Analysis No.	Dis-tribu-tional type	1	2	3	4	5	6	7	8	9	10	Con-stancy pCt. Nos. 1—10	11	12	13	14	15	16
Locality No.		13	7	9	2	33	61	61	61	61	61		61	11	12	73	73	73
1.																		
Empetrum nigrum	bsΓ	10_{10}	10_{10}	10_{10}	10_9	10_9	10_8	10_{10}	10_{10}	10_7	10_9	**100**	10_{10}	10_9	10_8	10_8	10_9	10_{10}
Vaccinium uliginosum	bsΓp	—	—	—	2	—	—	—	—	—	—	10	—	—	—	—	—	—
Juncus balticus	bsΓ	—	—	—	7	—	—	—	—	—	—	10	—	—	—	—	—	—
Elymus arenarius	bsx	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	—	—
2.																		
Calluna vulgaris	sbo_3	—	10_5	10_{10}	10_{10}	10_9	4	+	6	10_{10}	10_8	**90**	10_4	—	—	—	10_8	4
Erica tetralix	so_1	—	—	—	+	—	—	—	—	—	—	10	—	—	—	—	—	10_8
Genista anglica	sdo_1	4	—	—	—	9_5	—	—	—	—	—	20	—	—	—	—	—	—
Carex arenaria	so_2	7_2	4	9_2	10_4	10_4	9_2	10_2	6	9_3	10_1	**100**	1	4	4	—	8_1	8_0
Holcus lanatus	so_3	—	—	—	—	—	—	—	—	—	—	—	—	6	—	—	—	—
Corynephorus canescens	sdo_3(H)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	—	—
Armeria maritima	sbo_2	—	—	—	—	—	—	—	—	—	—	—	1	—	+	—	—	—
Galium saxatile	sbo_2	—	—	—	—	—	—	—	1	—	—	10	—	—	—	—	—	—
Hypochoeris radicata	so_3	1	—	—	—	—	—	—	—	—	—	10	—	—	—	—	—	—
Jasione montana	so_3	—	—	—	—	—	—	1	—	—	—	10	—	—	—	—	—	—
3.																		
Rosa spinosissima	sbc_3p	—	—	—	—	—	—	—	—	—	—	—	—	10_5	1	—	—	—
Hypochoeris maculata	sbc_3(⌐)	—	—	—	—	—	—	—	—	—	—	—	6_2	—	—	—	—	—
Pimpinella saxifraga	sbc_3p	—	—	—	—	—	—	—	—	—	—	—	—	—	6_2	—	—	—
Geranium sanguineum	sc_2	—	—	—	—	—	—	—	—	—	—	—	1	+	—	—	—	—
Erigeron acer	sbc_3	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
4.																		
Solidago virga-aurea	sbxp	—	—	—	—	—	—	—	—	—	—	—	—	—	6_1	—	—	—
Rumex acetosa	sbxp	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—
Polypodium vulgare	sbx	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—
5.																		
Salix repens	sx(L)p	—	—	—	4	2	—	—	—	—	—	20	—	—	—	10_6	10_6	10_5
Lotus corniculatus	sbx	—	3	9_4	+	—	+	—	+	1	—	60	—	—	8_3	1	1	—
Hieracium umbellatum	sbxp	—	—	1	—	—	—	1	+	—	—	30	—	—	1	+	—	—
— pilosella	sbxp	—	—	—	—	—	—	2	1	—	—	20	3	—	—	—	—	—
Campanula rotundifolia	sbaxp	—	—	—	3	—	—	1	—	—	—	20	—	—	—	—	—	—
Thymus serpyllum	sbxp	—	—	—	—	—	—	5	+	—	—	20	—	+	—	—	—	—
Anthoxanthum odoratum	sbxp	—	—	—	+	4	—	—	—	—	—	20	—	—	—	—	—	—
Festuca ovina	sbxp	—	—	—	—	—	—	—	—	—	—	—	5	—	—	—	—	—
Deschampsia flexuosa	sbx	—	—	—	—	1	—	—	—	—	—	10	—	—	—	—	—	—
Carex stolonifera	sbx	—	—	—	1	—	—	—	—	2	—	20	—	—	—	—	—	—
6.																		
Festuca rubra var. arenaria	sbx	—	2	—	—	3	—	—	+	—	—	30	2	5	10_5	10_6	10_3	10_2
Galium verum	sbx	—	—	+	—	—	—	+	+	—	—	30	7_0	3	2	—	—	—
Plantago maritima	sbxp	+	—	—	—	—	—	—	—	—	—	10	6_3	—	3	—	—	—
— lanceolata	sbxp	—	—	—	—	—	—	—	—	—	—	—	—	+	1	—	—	—
Achillea millefolia	sbxp	—	—	—	—	—	—	—	—	—	—	—	2	—	5	—	—	—

Table 8 a (continued).

Analysis No. / Locality No.	Distributional type	1 / 13	2 / 7	3 / 9	4 / 2	5 / 33	6 / 61	7 / 61	8 / 61	9 / 61	10 / 61	Constancy pCt. Nos. 1—10	11 / 61	12 / 11	13 / 12	14 / 73	15 / 73	16 / 73
Lathyrus pratensis	sbx	—	—	—	—	—	—	—	—	—	—	—	—	6	—	—	—	—
Vicia cracca	sbxp	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—
Luzula campestris	sbxp	—	—	—	—	—	—	—	—	—	—	—	2	2	1	—	—	—
Ammophila arenaria	sx	—	—	+	—	—	—	—	—	—	—	10	—	1	4	+	—	—
Agrostis stolonifera	sbxp	—	—	—	—	—	—	—	—	—	—	—	—	9_1	—	—	—	—
7.																		
Cladonia imp.-silvat.-mitis	—	10_{10}	10_{10}	9_5	—	—	10_5	10_6	10_{10}	5	3	**80**	—	—	—	—	—	—
— rangiferina	—	—	—	—	—	—	10_8	2	+	—	—	30	—	—	—	—	—	—
— uncialis	—	—	—	2	—	—	—	—	1	—	—	20	—	—	—	—	—	—
— furcata	—	—	—	—	—	—	—	2	—	—	—	10	1	—	—	—	—	—
— chlorophaea	—	—	—	—	—	—	1	1	+	—	—	30	—	—	—	—	—	—
— gracilis	—	—	—	1	—	—	+	—	—	—	—	20	—	—	—	—	—	—
Cetraria tenuissima	—	—	—	2	—	—	1	4	3	—	—	40	—	—	—	—	—	—
— glauca	—	—	2	1	—	—	—	—	—	—	—	20	—	—	—	—	—	—
Parmelia physodes	—	—	7_1	5	4	—	5	2	4	5	—	70	—	—	—	—	—	—
Peltigera canina and rufesc.	—	—	—	—	—	—	—	2	—	—	—	10	—	1	—	—	—	—
8.																		
Hypnum cupressiforme	—	4	6	10_6	2	8_5	2	4	3	7	9_4	**100**	1	—	6_2	—	—	—
Hylocomium schreberi	—	—	1	1	6	10_5	—	—	—	—	+	50	—	10_5	5	—	—	—
— splendens	—	—	—	—	—	2	—	—	—	—	—	10	—	2	—	—	—	—
— squarrosum	—	—	—	—	—	—	—	—	—	—	—	—	—	7	—	—	—	—
— triquetrum	—	—	—	—	—	2	—	—	—	—	—	10	—	2	—	—	—	—
Dicranum scoparium	—	—	—	4	—	—	2	1	—	1	5	50	—	—	—	—	—	—
Frullania tamarisci	—	—	—	—	—	—	—	—	—	—	2	10	—	—	—	—	—	—

Vegetation: Nos. 1—10: typical *Empetrum* or *Calluna-Empetrum* heaths. Nos. 4—5: not very dry. Nos. 7—9 illustrate the transition from an *Empetrum* pioneer heath surrounded by grey dune vegetation to a *Calluna-Empetrum* heath behind the dune vegetation. No. 10: exposed western side of an old raised shingle beach. Nos. 11—13: *Empetrum* heaths with continental plants or plants alien to heath vegetation (cf. text p. 43). Nos. 14—16: *Empetrum* dune heaths without ground layer (cf. text p. 47).

Species groups: 1: Northern species. 2: oceanic-suboceanic species. 3: subcontinental species. 4: widely ranging species belonging to main type A. 5: widely ranging species, more or less frequent in heaths. 6: widely ranging species alien to heath vegetation. 7: lichens. 8: bryophytes.

Species not mentioned in the table: Group 1: *Antennaria dioeca* + in No. 2. Group 3: *Pulsatilla pratensis* + in No. 8, *Thalictrum minus* + in No. 7. Group 5: *Veronica officinalis* + in No. 13, *Juniperus* 2 in No. 12, + in No. 13. Group 6: *Agrostis tenuis* 1 in No. 2, *Anthyllis vulneraria* 1 in No. 11, *Polygala vulgaris*, *Ran. bulbosus* 1 in No. 13. Group 7: *Clad. portentosa* and *spumosa* + in No. 6, 1 in No. 10, *Cl. alcicornis* + in No. 7, 1 in No. 11, *Cl. glauca* and *pityrea* 1 in No. 7, *Cl. major* 2 in No. 7.

vegetation. Where, on the other hand, the soil is covered with a lichen carpet, the *Empetrum* patches grow larger and merge into an *Empetrum-Cladina* heath which frequently covers extensive areas. Between this type of *Empetrum* heath and that of neutral-moderate acid soils, numerous transitions exist. In such stages, *Koeleria glauca* var. *intermedia* occurs in the heath. Examples of the *Empetrum-Cladina* heath are given in Table 8 a. The same table contains some later stages where *Calluna* is co-dominant. From these *Calluna-Empetrum* dune heaths a gradual transition leads to the *Calluna-Empetrum* heaths of the inland or diluvial sand areas near the coast (e. g. the heaths of Kaas). The three analyses from Rørvig (Nos. 7—9) alternate with dune sociations which are related to continental grassland communities (occurrence of *Thalictrum minus*, *Pulsatilla pratensis* or *Geranium sanguineum*).

A special type of *Calluna-Empetrum* heath is found e. g. at Rørvig on old raised shingle beaches in places exposed to the wind (Table 8, No. 10). In this type, the ground layer is reduced. Sometimes, however, *Frullania tamarisci* may be rather frequent. In more sheltered spots, *Empetrum* disappears and a *Calluna* heath is formed (cf. p. 64). A very similar distribution of heath types seems to be present on Hammeren (cf. Table 8b), where the rocky slopes exposed to wind are occupied by *Calluna-Empetrum*, while the top plateau is covered with *Calluna* heath of the G- or I-type. Both types have a rather reduced ground layer. In his paper on the Isle of Jungfrun, du Rietz (1925 a) mentions allied heaths with reduced ground layer on rocks exposed to wind from the open sea. In Halland too (Loc. 72), a *Calluna* heath almost without bryophytes and lichens was observed on old raised shingle beaches. At some distance from the coast the ground layer cryptogams increased in frequency (cf. furthermore, Tab. 22, Nos. 13—14 and Fig. 24).

A soil profile from the coast heaths at Rørvig (Fig. 16, p. 48) shows a rapid increase in the pH values with increasing depth. The effects of podsolation are almost lacking. The same seems to apply to other alluvial heaths. In a paper on the

Table 8 b. The heath of the exposed slopes and the top of the plateau at Hammeren (Bornholm, Loc. 68).

Analyses performed by H. Bahnson, E. Bille Hansen, M. Lange, and B. Simonsen during an excursion arranged by the Studenterraad in 1942. Method: S.

Analysis No.	Distributional type	1	2	3	4
Calluna vulgaris	sbo_3	7_5	10_7	9_8	10_9
Empetrum nigrum	bsΓ	8_6	10_7	8_7	+
Deschampsia flexuosa	sbax	2	2	2	1
Carex arenaria	so_2	1	2	—	—
Polypodium vulgare	sbx	—	+	+	3
Juniperus communis	sbx	—	+	+	2
Prunus spinosa	sx	—	—	—	+
Rumex acetosella	sbxp	—	—	—	+
Campanula rotundifolia	sbaxp	—	—	—	+
Hypnum cupressiforme	—	6_3	4	4	6_5
Dicranum scoparium	—	3	5	9_7	5
Hylocomium schreberi	—	—	—	1	+
— splendens	—	—	—	+	+
Polytrichum piliferum	—	—	—	—	+
Cladonia impexa	—	—	+	+	3
— silvatica	—	—	+	+	2
— rangiferina	—	—	+	+	1
— chlorophaea + fimbriata	—	1	+	2	1
— floerkeana	—	—	+	+	+
Cetraria tenuissima	—	—	+	+	—
Parmelia physodes	—	3	1	3	6_3

Vegetation: Nos. 1—3: slope exposed towards NW, inclination about 15—30°, pH 4.2. No. 4: plateau, pH 4.0. Nos. 1—4 form a profile extending from the lower parts of the slope (1) to the upper parts (3) and the plateau above the slope (4).

heath vegetation of Læsø, Mentz (1920) states that—despite the formation of a more or less thick surface-raw humus — nowhere anything in the line of a podsole profile occurred.

In the typical *Calluna-Empetrum* or *Empetrum* heaths, the continental element does not play any considerable part in the vegetation. Among the oceanic plants,

A_{0-1}
A_2
(a)
(b)
(c) →
(d)

Fig. 16. *Calluna-Empetrum* heath on old raised shingle beaches at Rørvig (Korshage).

	Soil profile:	pH
A_{0-1}	Surface raw humus	4.5
	Raw humus below the surface	4.5
A_2	A somewhat bleached greyish layer of sand between shingle	4.9
	(a) Yellow sand between shingle	5.9
	(b) — — — —	6.5
	(c) Narrow horizon, brownish	5.6
	(d) Yellow sand between shingle	6.3

The measurement extended over 1 m. B. photo 1940.

only *Carex arenaria* and *Calluna* are important, *Genista anglica* being rather local. In one locality (Table 8 a, No. 5) it reached the values 9_5 in a somewhat moist "low" between old shingle sand fulls covered with dry *Calluna-Empetrum* heath. *Genista anglica* is the most prominent guiding species of the D-type (Dutch-German heath series) and, hence, this *Calluna-Empetrum-Genista anglica* heath forms an interesting transition type between main types B and D.

Nos. 11—13 (Table 8a) are also transition heaths. As in the case of the pioneer heaths described from Skallingen, the acidity is low (pH 5.1 in No. 11); however, it never approaches pH 7. While many pioneer *Empetreta* contain so many plants alien to heath vegetation that the term heath vegetation may be abandoned, the somewhat older dune heaths must be classified as heaths, in spite of the occurrence of many alien species. The three examples given in Table 8 show a number of continental plants and, consequently, these heaths are deviating B-heaths or transitions to the main types H-I. A more detailed description of these heaths is found on pp. 71 and 75.

Before considering the position of the typical *Calluna-Empetrum* (or older *Empetrum*) heaths we may summarize some important geographical and biological features of *Empetrum*.

Empetrum nigrum s. l. is almost circumpolar; the low-arctic tetraploid bisexual subspecies *Empetrum hermaphroditum* Hagerup may be found all around the pole without noticeable interruptions; in Greenland, a marked increase in frequency seems to occur in southern and oceanic regions. The range of the diploid boreal-montane plants may have rather large gaps. Hultén (1937) assumes that diploids have survived the glacial age in different refugia south of the ice. The Danish-North-German biotypes have probably survived the last glaciation in western Europe. These biotypes may be somewhat oceanic and, if so, the almost complete agreement in the Danish areas of the oceanic *Erica tetralix* (cf. B. 1937 a) and *Empetrum* (Fig. 14) would be more intelligible. Some other facts are also in favour of the theory of the oceanic tendencies of *Empetrum*[1]. The species is very frequent in European oceanic and boreal regions and, in East America, it is most frequent towards the Atlantic. In North Germany it occurs, according to Grevillius and Kirchner, "vorwiegend im Westen, an der Ostseeküste stellenweise häufig, nach Südosten bald abnehmend". In the Baltic States south of Riga bay, the plant is very rare as compared with Denmark (see dot map in Hryniewiecki 1932, p. 330). The oceanic tendencies are, on the other hand, mainly found in the southern part of the range and, thus, one might suppose that the distribution was governed by the low summer temperatures in the proximity of the sea. In that case, the range would resemble that of arctic psychrophilous plants and we would not have to assume the occurrence of special oceanic races.

Turesson has shown that the oceanic races transpire more slowly than do continental races of the same species. Some oceanic species have also low transpiration rates as compared with less oceanic or continental species. The transpiration of heath shrubs has been studied by Boysen Jensen, Stocker, Firbas and Breitsprecher. From these studies, the following facts may be mentioned. In most cases, the clearly oceanic *Erica tetralix* transpires more slowly than *Calluna*; the continental *Rhododendron lapponicum* transpires much more rapidly than *Vaccinium vitis idaea* which, at most, is slightly continental; finally, *Empetrum* has rather low transpiration rates[2] and may frequently transpire even more slowly than *Erica*. Thus, the distribution of *Erica* and *Empetrum* in Denmark may partly be due to similarities in the water economy. It would be an interesting task to compare the transpirations of arctic or continental *Empetrum* plants with those of western Europe. The influence of frost also ought to be studied. Withering of *Empetrum* shoots exposed to frost was observed at Rørvig in 1940.

In more continental regions it seems a remarkable fact that *Empetrum* disappears from

[1] Cf. also Steffen (1935) who discusses whether *Empetrum*, *Cornus suecica* and others ought to be classified as atlantic-subarctic or not.

[2] The same appears from a single experiment performed by the writer on the Isle of Læsø.

the dry heath earlier than from the heaths of northern slopes (observed at Raageleje and Gilleleje; cf. also LIBBERT 1940 on the heaths of the Baltic Sea coast). In this connection, it should also be emphasized that *Empetrum* in a profile transection from Rørvig gets the highest F percentages in the very same vegetations where *Erica tetralix* reaches its maximal shoot density. Here, however, *Empetrum* is able to dominate in many dry heaths, either pioneer heaths in the dunes or heaths exposed to wind.

While the heaths rich in *Vaccinium vitis idaea* may show some continental affinities, those rich in *Empetrum* and without *Vaccinium vitis idaea* may have oceanic affinities. This is possibly of importance for the understanding of the regional differences mentioned above, while a local differentiation in heaths with *Empetrum* and heaths with *Vaccinium vitis idaea* and *Empetrum* must be due to edaphic factors, viz. moisture and, possibly, acidity.

The *Calluna-Empetrum* heaths are related to low-alpine heaths in Scandinavia (e. g. the *Calluna-Empetrum-Cladina* heath mentioned by SAMUELSSON 1917, pp. 154 and 156). To the south, the inland *Calluna-Empetrum* heath has been found in North-West Germany (N-Oldenburg, Ostfriesland, N-Emsland) by JONAS (1935) and by LANGERFELDT (1939, pp. 6—7). According to LANGERFELDT, this heath is very rich in *Cladina*; it is developed "auf Kieskuppen, Sandheiden und Windmulden" and, sometimes, on pronounced podsolated soils. From the analysis made by LANGERFELDT, it appears that this German heath is identical with the dry acid heaths of the inland dunes of Læsø and Jutland (B. 1941 a and 1941 b). The other Danish *Calluna-Empetrum* heaths (e. g. those described by MØLHOLM HANSEN 1932, p. 132, see Table 6, No. 5) may be absent or very local in Germany, being largely restricted to the mountains. In the Dutch-German lowland, the *Calluna-Empetrum* heath is replaced by the "*Calluneto-Genistetum typicum*". The "*Calluneto Genistetum Deschampsietosum flexuosae*" (NB. without *Genista*) described by LIBBERT (1940) from the coast of the Baltic (Vorpommern) sometimes contains *Empetrum* also. However, this heath is rather moist, containing *Erica tetralix, Nardus, Molinia,* and *Juncus squarrosus* and, thus, it is more related to moist heath types. The same is the case with the *Calluna* heath on the Lebanehrung in East Pommern (HUECK 1932). The *Calluna-Empetrum* or *Empetrum* heaths of moderately acid Danish coast dunes are closely related to the "*Calluneto-Genistetum empetretosum*" described by TÜXEN (1937), and allied types may occur also in Dutch dunes (cf. BIJHOUWER 1926, Table 5).

C. Heaths characterized by northern and continental species and frequently rich in lichens (*Arctostaphylos uva ursi,* group of *Empetrion boreale*).

Atlantic dwarf shrub heaths are present mainly in western Europe, where the continental element is reduced. Hence, it is natural that heaths characterized by continental species only in very few cases are of regional significance. If we do not limit our studies to Atlantic heaths but include arctic dwarf shrub heaths, it is evident that the importance of continental plants increases as we pass from the heaths of

Les Landes to those of arctic Norway or Greenland where, in particular, a continental species like *Cassiope tetragona* covers large areas. The only Scano-Danish C-heath of regional significance, the *Arctostaphylos* heath, has only few true continental species; widely distributed suboceanic species (e. g. *Calluna*) are dominating in all its sociations.

The C-main type is poor in guiding species. Only *Arctostaphylos uva ursi, Pulsatilla vernalis, Cladonia alpestris,* and *Cetraria nivalis* are significant. Furthermore, *Cladonia rangiferina* and *Cetraria islandica* seem to be particularly common in this type and may be of some importance for its characterization.

In Denmark, the *Arctostaphylos* heath was mentioned by Raunkiær (1909/10, 1934, p. 269) from Loc. 42, by Mølholm Hansen from Loc. 47, and by the writer (B. 1941 a) from Loc. 44—45. It is developed on dry places, on southern slopes (Mølholm Hansen), on the tops of low hills, and in level heaths exposed to wind. Outside Denmark, it occurs in West Sweden (profile p. 23), South Norway (B. 1940, p. 47) and North Germany. Libbert (1940, pp. 123—124) refers to a *Calluna-Arctostaphylos* sociation from Wilstedt, and Jonas (1935, p. 107) states that this heath type is already frequent west of the "Unterelbe". Within Denmark, the *Arctostaphylos* heath has a large distribution in the inland heaths of Jutland (e. g. Loc. 21, 26, 28, 41, 42, 44—47, 51). In the dune heaths, it is absent or very sporadic and only on the island of Læsø (Loc. 8) it may be locally frequent. In Jutland, it was observed only in the old dune heath at some distance from the coast (Loc. 14, Table 9, No. 1).

In Table 9 which contains some analyses of *Arctostaphylos* heaths, Nos. 1—4 are situated in places very exposed to wind. Here, *Calluna* is generally very low and poor; sometimes, however, it is very scattered (Nos. 7—9), possibly due to the dying out of old plants and subsequent bad conditions for the germination of seeds (cf. B. 1941 a). In the table, two heath types are distinguished, viz. one poor in phanerogams but rich in lichens, and one (No. 10) rich in phanerogams and mosses. Only this latter one, which has already been described in B. 1941 a (p. 139, Fig. 37, Table 43, No. 1) includes other guiding species than the arctic subarctic *Arctostaphylos, Cladonia alpestris* and *Cetraria nivalis.* It is certainly bound to relatively rich soil and forms a transition to the H-heaths.

The plant-geographical relations of the C-heath are very interesting. In the profile transection p. 12, we find the *Phyllodoco-Myrtillion* heaths near shrubs or on northern slopes, whereas the southern exposed slopes or the summit plateaux are occupied by the *Loiseleurieto-Arctostaphylion* heaths. According to Nordhagen, the latter have *Arctostaphylos uva ursi* as "Differentialart". The profile p. 23 and other profiles in B. 1941 a (Table 50, p. 167) show our A-heaths on the north side and the C-heaths on the south side and on the top of the ridge. Consequently, there seems to be an ecological agreement between the C-type and some of the alpine heaths belonging to the *Loiseleuria* group (cf. the *Arctostaphylos uva ursi* sociations of du Rietz 1925 d, pp. 29—31 and 63—64). Owing, however, to the great difference in temperatures etc. between the exposed, early snowfree alpine localities and the exposed, dry lowland habitats, the floristic similarity is not marked, only *Arctostaphylos,*

Table 9. Heaths of the *Arctostaphylos uva ursi* group of the *Empetrion boreale* (C. main type). Method: S.

Analysis No. / Locality No. / pH	Distributional type	1 26 3.9	2 26 3.7	3 21 —	4 21 4.0	5 21 —	6 14 4.1	7 47 3.7	8 47 4.0	9 47 3.6	10 45 4.4	Constancy pCt.
1.												
Arctostaphylos uva ursi	bsc$_3$┐)	10_7	10_7	9_5	7_3	10_{10}	10_{10}	10_8	10_5	10_7	8_6	**100**
Pulsatilla vernalis	bsc$_1$(H)	—	—	—	—	—	—	—	—	—	10_4	10
Carex ericetorum	bsc$_1$	—	—	—	—	—	—	—	—	—	3	10
Scorzonera humilis	sc$_2$	—	+	—	—	—	—	—	—	—	2	20
Hypochoeris maculata	sbc$_3$(┐)	—	—	—	—	—	—	—	—	—	+	10
2.												
Empetrum nigrum	bs┌	8_3	6_5	10_{10}	4	+	8_4	10_{10}	10_{10}	10_{10}	10_6	**100**
Vaccinium vitis idaea	bs(┐)	—	—	—	—	—	—	—	—	—	5	10
Trientalis europaea	b(al)sx	—	—	—	—	—	—	+	1	1	—	30
Antennaria dioeca	bsx	—	—	—	—	—	—	—	—	—	1	10
3.												
Calluna vulgaris	sbo$_3$	10_{10}	10_{10}	9_4	10_7	3_2	9_2	+	+	1	10_6	**100**
Genista anglica	sdo$_1$	+	+	—	+	+	1	1	1	2	—	**80**
— pilosa	sdo$_2$	+	+	—	—	6_2	—	+	+	+	7_1	70
Carex arenaria	so$_2$	—	—	—	—	—	3	—	—	—	—	10
— pilulifera	sbo$_3$	—	+	—	—	+	—	—	—	—	6	30
Sieglingia decumbens	sbo$_3$	+	+	—	—	—	—	—	—	—	1	30
Scirpus caespitosus	sbo$_3$	—	—	—	—	—	—	1	+	1	—	30
Galium saxatile	sbo$_2$	—	—	—	—	—	—	—	—	—	1	10
Hypericum pulchrum	so$_2$	—	—	—	—	—	—	—	—	—	1	10
4.												
Deschampsia flexuosa	sbax	+	+	—	+	7_1	4	1	+	+	4	**90**
Carex panicea	sbx	6	1	—	—	—	—	7_0	7_1	6	4	60
Festuca ovina	sbxp	—	—	—	—	1	—	—	—	—	3	20
Agrostis cf. canina	sbxp	2	+	—	—	—	—	—	—	—	—	20
Molinia coerulea	sbxp	—	—	—	—	—	—	+	—	—	—	10
Poa pratensis	sbxp	—	—	—	—	—	—	—	—	—	2	10
Luzula multiflora	sbxp	—	—	—	—	—	1	—	—	—	—	10
Campanula rotundifolia	sbaxp	—	—	—	—	—	—	—	—	—	2	10
Potentilla erecta	sbxp	—	—	—	—	—	—	—	—	+	1	20
Salix repens	sx(L)p	+	+	—	—	—	—	—	—	—	—	20
5.												
Cladonia silvatica	—	8_7	7_4			10_8	10_{10}	6_4	6_1	2	—	**90**
— impexa	—	9_5	8_3	} 10_{10}	10_{10}	5	5	10_5	10_8	10_6	7_3	**100**
— rangiferina	—	4	2			10_8	4	2	3	2	1	**100**
— alpestris	—	+	+	—	—	—	—	—	—	—	—	20
— uncialis	—	+	+	—	1	2	—	+	+	+	—	70
— squamosa	—	3	3	—	2	—	3	+	+	—	—	60
— chlorophaea (and fimbriata)	—	1	+	—	—	1	—	+	+	+	1	70
— gracilis	—	+	+	—	—	—	—	+	+	+	—	50
— cornuto-radiata (and glauca)	—	+	+	—	—	—	—	+	+	—	—	40
— destricta	—	—	—	—	—	—	—	+	1	+	—	30
— pityrea	—	—	—	—	—	1	—	—	—	—	—	10
Cetraria tenuissima	—	1	+	—	2	—	9_4	—	—	—	—	40
— islandica	—	2	+	—	—	7_2	9_4	—	—	+	—	50
— nivalis	—	+	—	—	—	—	—	—	—	—	—	10
Parmelia physodes	—	2	1	—	—	—	—	+	—	—	—	30

Table 9 (continued).

Analysis No. / Locality No. / pH	Distributional type	1	2	3	4	5	6	7	8	9	10	Constancy pCt.
Analysis No.		1	2	3	4	5	6	7	8	9	10	
Locality No.		26	26	21	21	21	14	47	47	47	45	
pH		3.9	3.7	—	4.0	—	4.1	3.7	4.0	3.6	4.4	
6.												
Hypnum cupressiforme	—	10_7	10_8	6_3	8_5	—	3	10_6	9_7	10_6	9_6	**90**
Hylocomium schreberi	—	+	—	9_5	—	—	6_1	1	+	1	7_5	70
Dicranum scoparium	—	+	—	—	—	—	3	+	+	+	—	50
— spurium	—	+	—	—	—	+	—	—	—	—	—	20
— rugosum	—	—	—	1	1	—	—	—	—	—	2	30
Blepharozia ciliaris	—	5	4	1	1	—	—	1	2	1	3	**80**
Leucobryum glaucum	—	—	—	—	—	—	—	+	+	+	1	40

Species groups and species not mentioned in the table: 1: continental-subcontinental species. 2: northern (montane) species; *Arnica montana* + in No. 1. 3: oceanic-suboceanic species; *Euphrasia gracilis* + in No. 2. 4: widely distributed species; *Solidago virga-aurea* + in Nos. 1—2, *Succisa pratensis* 2 in No. 10, *Hieracium pilosella* + in Nos. 6 and 10, *Viola canina*, *Polygala vulgaris* 1 in No. 10, *Ammophila arenaria* 1 in No. 6. 5: lichens; *Cladonia furcata* + in No. 1, *Cladonia floerkeana* + in Nos. 1—2, *Cladonia coccifera* + in No. 2, *Cladonia crispata* + in Nos. 7—9, *Cladonia portentosa* + in No. 9. 6: bryophytes; moreover *Cantharellus cibarius* 4 in No. 6. No. 10 has been published earlier in B. 41a (Tab. 43,1 and Fig. 37).

Vaccinium vitis idaea, Empetrum nigrum (s. l.!), *Deschampsia flexuosa* and *Cladonia rangiferina* being frequent in alpine as well as in lowland heaths.

In very oceanic regions, the heath type on dry slopes and related habitats is frequently dominated by *Erica cinerea*; in such heaths, *Arctostaphylos uva ursi* may be rather frequent (cf. B. 1940, p. 11). In more continental regions, our C-heath is replaced by *Pinus* woods rich in *Arctostaphylos* (Gräbner 1925, p. 254, du Rietz 1925 e, pp. 11—13, Pettersson 1940, p. 177) or *Arctostaphylos* heaths very rich in species (e. g. dry os-slopes in South Sweden, Sterner 1921, pp. 304—305) and on rocky ground on Gottland in the Baltic (du Rietz l. c., p. 28). To the south, there are transitions between our Danish *Arctostaphylos* heath and the *Genista pilosa* heaths (see p. 59). Typical transitions of this kind are described in B. 1941 a (p. 141, Fig. 39, Tables 43 and 58, No. 5) and in Table 9, Nos. 5 and 10.

With our C-type, we may perhaps finally class the *Calluna-Empetrum* heaths rich in *Cladonia alpestris* or *Cetraria nivalis* which occur in small patches in dry, exposed dune heaths on the island of Læsø (see B. 1941 b). In that case, however, only the ground layer belongs with certainty to the C-type.

Before leaving the C-type we may study the guiding species in detail.

Arctostaphylos uva ursi has a very problematic distribution. It was considered to be somewhat continental (B. 1937) but, after having seen the plant in western Norway, it was concluded that the species is a "boreal dry soil plant, without any connection either with oceanity nor with continentality" (B. 1940, p. 33). Its distribution in Denmark and Finmark in Norway as well as the occurrence in the northern parts of Central Europe favours the theory of its continental climatic requirements. Gräbner (1925, p. 44) writes: "Im Osten meist zerstreut bis Fürstenau, Lesum, Utlede, Hagen a. d. Unterweser". In Central Holland (Veluwe), it has been found in one place only in a region where also *Carex ericetorum*, *Hypochoeris maculata* and *Scorzonera humilis* reach more or less extremely western localities (Uittien 1932). It is frequent in most parts of Iceland, although it is rare in outer coast regions in the Northwest Country and the southern part of the land (Gröntved). In Sweden, its distribution has been discussed by Hård (1935, p. 183) who concludes that the species must have immigrated lately to the Vänern region. In Denmark, on the other hand, it is an old species, being found already in the Alleröd period (K. Jessen, 1920).

In order to interpret the contradictory facts in the distribution we may propound the following theory. After the last glaciation, the area of *Arctostaphylos uva ursi* was disrupted. Some populations inhabited continental regions and were mainly composed of continental biotypes, other populations survived the last glaciation in various oceanic regions (Ireland, West Norway) and were composed of biotypes fitted for more oceanic climates. After the retreat of the ice, the local areas were enlarged and were joined in many cases. The populations which immigrated to Denmark and Germany (or which survived the glaciation in these countries) were subcontinental and have not produced oceanic races in recent times. In West Norway, the presence of both oceanic and continental biotypes may be due to the rather continuous distribution from the sea to the mountains in the interior. The facts mentioned by Hård indicate a late immigration to the Vänern region, but give no evidence for this theory, since the distribution along the coasts of the lake Vänern and in the region northwest of Åmål to some extent coincides with that of the clearly continental *Ledum palustre* and a species such as *Viola stragnina*. The coasts of lake Vänern are relatively dry (cf. Fig. 24 in Hård) and, hence, the distribution of *Arctostaphylos uva ursi* may at any rate partly be explained as a result of the climate.

The autecology of *Arctostaphylos uva ursi* also leads to the assumption that it may be a subcontinental low-arctic-boreal plant. The *Pinus* woods rich in *Arctostaphylos uva ursi* recently described by Pettersson (l. c.) contain only one suboceanic and up to 50 per cent continental species. In the long list of species from the dry os-slope in Småland (Sterner 1922, p. 304) there are two suboceanic species and a large number of continental species (e. g. the two montane-continental species, *Trifolium montanum* and *Pulmonaria augustifolia*). The pH domain of *Arctostaphylos uva ursi* is large (Hård, l. c.).

The above theory is weakened by the fact that the variability of the species seems to be slight. However, we do not know anything concerning the ecological variability. The two races of *Luzula pilosa* differ almost only with respect to their biology (Fig. 10) and the same may be assumed for the hypothetical *Arctostaphylos uva ursi* races. Only in one locality, viz. Nørholm Hede, did two different biotypes occur in the same spot. They differed mainly as to the leaf length, one having 13.2 mm. and the other 15.6 mm. long leaves. In N.E. America, the variability may be larger; here, *Arctostaphylos uva ursi* and its two varieties *coactilis* and *adenotricha* are restricted to limestone areas (St. John 1922).

Pulsatilla vermalis is a continental alpine-boreal plant of acidic habitats (cf. B. 1941 a, pp. 137—142). Nordhagen (1936, p. 61) uses it as a "regionale Verbandscharakterart" in his *Juncion trifidi scandinavicum*, which generally succeeds the *Loiseleurieto-Vaccinion* in more alpine places. In central Jutland, too, *Pulsatilla vernalis* is rarely found in acidic grassland (B. 1941 a, Table 41, 2).

Cladonia alpestris has a continental low-arctic-subarctic range (Lynge 1921, B. 1941 b).

Cetraria nivalis is a subcontinental arctic plant (B. 1941 b, p. 25). The Danish individuals are frequently more pale yellow as compared with Norwegian alpine or arctic specimens.

Cladonia rangiferina is a northern species and shows continental tendencies in N.W.-Germany (Langerfeldt 1939; B. 1941 b, p. 29).

2. The Dutch-German heath series and its northern radiants.

As the writer himself has not studied the heaths in Germany or in the Netherlands, he will confine himself to mentioning the main features of the typical vegetation and, besides this, call attention to a number of heaths occurring in Denmark (more rarely also in southern Sweden) which may be regarded as northern radiants of the Dutch-German heath series.

According to Walter (1927), the German heath vegetation may be divided into three series, viz. the north-Atlantic, the south-Atlantic-pontine, and the alpine heath series. The north-Atlantic series seems to be identical with our Dutch-German heath series. The pontine heaths are developed near the continental timber line and are not composed of dwarf shrubs belonging to *bicornes*; more naturally, they may be classified as steppe communities. The alpine series has been dealt with by Pallmann and Haffter (1933) and by Gams (1940).

The heath vegetation of North-West Germany and the Netherlands is generally termed *Calluneto-Genistetum typicum* (Tüxen 1937). According to Schütt (1931, p. 28), the heath vegetation of the large heath reserve Lüneburger Heide in Germany is dominated by *Calluna* with an admixture of *Genista anglica, pilosa, Juniperus, Lycopodium complanatum, Lycopodium tristachynum, Potentilla erecta, Sieglingia, Nardus, Festuca ovina,* and a number of widely distributed mosses and lichens. A very similar picture of the vegetation is obtained from a study of Tüxen's 22 analyses from almost the same region (cf. Tüxen, l. c., p. 117). This typical *Calluna-Genista* heath is also found in the Netherlands (see analyses in Beijerinck 1940, p. 115).

Tüxen and Diemont (1936) studied the geographical relations of the typical *Calluna-Genista* heath. With increasing oceanity, this heath is replaced by the *Erica cinerea-Ulex europaeus* heath of northern France. With decreasing oceanity follows a *Calluna-Antennaria* heath which is found in low central European mountains below the *Fagus* zone.

In West Germany (Aachen), Schwickerath (1933) separates two *Calluna-Genista* heaths, viz. one oceanic heath characterized by *Genista anglica* and *Erica tetralix,* and a suboceanic one characterized by *Genista pilosa, Genista sagittalis,* and *Galium saxatile.* A similar type was described by Oberdorfer (1937, Ber. d. Deutsch. Bot. Ges. 55) from the Oberrhein region and by Libbert (1936) from the Halberstadt region on sandstone on the slopes of low mountains. Libbert considers *Antennaria* to be a character species. Thus, there seems not to be any great difference between his *Calluna-Genista pilosa* heath and Tüxen's *Calluna-Antennaria* heath which also, though scattered, contains *Genista pilosa* and which is found on slopes of sandstone mountains. In many cases, they may belong to the same main type.

Farther to the east, *Genista pilosa* disappears and only very few suboceanic plants are left in the heath. At the same time, continental plants may be characteristic. We have reached a vegetation which forms the border line between steppe and heath.

The status of the *Sarothamnus* heath is peculiar. In the areas dominated by

Calluneto-Genistetum, Sarothamnus does not occur with great frequency in the typical heath on podsolated soil, but attains its optimum in the heaths of sandy areas (inland dunes). East and south of the areas of the *Calluneto-Genistetum*, however, the *Sarothamnetum* may be looked upon as a regional type. According to Gräbner (1925, p. 243), it is even characteristic of some subcontinental areas: "Gerade hier nehmen die *Sarothamnus*-Bestände unter der Gesamtzahl der in jenen Gebieten vertretenen echten Heideformationen einen hervorragenden Platz ein". In the vertical zonation of the heath vegetation in the Black Forest, the *Calluna-Sarothamnus* heath, according to Bartsch (1940, 1941), is characteristic of grazed clearings in the low montane zone (altitude 350—800 m). Below this zone comes a mixture of subatlantic heaths and steppelike grassland and above this zone a high montane *Calluna-Genista sagittalis* heath with *Arnica montana* and *Carlina acaulis* (cf. Oberdorfer's *Genista sagittalis-Carlina* association). The uppermost heaths (altitude 13—1500 m) are subalpine (*Empetreto-Vaccinietum*).

The subalpine or high montane heaths of central Europe are closely related to the Scano-Danish series, in particular to the A-type. Tüxen's *Empetreto-Vaccinietum* from the summits of the Harz and Klement's *Callunetum* rich in lichens from the Erzgebirge are completely Scano-Danish (*Vaccinium vitis idaea, Empetrum* and *Cetraria islandica* are character species). On the other hand, the high montane heaths of the Black Forest contain species which are lacking in northern Europe (*Carlina acaulis, Jasione perennis* (suboceanic), *Genista sagittalis*) and which differentiate these montane-subalpine central European heaths from the Scano-Danish ones. The montane heath of Venn described by Schwickerath (1933) as a northern-montane subassociation occupies an intermediate position between the Scano-Danish and the Dutch-German heaths, but it comes very near to the former, containing *Trientalis, Vaccinium uliginosum, vitis idaea, Myrtillus* (!), *Empetrum, Arnica, Meum athamanticum* (subatlantic-montane), *Genista anglica* and *pilosa*. Tüxen classifies his *Empetreto-Vaccinietum* to the alpine *Empetreto-Vaccinietum* described by Pallmann and Haffter. However, this is hardly quite correct, the latter being separated by a great number of alpine plants (*Loiseleuria, Hieracium alpinum, Rhododendron ferrugineum*, etc.). At any rate, it would justify the classification of the Scano-Danish heaths to the subalpine heaths, which might lead to the confusion of rather well separated heath types.

The low montane and colline heaths of Central Germany are also related to Danish heaths, but here the regional geography is more complicated. A study of the flora in the *Calluna-Antennaria* heaths described by Tüxen and Pfalzgraf (1934) shows many widely distributed, sometimes suboceanic species and a few continental species, or many subcontinental, rather widely distributed species. There are very few typical southern heath plants, and the southern element (*Genista germanica, Genista pilosa, Lycopodium tristachyum*) obtains only low constancy and covering values. Heaths without these southern heath plants may be identical with a number of east-Danish, south-Baltic heaths of a suboceanic-subcontinental type. Thus, in the present case, neither the term Scano-Danish nor the term Dutch-German is convenient, since the vegetation lacks most Scano-Danish and Dutch-German guiding species. Consequently, we must classify many German *Calluna-Antennaria* heaths and a number of Danish heaths to a connecting heath series which may be called the south-Baltic-submontane (German) heath series. This latter series will be treated after the Dutch-German series.

After this review, it seems justified to work with the following four main types:

Genistion Dutch-German heath series	D. Oceanic: *Genista anglica* type E. Suboceanic: *Genista pilosa-Sarothamnus* type F. Subcontinental: *Genista germanica-tinctoria* type Suboceanic-montane: *Genista sagittalis* type.

The writer does not venture on a detailed treatment of these main types, but only endeavours to survey them and to describe the northern radiations, paying special attention to the occurrence of the guiding species for the D, E, and F-main types in Scandinavia.

D. Heaths characterized by southern oceanic species (*Genista anglica*-group of *Genistion*).

Heaths belonging to this main type cover large areas in North-West Germany and have earlier been much more widely distributed in North Holland also. Now, the area of the heath has been largely diminished by cultivation and foresting.

According to Tüxen, the *Calluna* heath characterized by *Genista anglica* has succeeded woods ("*Querceto roboris-Betuletum*").

Genista anglica has a typical oceanic range (map after Hannig in W. Christiansen, 1938). In Germany, the eastern limit coincides fairly well with the January isotherm of 1° C (Fig. 30 in W. Christiansen). It is not mentioned in any *Ericeto-Ledetalia* communities analyzed by Tüxen. Schwickerath (1933, 1940), on the other hand, mentions it, though scattered, in his *Ericion* communities. In Denmark, the species is scattered in many different heath types (cf. the Tables), but it attains the highest values of shoot density in certain alluvial heaths of the transition type between wet and dry heath (p. 48). *Genista anglica* may be rather dependent on the fertility of the soil (cf. the frequent occurrence in the alluvial heaths and in the *Calluneto-Genistetum* with *Orchis maculatus* (Diemont)). In *Sphagnum* bogs, it occurs only in spots where the water oozes out of the soil (B. 1941 a, p. 180). The occurrence or non-occurrence of *Genista anglica* may differentiate the D- and E-types and the D- and A-types from each other, hardly, however, the D- and the B-types, seeing that the species is scattered in most Danish as well as in German heaths (constancy 50 per cent, degree of covering: + — 1 in Tüxen, l. c., pp. 117—118; constancy 20 per cent, covering: + in W. Christiansen, l. c., p. 63).

Cuscuta epithymum is not a guiding species for the D-main type, but perhaps for *Genistion*. It is a widely distributed plant which, however, approaches its northern limit in Denmark. The frequency limit to the north seems to run through southern Jutland and may be valuable in combination with southern frequency limits of Scano-Danish guiding species in the same area (e. g. *Vaccinium vitis idaea*). In TÜXEN's *Calluneto-Genistetum* Nos. Ia, Ib, IIa and IIb, it reaches the following constancy percentages and covering values: 23, + —1; 17, +; 14, +, and 50, + —1. In the Dutch heaths, it is frequently found by JESWIET and DE LEEUW (1933), BEIJERINCK (1934), and WEEVERS (1940). In the French *Calluneto-Ericetum cinereae*, it covers from 1 to 3 and occurs in 20 per cent of the analyses (LEMÉE). In Denmark, it was lacking in Randbøl Hede. From Nørholm Hede, it is mentioned by MØLHOLM HANSEN, but it is not included in any of the numerous analyses. In southern Jutland, it is found in heaths between Thiset and Jenning (Loc. 51), between Stenderup and Allerup, in Arrild Hede, in the heath on the Isle of Rømø (Loc. 50) as well as in heaths at Tønder. In northern Jutland, it has only two localities in alluvial heaths and the heath covered hills of the Isle of Fur (Loc. 16), here attacking *Calluna* and *Empetrum nigrum* (JØRGENSEN and B.). Curiously enough, this rather southern species is used as character species for the high montane *Calluna-Genista sagittalis* association of the Black Forest (BARTSCH 1940).

E. Heaths characterized by southern suboceanic species (*Genista pilosa-Sarothamnus*-group of *Genistion*).

A number of *Calluna* heaths and other heaths lack the oceanic element but contain some suboceanic species. To the E-type we may also refer heaths with a representation of suboceanic and subcontinental species. The latter form the transition to the subcontinental heaths.

The E-type is mainly distributed east of the D-type, but may locally occur on somewhat better soils east of the large heath areas of central and western Jutland, but they are also met with in many places in the true heath districts. In the heaths of the main types B—C, the guiding species of the E-type occur mostly as subordinate elements.

The E-heaths are developed in regions naturally covered with woods (*Querceto sessiliflora-Betuletum, Abieto-Fagetum*). Very frequently, they represent successional stages after disforesting, burning or cultivation (see BARTSCH 1941, p. 141). The most important heaths belonging to the main type are the *Calluna-Genista pilosa* heath described from Germany by LIBBERT and occurring in the mountains of Croatia (HORVAT 1931; here, with the subcontinental *Genista germanica*) and the *Calluna-Sarothamnus* heath.

Genista pilosa has a suboceanic range. In the British Islands it is rare. According to SALISBURY (1932), it belongs to the western-central component which has its main home in West and Central Europe. In Sweden, it is rare, being found only in N.W.-Scania and Halland (see the map in HÅRD 1924, p. 140). In Denmark, it has a central-western distribution in Jutland and reaches the northern limit at the Limfjord (JESSEN 1931, p. 33). In France, it occurs in the alpine heaths of the central massif (BRAUN-BLANQUET 1923, p. 183). SCHMID (1936, p. 61) mentions it among the steppe wood plants which are able to grow on sandy soil.

In the heath vegetation, it covers larger patches than *Genista anglica*. It is rather constant in most heaths of Jutland with the exception of the dune heaths. In the Tönnesjö heath in Halland it is also rather constant (MALMSTRÖM). The greatest constancy and shoot density is attained in dry heaths where the humus layer is thin or absent, as e. g. in inland dune areas (*Calluna-Genista pilosa* soc., cf. B. 1941a, pp. 136—137, Plate VII, Fig. 2), in successional stages after burning and cultivation (B. 1941 a), or in dry hill slopes (LIBBERT 1936). It is able to grow in soils of varying acidity (Randbøl Hede pH 3.6—4.5, as subdominant from pH 4.2—4.5) or even in almost neutral soil (pH 6.3 according to KLIKA 1937). It dominates an initial stage in limestone gravel in the western Carpathians (KLIKA, l. c.) and, according to ALLORGE (1941 a), it is "surtout calcicole" in Spain. Thus, its pH optimum probably lies rather high. The *Genista pilosa* vegetation described by KLIKA does not belong to the Atlantic heath formation; the succession leads to continental grassland (the *Festuca pallens-Minuartia montana* ass.) with no other oceanic elements than *Genista pilosa* and many southern continental plants (e. g. *Scabiosa canescens, Pulsatilla grandis, Hutchinsia petraea*). Thus, as *Genista pilosa* tolerates the conditions in grassland of this kind, it is understandable that vegetations forming the transition between the southern heaths and the northern C-type are frequently rich in *Genista pilosa.* To the south, *Genista pilosa* may to a great extend replace *Arctostaphylos uva ursi.* At Vind (Loc. 27) and Vorbasse (Loc. 45, Table 9, No. 10) it is subdominant in heaths with much *Arctostaphylos* or *Pulsatilla vernalis.*

Lycopodium tristachyum (*chamaecyparissias*). According to SAMUELSSON (1919, Sv. Bot. Tidsskr. 13, p. 247), its distribution is suboceanic and rather southerly. It is a character species in the subatlantic heaths of Germany (OBERDORFER, TÜXEN) and rare in the Danish and Swedish heaths, there, probably, most on relatively fertile soils. Heaths with much *Lycopodium tristachyum* have been described from Randbøl Hede (B. 1941), Utoft (BØRGESEN and JENSEN, Fig. 7). Other examples from W. Sweden (Tönnersjö) are found in Table 10. The species prefers a not too closed *Calluna* heath, sometimes with a reduced ground layer. In the Randbøl Hede, it grows in a *Calluna-Cladina* heath; at Tönnersjö, however, in typical Scano-Danish B- C-heaths.

Table 10. Heath patches with *Lycopodium tristachyum* (Loc. 74). Method: D.

Arctostaphylos uva ursi	–	2	Calluna vulgaris	4	5
Vaccinium vitis idaea	2	2	Lycopodium tristachyum	3	1
— myrtillus	1–2	–	Deschampsia flexuosa	1	–
Antennaria dioeca	1	1	Potentilla erecta	1	1

Sarothamnus scoparius. It has its main region in S.W.-Europe; furthermore, it is frequent in the Dutch-German heaths. Its eastern limit has been mapped by CZECZOTT. ULBRICH's map (in W. CHRISTIANSEN) is somewhat misleading with regard to Scandinavia. The species is missing in central S.-Sweden (HÅRD) and in Denmark, it is hardly originally wild on the eastern islands and in the northernmost parts of Jutland (K. JESSEN).

Table 11. *Calluna-Sarothamnus*-heath at Hem (Loc. 38). Method: D.

1.		3.	
Calluna vulgaris	4–5	Cladonia impexa	1
Sarothamnus scoparius	3–4	— cornuto radiata	1–2
Carex arenaria	+	— glauca	+
Jasione montana	+	— chlorophaea	1
		— coccifera (pleurota)	1
2.		— floerkeana	+
Deschampsia flexuosa	1–2	— pityrea	+
Festuca ovina	1		
Rumex acetosella	+	4.	
Hieracium pilosella	+	Hylocomium schreberi	2–3
Campanula rotundifolia	+	Dicranum scoparium	1

Species groups: 1: suboceanic species. 2: widely distributed species. 3: lichens. 4: bryophytes.

In W.-France, it is very frequent in the tall *Ulex europaeus* heaths, e. g. on Belle-Ile-en-Mer (GADECEAU 1903). Farther to the east, it reaches similar heights in periods of mild winters; in cold winters, however, it dies down to the basal shoots which have been protected by snow.

In the heath regions of Jutland, *Sarothamnus* is lacking in heaths with a well developed hard-pan (MENTZ 1906). Here, it is able to dominate the vegetation in three types of localities.

Fig. 17. Horneby Fælled (Loc. 55). Patches of *Calluna* heath surrounded by dry acidic grassland with flowering *Pulsatilla vulgaris*. Photo. 1932.

a. Inland dunes, see B. 1941a (pp. 82, 83 and 88, Plate V). *Sarothamnus* is sometimes able to form low dunes (Loc. 28).

b. Old sandy fields. *Calluna-Sarothamnus* heaths on old fields or dry pastures are numerous in central Jutland in hilly districts where the leaching of the sandy soil is weak.

Table 12. *Calluna-Sarothamnus*-heath at Ravnstrup (Loc. 22). Method: S. S-E-slope, inclination 15°.

1.	
Calluna vulgaris	10_7
Sarothamnus scoparius	10_8
Genista anglica	+
Hypochoeris radicata	1
Carex pilulifera	1
— arenaria	+
2.	
Arnica montana	+
Antennaria dioeca	+
3.	
Chamaenerium augustifolium	6
Deschampsia flexuosa	8_3
Luzula multiflora	2
Hieracium pilosella	2
Potentilla erecta	1
4.	
Cladonia floerkeana and coccifera	3
Lecidea ssp.	+

Species groups: 1: oceanic-suboceanic species. 2: montane or northern species. 3: widely distributed species 4: lichens.

In the more fertile, somewhat clayey soils, *Calluna* is more scattered and *Sarothamnus* is very abundant. The *Calluna-Sarothamnus* heath may be exemplified by the analysis from the hills at Mossö (Loc. 38, Table 11); see, moreover, B. 1941 a (p. 60) and the very similar vegetation from Belgium (van Oye 1938, Bull. Soc. Roy. Bot. Belg. 70).

c. Glades. In Germany, *Sarothamnus* occurs in pine woods (Libbert 1933, p. 331) and in Switzerland, it is constant and rather abundant in the *Castanea sativa* woods (Lüdi 1941). After disforesting a *Calluna-Sarothamnus* heath arises (Faber 1933, Bartsch 1941). Tüxen describes a *Chamaenerium augustifolium-Senecio silvaticus* "Kahlschlaggesellschaft" where *Sarothamnus* is a character species. In Denmark, this mode of occurrence after disforesting is not frequent, possibly because the species neither grows in the oak woods nor in the conifer plantations. The analysis in Table 12 was made in heath covered hills between plantations at Ravnstrup. The area had presumably been burnt some years ago.

F. Heaths characterized by southern subcontinental species (*Genista germanica-tinctoria*-group of *Genistion*).

Heaths belonging to this type occupy only comparatively small areas of moderately acid soils and are situated in regions with more fertile soils than are present in true heath regions. The suboceanic element in this heath type is very reduced, being sometimes represented only by *Calluna* and a few other widely ranging suboceanic plants (or, perhaps more correctly, widely distributed with oceanic tendencies.)

It is beyond doubt that some difficulties arise from an attempt to classify heaths which are dominated by *Calluna*, but which otherwise contain a number of true continental species. In fact, physiognomically such vegetations resemble the Atlantic dwarf shrub heaths; ecologically, however, they may in many cases be more close to steppe communities. In the writer's opinion, the *Calluna* patches on many hills dominated by continental grassland do not belong to the Atlantic dwarf shrub heath, but should be looked upon as acidic (degenerated) varieties of continental grassland. The same opinion is held by Libbert (1938, pp. 118—119). However, it should be emphasized that a separation of such *Calluna* patches from the heaths mentioned here is sometimes difficult. The *Callunetum* of northern slopes in the Saale region (Meusel 1940, Table IX) may still belong to the true heaths; it contains e. g. *Genista pilosa, Jasione, Sieglingia, Pulsatilla vulgaris, Avena pratensis, Pimpinella saxifraga, Dianthus carthusianorum.*

The different F-heaths and their distribution appear from the description of the guiding species.

Genista tinctoria is subcontinental with a rather southerly range (for further details, cf. Jessen 1931, pp. 27—28). It is found on better soils in heaths (Mentz) as well as in steppe communities (Kleopow 1934). In Germany, it occurs also in oak and pine woods (see, e. g., Gassert 1934, p. 100) and in the *Calluna* variety of the *Violetum calaminariae* (Schwickerath). In the heaths of central Jutland it is found on burnt ground or old fields covered with heather or near roads (Randbøl area). In eastern Jutland, it frequently grows in hills clothed by fertile *Calluna* heath. At Aalborg, it was observed as a dominant in a steppelike community on a dry hill (B., unpublished).

Genista germanica has a similar subcontinental distribution, but the range is more southern and central European than that of *Genista tinctoria*. Ecologically, it is closely related to *Genista tinctoria*, occurring e. g. in the montane *Pinetum callunosum* of the Alps (SCHMID 1936) and, particularly, in the *Querceto-Betuletum* "rich in *Genista germanica*" (BRAUN-BLANQUET). In TÜXEN's *Calluna-Antennaria* heath, it reaches the constancy of 22 per cent, yet it is scattered. It occurs also in the related montane heaths of Croatia (HORVAT 1931). In Denmark it is very rare. Analyses of Danish heaths with *Genista germanica* are found in B. 1941 a, p. 104.

Pulsatilla vulgaris ssp. *germanica* has a subcontinental central European distribution. In eastern Europe it is replaced by ssp. *grandis*. According to GRÄBNER (1925, p. 230) the heaths rich in *Pulsatilla vulgaris* occur "an den Hängen, den sanften Lehnen oder den welligen Kuppen von Diluvialhügeln, deren obere Bodenschichten stärker ausgelaugt sind als bei den pontischen Hügeln". In Sweden, this species reaches the Uppsala region (here in dry subcontinental heath, cf. below); in Denmark, it occurs mostly in medium-dry grassland (cf. B. 1941 a), but also enters the open heaths on diluvial sandy hills (e. g. Fig. 17) or on barrows. A number of heather patches with *Pulsatilla vulgaris* (see Table IX, No. 1 in MEUSEL 1939) have so many continental species that they must be separated from the Atlantic heath formation (cf. above).

3. The South-Baltic-submontane heath series.

On p. 57, the advantage of collecting all heaths without northern or southern elements in a separate series was pointed out. This series is inserted between the Scano-Danish and the Dutch-German heath series, however, it does not reach the Atlantic areas where the B- and D-types meet and are mingled.

In Denmark, this series occurs in Jutland (rarely!), in Sealand, on the Isle of Møn, and on Bornholm (in the Baltic). To the south, in Germany, there may be a gradual transition from south-Baltic-submontane to suboceanic-subcontinental (Dutch-) German heaths. The series is also represented in southern Sweden and may be rather widespread along the Baltic coast and in dry acid localities in the interior. To the north, however, Scano-Danish guiding species will soon appear. Unfortunately, the writer has only access to a few observations from Sweden and, in the literature, no heath analyses from South Sweden are found.

The oceanic element is lacking in the Baltic-submontane heaths and among suboceanic plants, only *Calluna vulgaris* is of any great importance. All heaths may belong to one alliance called *Callunion balticum* (cf. below). The series may be further subdivided into geographical main types which show affinities to the main types of the Scano-Danish and the Dutch-German series.

G. Heaths characterized by suboceanic species, continental elements reduced (*Galium saxatile-Carex arenaria*-group of *Callunion balticum*).

Fig. 18 shows typical occurrences of this heath type. In Denmark, it is most frequent in alluvial areas (e. g. Loc. 35, 53, 54, 63, 64, 66, and 71) but it is also found in dry diluvial sandy hills (Loc. 55, 57, 59, and 65), cf. furthermore B. 1943 a.

Table 13. Heaths of the *Callunion balticum* (G main type) Method: S (R in 9—10).

Analysis No. / Locality No. / pH	Distributional type	1 / 55 / 4.2	2 / 65 / —	3 / 65 / —	4 / 57 / —	5 / 61 / —	6 / 61 / 4.1	7 / 63 / —	8 / 66 / 3.9	9 / 59 / —	10 / * / 4.3	Constancy pCt.
1.												
Calluna vulgaris	sbo_3	10_9	10_{10}	10_{10}	10_8	10_{10}	10_{10}	10_{10}	10_{10}	10	10	**100**
Carex arenaria	so_2	10_2	—	—	10_2	8_1	1	8_1	10_4	4	—	70
Galium saxatile	sbo_2	—	10_7	8_3	—	—	—	—	—	—	—	20
Sieglingia decumbens	sbo_3	—	1	3	—	—	—	—	—	—	10	30
Carex pilulifera	sbo_3	—	9_2	10_2	—	—	—	—	—	—	—	20
Hypochoeris radicata	so_3	+	—	—	—	—	—	—	—	—	—	10
2.												
Thymus chamaedrys	sc_2	—	1	1	—	—	—	—	—	—	—	20
Pulsatilla pratensis	sdc_1	—	—	—	3	—	—	—	—	+	—	20
Avena pratensis	sbc_2	—	—	—	3	—	—	—	—	—	—	10
Artemisia campestris	sc_1	—	—	—	+	—	—	—	—	—	—	10
Trifolium arvense	sc_3	—	—	—	+	—	—	—	—	—	—	10
Carex caryophyllea	sc_3	—	—	—	—	—	—	—	—	—	1	10
3.												
Empetrum nigrum	bsΓ	+	—	—	2	+	3	—	—	—	—	40
Antennaria dioeca	bsx	—	+	2	+	—	—	—	—	—	7	40
4.												
Deschampsia flexuosa	sbax	10_2	7_3	9_8	2	1	5	10_4	9_6	—	—	**80**
Festuca ovina	sbxp	—	10_9	10_9	5	—	—	—	—	9	10	50
Agrostis canina	sbxp	7_2	—	—	—	—	—	—	—	—	—	10
— stolonifera	sbxp	—	1	—	—	—	—	—	—	—	—	10
Anthoxanthum odoratum	sbxp	—	—	+	+	—	—	—	—	1	1	40
Poa pratensis	sbxp	—	3	2	—	—	—	—	—	+	—	30
Luzula campestris	sbxp	—	1	2	—	—	—	—	—	1	—	30
Hieracium pilosella	sbxp	1	4	5	2	—	—	—	—	—	3	50
— umbellatum	sbxp	2	—	—	2	—	—	—	—	—	—	20
Viola canina	sbxp	1	1	2	—	—	—	—	—	—	—	30
Veronica officinalis	sbxp	—	1	+	—	—	—	—	—	—	—	20
— chamaedrys	sbx	—	—	1	—	—	—	—	—	—	—	10
Campanula rotundifolia	sbxp	—	—	2	+	+	+	1	—	2	—	60
Potentilla erecta	sbxp	—	2	6_1	—	—	—	—	—	—	1	30
Achillea millefolia	sbxp	—	2	—	—	—	—	—	—	+	—	20
Thymus serpyllum	sbxp	—	—	—	+	—	—	—	—	—	—	10
Lotus corniculatus	sbx	—	—	—	+	—	—	—	—	—	—	10
Galium verum	sbxp	—	—	—	+	+	+	—	—	—	—	30
5.												
Cladonia silvatica	—	—	—	1	1	—	—	—	1	ground layer not analysed	ground layer not analysed	38
— tenuis	—	2	—	—	7_4	—	—	—	2			38
— impexa	—	1	—	—	2	—	2	2	4			63
— rangiformis	—	3	—	—	—	—	—	—	—			13
— chlorophaea	—	5	—	—	—	—	—	—	1			25
— cornuto radiata	—	3	—	—	—	—	—	—	—			13
— pityrea	—	1	—	—	—	—	—	—	—			13
Cetraria tenuissima	—	—	—	—	1	—	—	—	—			13
— glauca	—	3	—	—	—	—	—	—	—			13
Parmelia physodes	—	9_3	—	—	—	3	—	—	6_2			38

* near Dragør at Copenhagen.

Table 13 (continued).

Analysis No. / Locality No. / pH	Distributional type	1 / 55 / 4.2	2 / 65 / —	3 / 65 / —	4 / 57 / —	5 / 61 / —	6 / 61 / 4.1	7 / 63 / —	8 / 66 / 3.9	9 / 59 / —	10 / * / 4.3	Constancy pCt.
6.												
Hypnum cupressiforme	—	9_5	2	—	4	—	5	10_4	1			75
Hylocomium schreberi	—	7_4	9_6	9_6	8_3	—	2	10_8	10_9			88
— splendens	—	—	5	10_6	—	—	—	5	—	ground layer not analysed	ground layer not analysed	38
— triquetrum	—	—	—	—	1	—	—	1	—			25
— squarrosum	—	—	2	4	—	—	—	—	—			25
Dicranum scoparium	—	5	—	—	—	—	+	2	3			50
Lophocolea cuspidata	—	3	—	—	2	—	—	—	—			25

* near Dragør at Copenhagen.

Vegetation: Nos. 1—3: on diluvial hills, inclination 5—8° SW. Nos. 4—10: on alluvial soils. Nos. 9—10: according to RAUNKIÆR 1935, pp. 231 and 242 (Tab. 2, No. 6).
Species groups: 1: suboceanic species. 2: continental-subcontinental species. 3: northern or montane species. 4: widely distributed species. 5: lichens. 6: bryophytes.
Species not mentioned in the table: No. 1: *Solidago virga-aurea* 1, *Polypodium* +. No. 2: *Rumex acetosella*, *Stellaria graminea* 1. No. 3: *Carex hirta* +. No. 4: *Ononis repens*, *Plantago maritima* +. No. 7: *Juniperus* abundant, see Fig. 18. No. 8: *Juniperus* abundant, see B. 1942, Tab. 3. No. 9: *Festuca rubra* 1. No. 10: *Carex flacca* 1, *Agrostis tenuis* 1.

In Table 13, a number of analyses from Denmark are grouped. Where in initial stages in dune areas *Empetrum* is more frequent, transitions between the G- and the B- main types are formed. On Boderne (Loc. 71), the alluvial *Callunetum* contains the subatlantic *Carex arenaria* and *Euphrasia gracilis* and, furthermore, *Thymus serpyllum, Galium verum, Polypodium, Salix repens,* the common bryophytes, *Cladonia* and *Cetraria tenuissima.* In Sweden, similar heaths were observed at Johnstorp, Heljaröd and Skanør. On the border line between the uniform *Calluna* heath and a meadow dominated by *Agrostis-Deschampsia flexuosa,* the following heath was observed (Table 14).

Table 14. Heath at Heljaröd near Engelholm (Sweden). Method: D.

1.	
Calluna vulgaris	5
Galium saxatile	2
Achillea millefolia	1
Thymus serpyllum	1
Potentilla erecta	1
Lotus corniculatus	1
2.	
Deschampsia flexuosa	3
Carex hirta	1–2
Agrostis stolonifera	1
Festuca ovina	1
Veronica officinalis	1
3.	
Hylocomium schreberi	4
— splendens	1
— triquetrum	1
Dicranum rugosum	1

Species groups: 1: suboceanic species. 2: widely distributed species. 3: bryophytes.

While the heaths of level or gently sloping ground (Table 13) are related to the B-heaths and, in many localities, merge into typical Scano-Danish B-sociations, those of northern slopes are ecologically closely related to the A-heaths. Perhaps, the latter should have been separated in a special main type characterized by *Polypodium, Rumex acetosa, Lonicera periclymenum, Hylocomium triquetrum,* and *Lophocolia bidentata,* which were mentioned on p. 31 as characteristic A-heath plants. In the present treatise, however, they are classified only as a variety of the G-type. Transitions between A- and such northern slope varieties of the G-type may be found

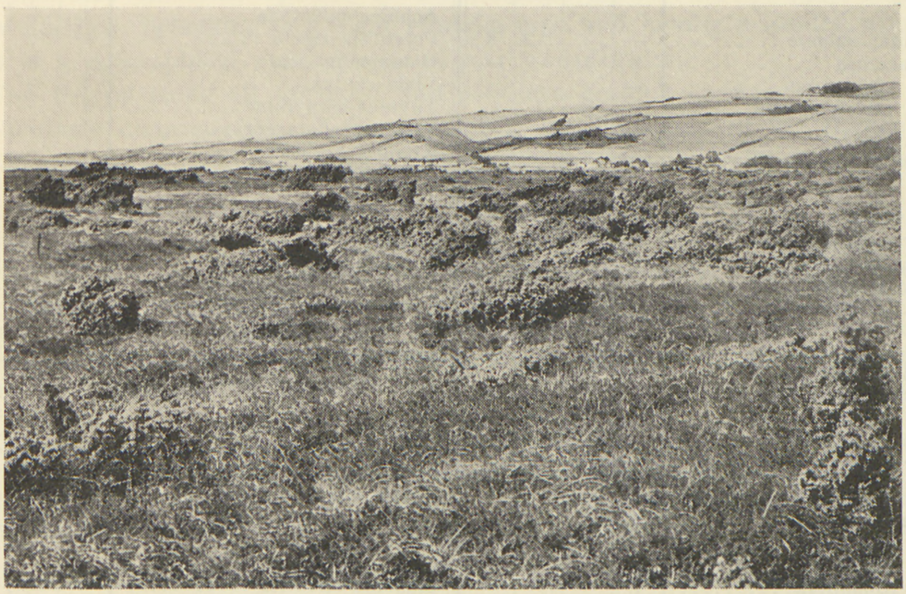

Fig. 18. *Calluna-Deschampsia flexuosa-Carex arenaria* heath with scattered junipers on the alluvium at Dragsholm (Loc. 63). In the background, cultivated land on hills accumulated at the edge of the ice (Vejrhøj, 121 m. above the sea); to the left, Sejrø Bugt (the northern part of the Great Belt). After B. 1943 a.

in Table 4 of Hammer Pedersen (1938). In Table 15, four examples of the variety are collected.

In a number of analyses from Denmark, we find *Antennaria dioeca* which was used as a character species in the *Calluna-Antennaria* ass. of Tüxen. A study of the relations between this German heath and the above-mentioned Danish vegetations must begin with an examination of the distributional types in the *Calluna-Antennaria* heaths. We may use Tüxen's two tables (pp. 121—122) and the description in Pfalzgraf (1934). In Tüxen's 21 analyses, the following suboceanic plants occur: *Calluna, Sieglingia* (constant!), *Genista pilosa* (constancy 11 and 25 per cent), *Lycopodium tristachyum* (rare), *Carex pilulifera, Galium saxatile, Hypochoeris radicata,* and *Leucobryum glaucum* (*Nardus* variety). The continental element is represented exclusively by *Genista germanica.* On the other hand, Pfalzgraf's heaths from Meissen (altitude 6—700 m., pH 4.6, 5.2) contain only very few suboceanic plants (*Calluna, Trifolium minus*) and a large contingent of continental "Bromion" species, viz. *Avena pratensis, Koeleria cristata, Pimpinella saxifraga, Helianthemum chamaecistus, Silene nutans,*

Table 15. Northern slope variety of G main type. Method: D.

Analysis No.	1	2	3	4
Locality No.	56	60	69	71
Exposure	NW	NW	NE	N
Slope	35°	30°	15°	30°
1.				
Polypodium vulgare	—	+	1–2	3
Rumex acetosa	1	1	—	—
Solidago virga-aurea	—	+	—	—
Lonicera periclymenum	—	—	1	—
Fragaria vesca	2	—	—	—
2.				
Calluna vulgaris	5	5	5	5
Carex arenaria	1	—	—	1
Sieglingia decumbens	1	—	—	—
Saxifraga granulata	—	1	—	—
3.				
Pimpinella saxifraga	+	—	—	1
Trifolium medium	1	—	—	—
Viscaria vulgaris	—	+	—	—
Artemisia campestris	—	—	—	1
4.				
Deschampsia flexuosa	2	1	1	—
Festuca ovina	1–2	1	—	—
— rubra	+	—	—	—
Agrostis stolonifera	1	—	—	—
Anthoxanthum odoratum	—	+	—	1
Carex flacca	+	—	—	—
Campanula rotundifolia	1–2	1	—	—

Analysis No.	1	2	3	4
Locality No.	56	60	69	71
Exposure	NW	NW	NE	N
Slope	35°	30°	15°	30°
Achillea millefolia	1	—	—	—
Potentilla erecta	+	—	—	—
Ranunculus acer	+	—	—	—
Viola canina	1	—	—	—
Thymus serpyllum	1	—	—	—
Veronica chamaedrys	1	—	—	—
Knautia arvensis	+	—	—	—
Galium verum	1	—	—	1
5.				
Hylocomium schreberi	4	+	2	4
— splendens	3	2	1–2	—
— triquetrum	3	3	4	—
— squarrosum	1	—	—	—
Pseudoscleropodium purum	—	1	—	—
Dicranum rugosum	+	—	—	—
— scoparium	—	+	—	1
Hypnum cupressiforme	—	—	1	—
Camptothecium lutescens	—	1	—	—
Catharinaea undulata	—	+	—	—
Lophocolea bidentata	—	1	—	—
6.				
Cladonia silvatica	—	1	1	—
— rangiferina	—	—	1	—
— rangiformis	—	—	—	+
Peltigera canina	+	—	—	3

Vegetation: Nos. 1—2: sandy diluvial hill-slopes, pH 4.7 (No. 1). No. 3: rocky ground at Bobbeaa. No. 4: dune slope in old blow-out. No. 1: 4 sq. m. Nos. 2—4: 1 sq. m.
Species groups: 1: northern slope species (cf. main type A). 2: suboceanic or west-central European (*Sax. granulata*) species. 3: continental-subcontinental species. 4: widely distributed species. 5: bryophytes. 6: lichens.

Viscaria vulgaris, Dianthus superbus, Galium boreale, and *Campanula glomerata.* No doubt, the *Calluna-Antennaria* heaths of Germany are no unity. Some of them belong to the suboceanic E-type (cf. p. 58). The Meissner heaths which lack Dutch-German guiding species but include *Vaccinium myrtillus,* belong most naturally to the I-type (cf. below) or may perhaps only be regarded as a degeneration stage of a *Bromion* community. Finally, many *Calluna-Antennaria* heaths without *Genista pilosa* or other southern suboceanic species may belong to the G-type.

The rather curious behaviour of the *Calluna-Antennaria* heath is primarily due to the unlucky choice of character species. *Antennaria dioeca* is a widely distributed eurasiatic boreal plant ranging from Iceland, West Norway (where it is frequent) to the central parts of the continent. In central Europe and in England, it is montane. In Denmark, it is not particularly frequent in the heath, it attains the greatest abundance, however, in certain dry grassland communities. *Lycopodium clavatum* is also widely distributed and is, besides, used as a character species in the *Calluna-Genistetum*. The two other character species are suboceanic (*Lycopodium tristachyum*) or continental (*Gen. germanica*). It is inevitable that the value of widely ranging character species is very limited and that the value of two character species with opposite distributional tendencies must also be very low. On the other hand, the most important character species of the *Calluneto-Genistetum*, viz. *Gen. anglica*, is well established, belonging to a clear climatic type and having a limited area. This species is a geographical guiding species par excellence.

The G-type lacks all northern and southern guiding species, and no species is particularly characteristic of this type. For the limitation of the G-type *Carex arenaria* may be of some importance and the same is the case with *Gallium saxatile*.

Carex arenaria. According to Hård (1935), it is "eu-oceanic". The present writer, however, terms the species suboceanic, since it is frequent in rather continental areas (e. g. Øland, Sweden) and penetrates to the Leningrad region. To Sterner's map (in Acta Flora Suecica I, p. 211) numerous localities in Ireland should be added (Präger). Furthermore, the species is closely related to the central European *Carex ligerica* and the continental *Carex colchica*. On the variability of the distinguishing characters, cf. Fettweis (1938, in Decheniana vol. 97 B, p. 85).

Galium saxatile. In contrast to the rather southerly *Carex arenaria* this species is rather northerly and suboceanic. It is widely distributed in different heaths and is of value for the limitation of suboceanic types from subcontinental ones (G-I) and for the limitation of relatively northern and southern heaths in France (Allorge and Gaume, 1931, p. 35; B. 1940, p. 22).

H. Heaths characterized by boreal continental species (*Lycopodium complanatum-Carex ericetorum*-group of *Callunion balticum*).

Under this heading we collect a number of heaths which are related to those of the C-type. Compared with the *Arctostaphylos* heath, they occur mainly in localities with richer soils and are not particularly rare in hilly districts. None of the H-heaths occupy large areas. In the following, both typical H-heaths and such transition heaths where the H-guiding species are very scattered are described. Thus, the material elucidates the occurrence of the boreal continental element in the north-Atlantic heath formation. The H-type may perhaps be subdivided into two groups, viz. one group with relations to woods (a), and one group with relations to herbaceous hillside vegetation (b). Finally, some dune heath sociations are related to the H-type and may be mentioned here (c).

a. *Calluna-Lycopodium complanatum* soc. In Sweden, *Lycopodium complanatum* is mainly a plant of conifer woods (Samuelsson 1919). In Denmark, heaths with *Lycopodium complanatum* are frequently found in slopes with a northerly exposure or in luxuriant tall *Calluna* heaths. The ground layer consists of mixed bryophytes and lichens, and the vegetation has a great resemblance to the A-heaths. After burning,

Table 16. Heaths of the *Callunion balticum* (H main type) and related transition heaths. Method: D:

Analysis No. / Locality No.	Distributional type	1 / 79	2 / 6	3 / 6	4 / 6	5 / 45	6 / 6	7 / 6	8 / 5	9 / 6	10 / 39
1.											
Lycopodium complanatum	bsc$_2$	5	4	2	2	1–2	3	4	—	—	—
Carex ericetorum	bsc$_1$	—	—	2	—	—	—	—	3	3	1
— montana	sc$_3$Mo	—	—	1–2	—	—	—	—	—	—	—
Hypochoeris maculata	sbc$_3$(┐)	—	—	—	—	—	—	—	—	—	1
Scorzonera humilis	sc$_2$	—	1	—	—	—	—	—	—	—	+
2.											
Vaccinium vitis idaea	bs(┐)	2	—	—	2	1	—	—	—	—	—
Empetrum nigrum	bs┌	—	1	—	1	1	4	—	—	—	—
Antennaria dioeca	bsx	—	1	—	—	—	—	—	1	1	—
3.											
Vaccinium Myrtillus	b(al)sx	1	—	—	—	—	1	4	—	2	—
Trientalis europaea	b(al)sx	—	—	—	—	—	1	—	—	—	—
Luzula pilosa	sbx	—	—	—	—	—	1	1–2	—	—	—
Melampyrum vulgatum	bsx	—	—	—	—	—	2	2	—	—	—
4.											
Calluna vulgaris	sbo$_3$	4	5	5	5	5	—	—	4	4	5
Sarothamnus scoparius	sdo$_3$	—	—	—	—	—	—	—	—	—	2
Genista pilosa	sdo$_2$	—	—	—	—	1–2	—	—	—	—	1
Carex pilulifera	sbo$_3$	—	—	—	—	—	—	—	—	—	1
— arenaria	so$_2$	—	—	—	—	—	—	—	1	—	—
5.											
Juniperus communis[1]	sbx	—	—	—	—	—	1	3–4	—	—	—
Deschampsia flexuosa	sbax	1	1	1	1	1	1	1	—	—	1
Festuca ovina	sbxp	—	—	—	—	—	—	—	—	1	—
Agrostis canina	sbxp	—	—	—	—	—	1	—	1	—	—
Luzula multiflora	sbxp	—	—	—	—	—	—	—	—	—	1
Lotus corniculatus	sbx	—	—	—	—	—	—	—	1	1	—
Potentilla erecta	sbxp	—	—	1	—	1	—	—	—	—	—
6.											
Cladonia impexa	—	1	3	3	1	1	—	—	1	1	1
— silvatica [*mitis]	—	1	4	3	2	2	—	—	5*	2	—
— floerkeana	—	—	—	—	—	—	—	—	—	—	1
— chlorophaea	—	—	—	—	—	+	—	—	—	—	1
7.											
Hylocomium schreberi	—	—	4	4	5	4	3	2	3	2	—
— splendens	—	—	—	—	—	—	1	—	—	—	—
Hypnum cupressiforme	—	—	1	1	1	4	—	3	1	2	—
Blepharozia ciliaris	—	—	—	1	1	—	—	—	1	1	—
Lophocolea bidentata	—	—	—	—	—	—	—	1	—	—	—
Jungermannia barbata	—	—	—	—	—	—	—	—	—	1	—
Pohlia nutans	—	—	—	—	—	—	—	—	—	—	1
Polytrichum piliferum	—	—	—	—	—	—	—	—	1	—	—

[1] in the scrub layer.

Lycopodium complanatum is sometimes abundant in the *Calluna* stages of the succession. Observations of the *Calluna-Lycopodium complanatum* soc. are tabulated in Table 16, Nos. 1—5.

Another boreal plant otherwise found in continental mesophytic thin woods (cf. STERNER 1921, p. 406) occurs in the heaths of the Halland ridge. Here (Troldehallar, Loc. 79), *Calamagrostis arundinacea* enters a *Callunetum* on a scree facing east, situated near a beech wood. The acidity of the soil is high (3.8), and moreover the vegetation contains *Deschampsia flexuosa* and *Solidago virga aurea.* In Sweden, this may be a rather local behaviour of *Calamagrostis arundinacea*; in Denmark, the plant is almost exclusively observed in woods or oak scrubs, being very rare in the A-heaths (Table 2, No. 13). In East Prussia, however, it occurs in the *Callunetum* (cf. below). In the same manner or even more frequently, *Calamagrostis epigeios* in a sterile stage enters some heath slopes in the vicinity of scrubs (Loc. 5, 24, and 27). This species is not a true boreal continental plant, although it is sometimes reckoned among the subarctic steppe plants (PODPERA, 1928). Furthermore, it is very frequent in Dutch dune heaths (Berger duinen, see BIJHOUWER 1926, Tables 5 and 6) and, sometimes, also in Danish dune heaths (e. g. Svinkløv, Loc. 11: *Calluna-Hylocomium* soc. with *Calamagrostis epigeios, Geranium sanguineum* (subcontinental) and *Rosa spinosissima*).

b. The *Calluna-Carex ericeterum* soc. was observed at Tolne on the top of a dry heath-covered hill near open sand (Table 16, No. 8). The soil acidity is low (pH 5.3). In the Gerum heath, it is developed on burnt areas (Table 16, No. 9). The sociation occurs also in North Sealand (Loc. 59) on dry slopes.

Calluna heaths with scattered *Carex ericetorum* were observed at Vrads on southern slopes (Table 16, No. 10), while the northern slopes are covered with a *Calluna-Vaccinium myrtillus-Hylocomium* sociations with *Luzula pilosa.* A corresponding south slope heath was analyzed near Haderup (Loc. 30, Fig. 19), where *Carex ericetorum, Hypochoeris maculata,* and *Viscaria vulgaris* enter a *Calluna-Carex arenaria* soc. (Table 17). pH measurements of the soil gave rather high values.

Calluna heaths with a rather great number of *Viscaria vulgaris* were observed at Bindeballe on dry slopes (Loc. 44, B. 1941, p. 60) and at Villingebæk (Loc. 55) on hills south of the locality shown in Fig. 17.

Undoubtedly, most of the Danish H-heaths are westerly varieties of a more typical vegetation. Unfortunately, only rather few analyses of such heaths are at hand. The very easterly heaths have been analyzed by DU RIETZ (1930, Table 6), JURASZEK ("*Xerocallunetum*"), and STEFFEN (1931). These vegetations from Uppland (Sweden), East Prussia, and Poland are of the greatest interest, showing an obvious relationship

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Table 16.

Vegetation and localities: Nos. —5: typical *Callunetum* with *Lycopodium complanatum.* Nos. 6—7: transition to the A main type. Nos. 8—9: *Calluneta* with *Carex ericetorum.* No. 10: transition to the E main type. — No. 1: Snekkebakker Tosjö Sogn; the vegetation covers many square metres. Nos. 2—4: Gerum heath, inclination 10°N. No. 5: Aakærhus, pH 4.8—4.9. Nos. 6—7: Flade Bakker near scrubs of beech, *Juniperus* very frequent. No. 8: on a dry top near open sand, pH 5.3. No. 9: gently sloping ground; the vegetation had been burnt in 1934 or 1935, it was analyzed in 1937. pH 4.5. No. 10: dry southern slope near a road.

Species groups and species not mentioned in the table: 1: continental-subcontinental species. 2: northern species. 3: northern and A type species (moreover *Arnica montana* 1 in No. 9). 4: suboceanic species (moreover *Jasione montana* and *Corynephorus canescens* 1 in No. 8). 5: widely distributed species (moreover *Thymus serpyllum, Rumex acetosella* 1 in No. 8, *Anemone nemorosa* 1 in No. 6). 6: lichens (*Parmelia physodes* 1 in Nos. 1 and 6, *Cladonia destricta* 1 in No. 9). 7: bryophytes.

Table 17. *Callunetum* on dry southern slope at Haderup. Method: S. Inclination 15—20° (cf. Fig. 19). pH 4.5, 4.7, 5.0.

1.	
Carex ericetorum	1
Viscaria vulgaris	+
Silene nutans	3
Genista tinctoria	1
2.	
Calluna vulgaris	10_9
Carex arenaria	9_4
Hypochoeris radicata	2
3.	
Empetrum nigrum	+
Antennaria dioeca	+
4.	
Deschampsia flexuosa	5
Luzula multiflora	1
Festuca ovina	+
Campanula rotundifolia	2
Hieracium pilosella	+
Solidago virga-aurea	+
5.	
Hylocomium schreberi	8_3
Hypnum cupressiforme	3

Species groups: 1: continental-subcontinental species. 2: suboceanic species. 3: northern-montane species. 4: widely distributed species. 5: bryophytes.

between the main types C, H, I and F. The Swedish heath contains C-guiding species (*Cetraria nivalis, Cetraria cucullata*[1]), H-species (*Carex ericetorum* with great constancy), and a single southern continental species (*Pulsatilla vulgaris*). In the *Xerocallunetum*[2] of Poland, the northern *Arctostaphylos uva ursi* (constancy 60 $^0/_0$), the boreal *Carex ericetorum* (constancy 80 $^0/_0$) met with the southern continental plants *Genista germanica* (constancy 20 $^0/_0$) and *Pencedanum oreoselinum* (constancy 60 $^0/_0$). The latter was also found in the heath of Loc. 66. With the exception of *Calluna*, the Swedish heath lacks all suboceanic plants. On the other hand, the *Xerocallunetum* contains 6 suboceanic (o_2 and o_3) plants (*Calluna, Sarothamnus, Teesdalia nudicaulis, Corynephorus canescens, Spergula vernalis,* and *Jasione montana*); it lacks, however, northern or montane plants such as *Vaccinium vitis idaea* and *Antennaria*, which occur in the Swedish heath. In spite of dissimilarities, both heaths may most naturally be assigned to the H-type.

The *Callunetum* described by Steffen from East Prussia is an open pine wood with *Calluna* heath as subvegetation. Here, the continental northern-boreal elements are represented by *Lycopodium complanatum, Carex ericetorum, Calamagrostis arundinacea* (constancy 50 $^0/_0$), *Arctostaphylos uva ursi* and *Pirola secunda*; to the southern continental element belong a good many species (e. g. *Anthericum ramosum, Peucedanum oreoselinum, Pirola umbellata, Pulsatilla patens, Scorzonera humilis, Polygonatum officinale*). The vegetation is most naturally assigned to the H-type, although it approaches the I-type (cf. below) and includes both continental plants from woods and herbaceous vegetation (a and b subtypes). The suboceanic element counts two species only (*Calluna* and *Carex pilulifera*).

c. *Calluna* heaths with *Hypochoeris maculata* as a subdominant have been described from Randbøl Hede, where they occur as a successional stage after burning and cultivation (B. 1941 a, p. 102). *Hypochoeris maculata* is moreover found in sub-

[1] Furthermore, guiding species for *Loiseleurieto-Arctostaphylion* and related alpine grass heaths.
[2] Juraszek 1928, Nos. 1—5.

climax heaths on fertile soils, but there mostly scattered. Only in certain alluvial areas is it abundant in old heaths. Thus, on Dybesøtangen (Loc. 61), the low wind-swept heath (Table 8a, No. 11) is adorned by the rosettes or flowering individuals of *Hypochoeris maculata*. The soil acidity is low (pH 5.1). This vegetation may be compared to the exposed *Empetreta* of Læsø (B. 1941 b), however, it is a more southern type without arctic-alpine lichens.

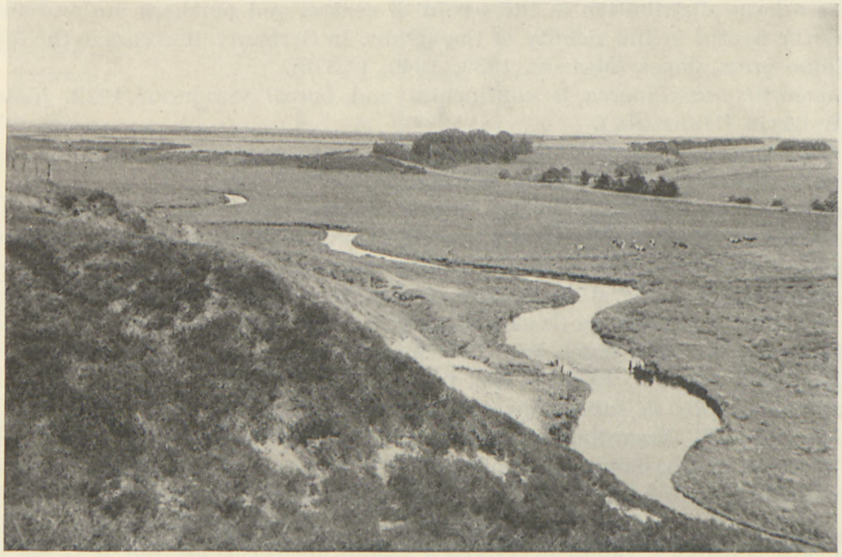


Fig. 19. *Calluna-Carex arenaria* heath on dry southern slope near the river Haderup Aa, cf. analysis Table 17. B. photo 1934.

In other heaths or related heaths of Jutland, patches can be found where *Rosa spinosissima* is abundant or more scattered. The few observations available indicate that such patches are not particularly dry and the vegetation is sometimes found on the north side of dunes (Table 8a). At Kaas (Loc. 24), the burnet rose grows in small patches in *Calluna-(Hylocomium)* soc. with *Empetrum, Deschampsia flexuosa, Carex arenaria, Potentilla erecta, Hypnum cupressiforme*, and *Pelligera canina*. The soil of the dune heaths is only moderately acid and the vegetation comes rather close to that of British limestone heaths, of which the burnet rose is characteristic (cf. Tansley 1939, p. 473).

Undoubtedly, the *Lycopodium complanatum-Carex ericetorum* group is a rather inhomogeneous type and its most marked representatives are not clearly separated from the more northern (C-type) and southern (F and I-types) continental main types. The close relationship between the C-, F-, H- and I-types is discussed in greater detail on p. 113.

Guiding species and other continental species in the H-heath type.

Lycopodium complanatum is boreal and subcontinental (cf. Hård 1935, p. 356; B. 1938, p. 60; Hultén 1941, pp. 68—69).

Carex ericetorum is boreal and continental (further details in Hultén 1937, Sterner

1922, Uittien, 1932, B. 1941a, p. 140). In Denmark it is moreover found in continental grassland. In Poland, it is very constant in the *Pineto-Cladinetum, Xerocallunetum, Thymetum augustifolii, Corynephoretum,* and *Calamagrostidetum epigeios* (Juraszek 1928).

Carex montana has a problematic distribution (Hård 1924, 1935). In N.W.-Germany, it is rare; continental and northern according to Matthews. It reaches an eastern limit at Pskow (Kupffer); Hermann (1936, p. 34) states that the eastern limit runs through Bulgaria. Nevertheless, it occurs in Russia, Sibiria, Caucasia, and the Altai mountains (Komarow). Locally, it may be rather frequent in the Tönnersjö heath in Sweden (Malmström). In Denmark, it has a large distribution in the scrubs of central and northern Jutland and it sometimes enters the heaths in the vicinity of the scrubs. In Germany, it occurs in the forest steppe and the alpine grass slopes (Meusel 1939, 1940, p. 379).

Calamagrostis arundinacea is continental and boreal (Sterner 1922, plate 22) and alpine in Bulgaria (Hermann).

Viscaria vulgaris is eurasiatic, continental in Norway and continental-northern in the British Islands (Matthews); in South Europe, it is very rare.

Hypochoeris maculata is eurasiatic, subcontinental and rather northerly. In England, it is rare and submontane. Podpera mentions it among the subarctic steppe plants. Furthermore, it has a large distribution in woody steppe communities in central and eastern Europe. The total range ought to be studied more closely in connection with investigations of the variability in different regions. In Czechoslovakia, it exhibits a noteworthy variability (Domin 1938); in Denmark it varies much less. For further details, cf. Uittien 1932, pp. 285—286, Hård 1935, p. 257, Meusel 1939, p. 232, and B. 1941a, p. 140.

Scorzonera humilis is subcontinental with a Baltic-central European range (Sterner 1922, pp. 240 and 407). According to Sterner, it is a species of mesophytic thin forests. In Denmark, it occurs in grassland communities, fertile heaths, and oak scrubs. It is particularly frequent in the H-I-main heath types; in the Randbøl area, it grows abundantly near roads where the supply of dust causes an increase in pH and in the fertility of the soil. The species occurs with low constancy values in Tüxen's *Calluneto-Genistetum*, but it is not mentioned in the *Calluna-Antennaria* heath. Tüxen refers to it among the *Calluneto-Genistetum* character species, however, its value must be very limited, since *Scorzonera* is continental and the *Calluneto-Genistetum* is oceanic.

Rosa spinosissima (*pimpinellifolia*) is very polymorphous; its different races are incompletely known. It has a large eurasiatic range and shows continental tendencies (cf. Matthews). In central and southern Europe it is montane. The species is absent in Sweden, N.E.-Germany, eastern Denmark and Norway, except the southern coast districts from Bergen to Langesund. The gap coincides fairly well with the area of the latest glaciated regions. In Denmark and the British Islands, it is most abundant in calcareous dune areas. In Iceland it is found in five localities (Grøntved 1942, Fig. 113).

I. Heaths characterized by continental-subcontinental, sometimes southern-continental species, suboceanic element reduced. *Filipendula-hexapetala*-group of *Callunion balticum.*

When in northern Sealand sandy slopes incline to the north, the variety of the G-type mentioned on p. 65 may be developed. Sometimes, however, fairly true A-heaths (Table 2, No. 16-17) also occur. When the slope is southern, eastern or western, other types with a number of continental plants are found. The latter as well as a few larger heaths of dry level ground belong to a subcontinental heath

Table 18. Heaths of the *Callunion balticum* (I main type). Method: D.

Analysis No. / Locality No.	Distri-butional type	1 / *)	2 / 57	3 / 58	4 / 60	5 / 69	6 / 68	7 / 78	8 / 78	9 / 68	10 / 68	Con-stancy pCt.
1.												
Filipendula hexapetala	sc_2	1	2–3	—	2	1	1	—	1	1	1	**80**
Avena pratensis	sbc_2	1	1–2	—	1	—	—	—	—	—	—	30
Poa angustifolia	sbc_2	+	1	—	—	—	—	—	—	—	—	20
Phleum nodosum	sc_3	—	—	—	—	—	1	—	—	—	—	10
Carex caryophyllea	sc_3	—	—	1	—	—	—	—	—	—	—	10
Pimpinella saxifraga	sbc_3p	+	—	1	1	—	—	—	—	—	1	40
Silene nutans	sc_3	—	—	—	—	—	—	—	—	+	—	10
Dianthus deltoides	sbc_3	—	—	—	1	—	—	—	—	—	—	10
Viscaria vulgaris	sbc_3	1	—	—	—	—	—	—	—	—	—	10
Potentilla pentaphylla	sdc_1	—	—	—	1	—	—	—	—	—	—	10
Agrimonia eupatoria	sc_3	—	—	—	—	—	—	1	—	—	—	10
Lathyrus silvester	sc_2	—	—	—	—	—	—	1	—	—	—	10
Vicia lathyroides	sdc_2	—	—	—	1	—	—	—	—	—	—	10
Hypericum perforatum	sbc_3	—	—	—	1	1	—	—	—	—	—	20
Geranium sanguineum	sc_2	—	—	—	—	—	—	—	—	2	1	20
Pulsatilla pratensis	sdc_1	+	—	2	—	—	—	—	—	—	—	20
Sedum maximum	sbc_3	—	—	—	—	1	—	—	—	—	—	10
Cynanchum vincetoxicum	sc_1	—	—	—	—	1–2	—	—	—	—	—	10
Melampyrum arvense	sdc_1	—	—	—	—	—	1	—	—	—	—	10
Centaurea jacea	sc_2p	—	—	—	—	—	1	—	—	1	—	20
Hypochoeris maculata	sbc_3(┐)	1–2	—	—	—	—	—	—	—	—	—	10
Scabiosa columbaria	sc_2	—	—	1	—	—	—	—	—	—	—	10
Veronica spicata	sc_1	—	—	—	—	1	—	—	—	—	—	10
2.												
Calluna vulgaris	sbc_3	**4**	**4**	**5**	**5**	**5**	**5**	**5**	**5**	**4**	**5**	**100**
Hedera helix	so_3L	—	—	—	—	—	—	—	—	4	2	20
Lathyrus montanus	so_3	—	1	—	—	—	—	—	—	—	—	10
Carex arenaria	so_2	1	—	—	1	—	—	—	—	—	—	20
Jasione montana	so_3	+	—	1	—	—	—	—	—	—	—	20
3.												
Deschampsia flexuosa	sbax	+	1	—	—	—	2	1	1	1	—	60
Anthoxanthum odoratum	sbxp	1	—	1	1	—	—	—	—	—	—	30
Agrostis tenuis	sbxp	+	1	—	—	—	1–2	—	1	—	—	40
Festuca ovina	sbxp	—	1	—	—	—	—	—	—	—	—	10
— rubra	sbxp	—	—	1	1	—	—	—	—	—	—	20
Potentilla erecta	sbxp	—	+	—	—	—	—	1	—	—	—	20
Campanula rotundifolia	sbaxp	+	—	1	1	—	1	—	—	—	1	50
Veronica officinalis	sbxp	—	—	—	—	1	—	—	—	—	—	10
Hieracium umbellatum	sbxp	—	—	—	—	—	1	—	—	—	1	20
— pilosella	sbxp	—	—	1	—	—	—	—	—	—	—	10
Thymus serpyllum	sbxp	+	—	—	—	—	—	—	—	—	—	10
4.												
Polypodium vulgare	sbx	—	—	—	—	—	—	—	—	—	1	10
Rumex acetosa	sbxp	—	1	—	1	—	—	—	—	—	—	20
Solidago virga-aurea	sbxp	—	—	—	—	—	—	—	—	1	1	20
5.												
Galium verum	sbxp	+	1	—	2	—	—	—	—	—	—	30
Achillea millefolia	sbxp	—	1	1	1	—	—	—	—	—	—	30

*) Galgebakke at Næstved south of Loc. 65. 8 sq. m.

Table 18 (continued).

Analysis No. / Locality No.	Distributional type	1 *)	2 57	3 58	4 60	5 69	6 68	7 78	8 78	9 68	10 68	Constancy pCt.
Plantago lanceolata	sbxp	—	—	—	1	—	—	—	—	—	—	10
Ononis repens	sx(o)	+	—	—	1	—	—	—	—	—	—	20
Knantia arvensis	sbx	—	—	—	1	—	—	—	—	—	—	10
Stellaria graminea	sbx	—	1	1	—	—	—	—	—	—	—	20
Dactylis glomerata	sbxp	—	—	—	1	—	—	—	—	—	—	10
Briza media	sbx	—	—	—	1	—	—	—	—	—	—	10
Rubus idaeus	sbx	—	—	—	—	—	—	1	—	—	—	10
Scrophularia nodosa	sbx	—	—	—	—	—	—	1	—	—	—	10
6.												
Pseudoscleropodium purum	—	—										10
Hylocomium schreberi	—	+	} 4	3	—	—	—	—	—	—	—	30
— splendens	—	—										10
Camptothecium lutescens	—	—	—	—	4	—	—	—	—	—	—	10
Hypnum cupressiforme	—	3	—	—	—	4	—	—	—	—	—	20
Dicranum scoparium	—	—	—	+	—	1	—	—	—	—	—	20
7.												
Juniperus communis	sbx	—	—	—	—	—	—	2	1	—	—	20
Prunus spinosa	sx	—	—	—	—	—	3	2	3	1	—	40

*) Galgebakke at Næstved south of Loc. 65. 8 sq. m.

Vegetation and localities: Nos. 1—4: sandy soil. Nos. 5—10: sandy or somewhat clayey soil on rocky ground. — No. 1: level area, pH 4.9. No. 2: eastern slope. No. 3: southern slope (inclination 10°); pH 5.2. No. 4: south-western slope (inclination 20°); pH 5.7. No. 5: south-eastern slope (inclination 15°); pH 5.1. No. 6: western slope. Nos. 7—8: south-western slopes (inclination 5 and 10°). Nos. 9—10: western slopes (inclination 30—40°).
Species groups: 1: continental and subcontinental species. 2: suboceanic species. 3: widely distributed species frequent in heaths. 4: widely distributed species frequent in the A-type and related heaths. 5: widely distributed species alien to heath vegetation. 6: bryophytes. 7: scrub layer.
Species not mentioned in the table: No. 1: *Primula veris, Avena elatior, Cladonia tenuis, Evernia prunastri, Parmelia physodes* +. No. 4: *Vicia hirsuta* 1. No. 5: *Cladonia chlorophaea* and *Parmelia physodes* 1. Nos. 9—10: *Stellaria holostea* 1.

which, geographically, may be placed between the H- and the F-types. In Sweden, I-heaths are found in patches on the southwestern slopes of Kullen, while very typical A-heaths occur on the northern slopes. The boundaries between the H-, I- and F-heaths are less marked. The typical I-heath is composed of *Calluna* (frequently the only suboceanic plant) and a number of subcontinental, continental and widely distributed plants. The most constant subcontinental species is *Filipendula hexapetala*. This species and other continental plants are valuable in the separation of the I-type; they are not true heath guiding species, since their optimal development falls outside the heath. The same is the case with *Rosa spinosissima* and, to some extent, with *Hypochoeris maculata* and *Thymus chamaedrys*. The latter is sometimes found in great quantities in *Calluneta* in East Jutland on fertile soils (B. 1941 a, p. 60). In locality 52, a *Calluna-Thymus chamaedrys* was observed with *Hieracium pilosella* and *Festuca ovina*. This vegetation also belongs to the subcontinental, rather southerly I-main type.

In Table 18, a number of heath analyses representing typical I-heaths are collected. They are taken from rather small patches and are selected in order to show places where the continental plants are particularly numerous. Nos. 9—10 deviate from the others, being ecologically related to the A-type (occurrence of woodland species (*Hedera, Stellaria holostea, Polypodium*) and *Solidago*). Nos. 5—8 come from rocky ground exposed to wind, where *Prunus spinosa* and *Juniperus* are very abundant. No. 5 was observed on the dry summits of the rocky slopes of Kleven. Nos. 1—4 are examples of heaths from the dry grassy slopes or hills of Sealand. The pH values from the I-heaths are comparatively high. The continental plants *Pulsatilla pratensis, Cynanchum, Melampyrum arvense, Veronica spicata,* and *Potentilla heptaphylla (opaca)* must generally be looked upon as intrusions from alvar- or steppe-like communities. The subcontinental species, e. g. *Filipendula hexapetala, Geranium sanguineum, Avena pratensis* may, however, sometimes occur almost as true heath plants. Near Skansehage (Loc. 61), *Filipendula* and *Avena* are found in the alluvial *Callunetum*, and in Loc. 62 patches of a *Calluna-Geranium sanguineum* soc. occur.

From these typical I-heaths there is only a small step to steppe-like grassland. To the I-main type we may, however, furthermore refer most of the larger heaths on archaean rocks of Bornholm (Fig. 20)[1]. These are largely dominated by *Calluna* and by widely distributed species with scattered subcontinental and continental plants. The composition of the vegetation will appear from the following list (a. Ringebakker, Warming 1914, pp. 291—292; b. Slotslyngen, Warming l. c., p. 305; c. Slotslyngen (B.); d. Højlyngen, Warming, l. c., pp. 326—327; e. Højlyngen at Kleven (B.).

Suboceanic: *Calluna* (a—e, dominant), *Aira praecox* (a, b), *Aira caryophyllia* (b), *Sieglingia* (c, e), *Carex pilulifera* (d), *Hypochoeris radicata* (a, b, e), *Lathyrus montanus* (a—c), *Leucobryum glaucum* (a, c).

Continental and subcontinental: *Avena pratensis* (a: frequent. c, d), *Carex ericetorum* (d), *Carlina vulgaris* (a, b), *Circium acaule* (a, b, d), *Cynanchum vincetoxicum* (c, e), *Filipendula hexapetala* (a, b, e), *Galium boreale* (a, d), *Helianthemum chamaecistus* (a, b), *Hypericum maculatum* (a, d), *H. perforatum* (e), *Hypochoeris maculata* (a), *Lithospermum officinale* (a), *Lycopodium complanatum* (d), *Scorzonera humilis* (a, c, d, e), *Sedum maximum* (d, e), *Silene nutans* (a), *Trifolium medium* (a, d), *Veronica spicata* (e), *Vicia cassubica* (d), *Viscaria vulgaris* (a, b) and the southern species *Orchis sambucinus* (d).

Widely destributed: *Achillea millefolia* (d), *Anemone nemorosa* (a, b, d), *Antennaria dioeca* (frequent a, b, d), *Anthoxanthum* (a, b, d, e), *Anthyllis vulneraria* (a, b), *Campanula rotundifolia* (c, e), *Chamaenerium augustifolium* (e), *Convallaria majalis* (a), *Deschampsia flexuosa* (frequently subdominant a, b, c, d, e), *Dryopteris filix mas* (d), *Festuca ovina* (a, b), *Galium verum* (a, d), *Hieracium umbellatum* (a, b, c, d), *H. vulgatum* (a), *H. pilosella* (b), *Leontodon autumnalis* (d), *Lotus corniculatus* (a, b, d), *Luzula pilosa* (b), *Lycopodium clavatum* (d), *Molinia coerulea* (c), *Nardus* (c, e), *Orchis maculata* (d), *Plantago lanceolata* (b), *Platanthera bifolia* (a), *P. chlorantha* (a, b), *Polypodium vulgare* (a, b, c, d, e), *Potentilla erecta* (a, b, c, d, e), *Pteridium* (c, d, e), *Ranunculus acer* (d), *Rubus idaeus* (e), *Rumex acetosa* (a, d), *R. acetosella* (a, d), *Salix repens* (e), *Solidago virga-aurea* (a), *Veronica officinalis* (a, b), *Viola canina* (e) and *Vicia cracca* (a, b, d).

Northern: *Geranium silvaticum* (b), *Vaccinium myrtillus* (c, d, e), *Empetrum* (very rare in small patches, c).

[1] On the heaths of Bornholm cf. furthermore Gelting (1943).

Very characteristic are the numerous trees and shrubs. In the heaths at Kleven: *Juniperus* and *Betula verrucosa* (abundant), *Corylus, Quercus* (rare), *Populus tremula* (frequent), *Carpinus, Pyrus malus, Crataegus oxyacantha, Sorbus aucuparia, Sorbus suecica, Prunus spinosa, Cerasus avium* and conifers (from the plantations in the neighbourhood). Most heaths are rich in bryophytes (*Hypnum cupressiforme, Hylocomium schreberi. splendens, Dicranum, Blapharozia ciliaris* are found), but in "Slots-

Fig. 20. From the heaths in the central archaean rock areas on the Isle of Bornholm. Sigw. Werner photo.

lyngen", *Calluna-Cladina* heaths also occur (*Cladonia rangiferina, silvatica, impexa, coccifera, Cetraria islandica, tenuissima*).

In Loc. 62, *Corylus* and *Rosa canina* are scattered, and *Juniperus* is abundant in the heath which here also has a continental stamp.

Outside Denmark, I-heaths may possibly occur in southern Sweden along the Baltic coast; in Germany, the Meissen heath may belong to this type (p. 66).

4. Remarks on the occurrence in the heath of a number of widely distributed species.

Lycopodium clavatum has a very wide range and is very variable. Judging from the maps in Hultén (1941, p. 118), it is not improbable that some varieties are suboceanic and others (e. g. var. *monostachyon*) continental. In Denmark and Sweden it is most frequent in hilly and fertile heaths (Loc. 4—6, 10, 17, 19, 44, 70, 74, and 79; cf. also Table 4, Nos. 1—8).

Pteridium aquilinum. Only as a collective species, bracken is "cosmopolitan". Otherwise, the fern is unable to inhabit desert and arctic-alpine climates. In the most continental areas of Central Asia, it is very rare and perhaps restricted to mountains with greater air humidity (cf. the map in Fomin 1930). In Great Britain, it seems to reach the greatest abundance.

The species is almost exclusively limited to young heath areas rich in scrub or wood and it reaches its highest F percentages in northern slopes, near scrubs or near the bottom of slopes (cf. Fig. 21).

In rocky districts, it is particularly abundant in the scree (in Norway near Flekkefjord, on Bornholm Loc. 69, 70 (Warming 1914, Fig. 19), at Troldehallar (Loc. 79)). The stony soil must suit it well; thus, on the old raised stony beaches of Ulvshale (Loc. 66), bracken forms

Fig. 21. *Pteridietum* and *Calluna-Pteridium* heath on Gern Bakker (Loc. 36). The stick is divided in white and red areas of 10 cm. B. photo 1934.

a characteristic vegetation together with heather and juniper. The heath slope vegetation rich in *Pteridium* may be exemplified the Nos. 1—4 of Table 19. The occurrence of *Pteridium* at the bottom of a slope is shown in the following profile.

Southern slope of Gern Bakker (Loc. 36). Inclination 15—20°. (cf. Fig. 21).
(From the top of a hill to a wet hollow).

	Distance in m.
Calluna-Cladonia impexa soc. (*Empetrum-Vaccinium vitis idaea*)	10
Vaccinium vitis idaea-Cladonia impexa soc. (*Deschampsia flexuosa*)	3
Empetrum-Vaccinium vitis idaea-Cl. impexa soc. (*Pteridium, Hyl. schreb.*)	12
Empetrum-Pteridium-Hyl. schreb. soc. (Table 19, No. 3)	3
Pteridium-Deschampsia flexuosa-Hyl. schreb. soc	3
Calluna-Pteridium-Hyl. schreb. soc	6
Molinia-Pteridium soc	1
Pteridium-Vaccinium myrtillus-Molinia soc.	1.5
Pteridium-Molinia-Myrica soc	4

	Distance in m.
Small road *Nardus* soc.	1
Deschampsia flexuosa-(Nardus) soc.	6
Calluna-Hyl. schreb. soc.	4
Calluna-Molinia-Myrica gale soc.	3
The same, but also abundant *Erica tetralix*	3
The same, but also *Narthecium, Drosera rotundifolia, Juncus squarrosus*	3
Narthecium-Sphagnum magellanicum soc.	

At the lake Flyndersö (Loc. 21), the *Calluna-Cladina* heath is similarly succeeded by a *Calluna-Pteridium-Hylocomium schreberi* heath which, at the bottom of the slope, is followed by *Juniperus-Pteridium* scrub with *Majanthemum* in the field layer.

Pteridium societies in acidic woods or scrubs have been described from Kaas (Loc. 24, cf. JØRGENSEN and B, Fig. 6), Langskoven near Hald (OLSEN 1938, Fig. 6), Fitting Krat (B. 1941), Ulvshale (Loc. 66, B. 1942) and the slopes at Flyndersø. Here, this society occurs at the bottom of a slope, not in the drier parts of the scrubs. *Pteridium* societies from British, Dutch and German woods have been described by TANSLEY (1939, Plates 16 and 27), VLIEGER (1937), and TÜXEN (1938, Fig. 2).

As may be seen from Table 19 and the profile transection, bracken can be subdominant or dominant in widely different heaths, wet and rather dry heaths, typical A-heaths (Table 3, Nos. 11-15 and Table 19, No. 1) and other heaths. The *Empetrum-Pteridium* soc. (Table 19, No. 3) belong most naturally to the B-type, while the *Calluna-Pteridium* heaths may sometimes belong to other types (e. g. G- and H-types).

Juniperus communis is a circumpolar, polymorphous species. In the Enebærdalen at

Table 19. Heaths with frequent occurrence of *Pteridium aquilinum*. Method: R. (S in No. 3).

Analysis No. / Locality No. / Exposure / Slope	Distributional type	1 37 W 40°	2 37 S 40°	3 36 S 20°	4 23 SW 25°
1.					
Calluna vulgaris	sbo$_3$	6	10	3	10
Galium saxatile	sbo$_2$	1	+	—	—
Carex arenaria	so$_2$	—	—	—	3
2.					
Vaccinium myrtillus	b(al)sx	6	—	—	—
Blechnum spicant	bso$_2$hy	1	—	—	—
Solidago virga-aurea	sbxp	1	—	—	—
3.					
Empetrum nigrum	bsΓ	—	—	10$_{10}$	+
4.					
Pteridium aquilinum	sbx(cosm)	9	7	8$_1$	3
Deschampsia flexuosa	sbax	7	1	9$_2$	5
Rubus idaeus	sbx	4	—	—	—
Potentilla erecta	sbxp	+	+	—	—
Molinia coerulea	sbxp	+	—	—	+
Chamaenerium angustifolium	sbax	—	—	—	3
5.					
Hylocomium schreb.	—	4	3	9$_4$	10
Hypnum cupressiforme	—	4	8	5	7
Dicranum rugosum	—	1	—	2	—
— scoparium	—	1	3	—	—
6.					
Cladonia impexa	—	+	—	2	4
— chlorophaea	—	1	—	—	—

Species groups: 1: suboceanic species. 2: A-type species. 3: northern species. 4: widely distributed species. 5: bryophytes. 6: lichens. In the scrub layer *Salix cinerea* and *Juniperus* in No. 1. pH 3.9 in No. 3.

the lake Hald Sø (Loc. 23), the variability is very conspicuous; here, erect, pillar shaped, prostrate individuals and intermediate types grow side by side in the valley. The variability must certainly be the result of genetic, not environmental factors.

Abundance of *Juniperus* is obtained in oak woods (Hald Egeskov, Gindeskov), fertile heaths and, particularly, such heaths which have been grazed and not burnt (cf. B. 1942, 43a). Finally, the juniper is very frequent in certain dry pastures, e. g. on the sandy parts of Møns Klint (Loc. 67) or at Jyderup and Gilleleje (Loc. 56) on Sealand. A special vegetation, frequently with much heather and juniper, is found on rocky ground in Sweden and on Bornholm.

The vegetations which are dominated by *Juniperus* may be low and heathlike. In most

Fig. 22. Bramslev Bakker at the Mariager Fjord. In the foreground, a *Calluna* heath on rather fertile and dry soil with much grass and *Ononis repens* (flowering). In the background, tall and frequently very dense and dark *Juniperus* scrubs with more or less heathlike ground flora. B. photo 1934.

cases, however, they reach such heights that the term scrub is more correct. The scrubs are very different with regard to the composition of the field-ground layers. The vegetation may be completely heathlike or composed of plants alien to heath, containing dry heath or wet heath plants. A few examples will elucidate these large differences.

1. Korsdalen in Hammer Bakker (Loc. 10), cf. Mølholm Hansen 1926, p. 281. The ground flora shows affinities to the heaths of main type A.

2. Hovs Hallar (Loc. 75). Typical A-heath society of *Vaccinium myrtillus, Dryopteris linnaeana,* and *Oxalis acetosella.*

3. Heath at Nakke (Loc. 62, cf. photo in B. 1939). *Trientalis* soc. (deep shade), *Deschampsia flexuosa* soc. with *Carex arenaria* and *Chamaenerium angustifolium. Hylocomia* very frequent, in particular *Hylocomium squarrosum.* On wet soil, *Hydrocotyle, Myrica, Molinia,* and *Holcus lanatus.*

4. Bramslev Bakker (Loc. 18). Southern heath slopes with beautiful *Juniperus* scrubs (Fig. 22). Ground vegetation varying from typical heathlike vegetations (viz. *Vaccinium myrtillus-, Deschampsia flexuosa-Trientalis* soc. with *Lathyrus montanus, Hylocomium schreberi-splendens-* or *triquetrum* soc.) to woodlike vegetations (*Holcus mollis, Lactuca muralis*)

and grassland vegetations (*Veronica officinalis, Ranunculus bulbosus, Pimpinella saxifraga, Plantago lanceolata, Briza media, Cynosurus, Festuca ovina*, and many others). Undoubtedly, the latter as well as the *Junipereta* of Møn do not belong to the heath vegetation or related scrub vegetations.

VI. North-Atlantic wet heath and bog communities.

Wet heaths are dependent on water near the surface or a water-logged soil. Their area corresponds to that of the dry heath (Fig. 1). Bogs (raised bogs and *Sphagnum* bogs in the heaths (Hedemoser)) are frequent in the same regions, but their area exceeds that of the heath, ranging through the whole Scandinavian peninsula and along the Baltic Sea to northern USSR.

Already Galløe and Jensen (1906) distinguish between wet heath and bog or moss vegetations (denoted as "moor" in Mølholm Hansen 1932, p. 190). The boundary between these formations may, however, be difficult to draw in many cases. Employing the terminology of Tüxen, the boundary separates the *Ericeta* from the *Sphagnata*. It must here be emphasized that no sharp floristic or ecological limit exists, seeing that many species are common to bogs and heaths and that, furthermore, the distributional types of bogs and heaths are related. Besides, it is evident that the similarity between wet heath soils with a thick layer of peat and bogs is very great. The writer agrees with Nordhagen (1936) in the view that all wet heaths and bogs should most naturally be united into one large formation ("*Ledetalia palustris*" or "*Ericeto-Ledetalia*", as proposed by Tüxen). Using distributional types, this formation might be subdivided into regional main types. In his paper on bog vegetation, Schwickerath (1940, 1941) makes an attempt of similar kind, emphasizing the use of so-called "geographische Differentialarten". In many respects, his "*Sphagnion atlanticum*" and "*Sphagnion continentale*" correspond to main types or alliances like those treated here.

The geographical distribution of the different bog types of Europe has been studied by many scientists (e. g. Osvald 1925, v. Bülow 1929, Gams and Ruoff 1929). In this connection, the map sketched by Gams and Ruoff (Fig. 33) showing the areas of the main bog types in the countries round the Baltic Sea is of special interest. To a fairly great extent, the different bog types are here separated by floristic boundaries, e. g. the *Erica tetralix-Ledum palustre* boundary (Granlund 1925) and the *Scirpus caespitosus-Chamaedaphne* boundary (Thomson 1924). Consequently, regional wet heath types based upon plant distributions may coincide with bog types. This is particularly the case west of the *Erica-Ledum* boundary, while bogs and wet heaths are rather well separated east of this boundary. Here, the area of the wet heath is very restricted.

As in the case of the dry heath, wet heaths and bogs are classified according to the presence (or absence) of northern, oceanic, and continental species. Wet heaths and some bogs with a large contingent or frequent occurrence of boreal species belong to types corresponding to the Scano-Danish dry heath series.

The wet heath is here assumed to include at any rate some heaths of the "*Calluneto-Genistetum molinietosum*" (Tüxen) which is found in places with moderately moist soils and, sometimes, contains *Erica tetralix* and other wet soil plants in rather large quantities.

1. Atlantic series. Wet heaths and bogs west of the *Erica-tetralix-Ledum palustre* boundary.

To this large group belong a great number of sociations on wet heaths or bogs in the British Islands, South-West Scandinavia, Holland, and North-West Germany. The main types J, K, L correspond to the A- and B-types within the dry heath series, while the M-type corresponds to the D-type. The group is called *Ulicio-Ericion tetralicis,* however, it does not cover the *Ulicio-Ericion* of Tüxen (cf. below).

J. Wet heaths and bogs characterized by northern-oceanic species (*Myrica-Narthecium*-group of *Ulicio-Ericion tetralicis*).

Myrica gale is able to dominate rather different vegetations. In bogs, it is abundant on gently sloping ground, where the soil water flows slowly. However, it may, though more rarely, dominate bogs with stagnant water (cf. Mølholm Hansen 1932, Table 7 a, Nos. 1—5; Jessen 1939, p. 663). In the wet heath, we find also two different vegetations, viz. a *Myrica-Molinia-*(*Narthecium*) vegetation on sloping ground, which corresponds to the moister *Myrica* bogs on slopes, and a *Myrica-*(*Molinia*) vegetation on level alluvial ground. The latter does not correspond to the moister *Myrica* bog described by Mølholm Hansen and Jessen, which grows on infertile peat, while the *Myrica* vegetation of alluvial ground occurs on relatively fertile soils. The two wet heath vegetations with abundant *Myrica* are closely related, both inhabiting places with rather favourable soils.

In the *Myrica* heaths, only two guiding species, viz. *Myrica* and *Narthecium*, occur. In bogs, *Narthecium* frequently replaces *Myrica* as the dominating species. Furthermore, it forms (e. g. Loc. 8 near Holtemmen) a very dense, meadowlike vegetation with scattered *Myrica* and *Erica* on alluvial wet soil. The latter vegetation and the *Erica-Narthecium* heath (Table 21) are related to the *Myricetum* of alluvial ground.

Myrica-Narthecium vegetations of locatities characterized by oozing or slowly flowing soil water.

There is a gradual transition from the rather dry *Myrica-Molinia* heath of the Randbøl Hede (B. 1941 a, pp. 176—178) through the *Myrica-Molinia-Narthecium*

Table 20. *Myrica-Narthecium*-group of *Ulicio-Ericion tetralicis* (Main type J). Method: S.

Analysis No. / Locality No.	Distributional type	1 / 21	2 / 36	3 / 36	4 / 61
1.					
Myrica gale	$bso_2(\Gamma)$	8_4	7_2	3	10_8
Narthecium ossifragum	sbo_1	2	10_6	10_8	—
Molinia coerulea	sbxp	10_8	10_4	2	6_4
Gentiana pneumonanthe	$so_3(L)$	+	—	—	—
2.					
Empetrum nigrum	$bs\Gamma$	10_7	2	—	—
Vaccinium uliginosum	$bs\Gamma p$	—	—	—	1
Oxycoccus quadripetalus	bsxp	1	3	—	—
Betula pubescens	$bsxp(o_3)$	—	—	—	2
Eriophorum vaginatum	bsx	1	3	—	—
Menyanthes trifoliata	bsx	—	—	1	—
3.					
Erica tetralix	so_1	5	10_8	1	9_6
Calluna vulgaris	sbo_3	8_5	6_1	—	9_8
Scirpus caespitosus	sbo_3	—	—	—	1
Carex arenaria	so_2	—	—	—	5
— pilulifera	sbo_3	—	—	—	+
Sieglingia decumbens	sbo_3	—	—	—	1
Juncus bulbosus	sbo_2	—	—	+	—

Analysis No. / Locality No.	Distributional type	1 / 21	2 / 36	3 / 36	4 / 61
4.					
Salix repens	sx(L)p	—	—	—	6_3
Juniperus communis	sbx	3	—	—	—
Carex stolonifera	sbx	1	—	—	—
— echinata	sbx	—	—	1	—
Eriophorum angustifolium	sbax	—	4	4	—
Deschampsia flexuosa	sbax	1	—	—	—
Agrostis canina	sbxp	—	—	9_2	—
Nardus stricta	sbx	2	—	—	—
Luzule multiflora	sbxp	1	—	—	—
Potentilla erecta	sbxp	1	1	—	4
Drosera rotundifolia	sbx	—	+	10_8	—
5.					
Hylocomium schreberi	—	5	2	—	5
— splendens	—	—	—	—	2
Hypnum cupressiforme	—	5	4	—	10_{10}
Dicranum rugosum	—	—	—	—	1
Sphagnum angustifolium	—	—	} 8_6	—	—
— magellanicum	—	—	}	10_{10}	—
Cladonia impexa	—	—	—	—	1

Species groups: 1: Oceanic and widely distributed species frequent in the J-type. 2: northern species. 3: oceanic-suboceanic species. 4: widely distributed species. 5: bryophytes and lichens. — pH 4.4 in No. 2.

heath of the Nørholm Hede (Mølholm Hansen, 1932, Table 7 a, Nos. 9—10; Töndersjöhed Malmström 1937), the closely related vegetation near Flyndersø (Table 20, No. 1) and the *Narthecium* heath of the Randbøl Hede (B. 1941 a, Table 65, No. 1) to the *Myrica-Narthecium* or *Narthecium-Sphagnum* bogs (Table 20) which are most beautifully developed on the slopes of Gern Bakker (Loc. 56) or other places in the hilly districts of Jutland (Fig. 23) or western Sweden.

Myrica-Narthecium vegetations of alluvial ground.

Raunkiær (1934, pp. 320—321) mentions a *Myrica* scrub from Loc. 1: "a densely closed formation about 40—70 cm high growing on the boundary between the meadow and the heath". The ground was covered with dead leaves of *Myrica* and the number of phanerogams was considerable. An almost similar vegetation clothes large areas between Nykøbing and Rørvig (Loc. 61, Table 20, No. 4) and the Læsø Nordmark in the neighbourhood of the old village of Hals. On the Isle of Læsø, are found transitions from this *Myrica* scrub (frequently *Myrica-Molinia* soc.) to the meadowlike, dense *Narthecietum* mentioned above. This type and the *Erica-Narthecium* heath found in Thy (Loc. 14, Table 21) occur on wetter soils than the *Myrica* scrubs. Outside

Denmark, *Molinia-Myrica* vegetations on alluvial ground have been described from Dutch dune heaths (Bijhouwer 1926, pp. 26 and 61).

The vegetations of the *Myrica* type differ from the *Erica-Empetrum-Vaccinium uliginosum* heaths with respect to the ecology (more fertile soils) and the content of distributional types. In the following, the area and ecology of the guiding species will be considered in greater detail.

Fig. 23. *Narthecium* bog on gently sloping ground clothing the bottom of a valley in the heaths of Vrads (Loc. 39). At the boundary between bog and heath *Juncus conglomeratus* and *Nardus*. *Juniperus* to the right. B. photo 1941.

Myrica gale has a northern oceanic range (map in Czeczott). The Pacific plant probably belongs to a special variety (*tomentosa* DC; cf. Hultén 1927—1930). In most ombrogene, raised bogs, *Myrica* belongs to the lagg or drainage channels and, thus, the occurrence in the Store Vildmose and other ombrogene bogs may be a rather local phenomenon[1]. On the other hand, *Myrica* is abundant in *Sphagnum* bogs with flowing soil water (B. 1941a, pp. 199, 203—204, and above). The optimal development is reached in the *Myrica* scrubs which, according to Jonas (1935, p. 117), are related to the *Alnetum glutinosa* (cf. also Tüxen's *Salix aurita-Frangula* ass. and the *Myrica* scrubs described from the beaches of the lake Tåkern in Sweden (Naumann)); in such communities *Myrica* approaches its southern limit in the "Rheinstromgebiet" (Schwickerath 1936). The occurrence of *Myrica* in heaths or bogs appears from the profile p. 77.

Narthecium ossifragum has a marked oceanic range (for further details, cf. Jessen 1935,

[1] Cf. Jonas (1935, p. 140): "Nach meinen Beobachtungen besitzen nur Hochmoore mit entrophen Anfangsstadien als Relikt an Kölken und in Laggen *Myrica gale* Gebüsch. Unseren typischen, von Anfang an oligotrophen Hochmooren fehlt *Myrica gale* ganz".

p. 79). MATTHEWS classifies it among the northern oceanic elements and this may be correct, since the abundance of the species is greatest in the northern part of its area. It reaches the Faroes and northern Norway (69°42′) where *Erica tetralix* is missing. In western Europe it occurs in the wet heaths of North France (LEMÉE, Tables 50—51) where *Myrica* is absent. The *Narthecium-Sphagnum* bogs (or *Narthecium* bogs with reduced ground layer) may be found within the total range of *Narthecium* (SCHWICKERATH 1940), while wet heaths with *Narthecium* seem to be more rare farther south. Generally, the bogs belong to the soligene (ombrosoligene) type. Thus, *Narthecium* reminds us ecologically of *Myrica*, but it is probably more oligotrophic and is able to grow in moister habitats than *Myrica*. The *Narthecium* meadows and *Erica-Narthecium* heaths of alluvial soils are perhaps limited to Jutland and Læsø.

In connection with the two guiding species, we shall here more closely describe *Molinia coerulea* and *Gentiana pneumonanthe*. They are not guiding species, but they show optimal development within the *Myrica* type.

Molinia coerulea is widely ranging and very polymorphous (cf. H. PAUL 1937). The greatest abundance of the races occurring in the heath is obtained in wet places where water oozes out (B. 1941a, Table 53, No. 9, Table 58, Nos. 0—1, Table 60, No. 2, Table 63, No. 6, Table 67, No. 8; profiles pp. 63, 166, 167, 171, 177, 195), on wet ground frequently covered with water during the winter, and on moderately acid soils (B. 1941a, pp. 193—197), and, finally, on old fields from the 17th century (B. 1941a, pp. 125—120, 225—226). In the present paper, the occurrence of *Molinia* is shown especially on p. 77. The picture of the ecology of *Molinia* corresponds to that obtained by the studies of JEFFERIES: *Molinia* is neither a marked oxylophyte, nor is it associated with pronounced oligotrophic habitats; it may, if anything, be classified among the mesotrophic plants. It would be an interesting task by means of cultivation experiments to compare the *Molinia* biotypes occurring in the "basikline" and "azidokline Subassoziationsgruppe" of the *Molinietum coeruleae* described by KOCH and TÜXEN. According to H. PAUL, the two subspecies (*coerulea* and *litoralis*) are well separated when growing side by side in a garden.

Gentiana pneumonanthe has a problematic range (HÅRD 1935, p. 246). In the Scano-Danish area it has a typical oceanic distribution; south of Scandinavia it is widely distributed and it occurs frequently even in Russia (KORSCHINSKY 1898, p. 291), however, it is lacking in Ireland and Scotland. The area reminds us somewhat of those of *Fagus silvatica*, *Teesdalia nudicaulis*, and *Corynephorus canescens* which, south of Denmark-Sweden, extend to Russia but in the British Islands show varying degrees of restriction and are denoted as "continental" by MATTHEWS (1937). Thus, *Gentiana pneumonanthe* may be a central-European plant, with suboceanic tendencies to the north[1]. In the heath, it follows *Myrica*, *Narthecium*, and *Molinia* (B. 1941a, pp. 169—171, 192—197); cf. also pp. 86 and 95 in the present paper. It is used as a character species in the acidic group of the "*Molinietum coeruleae*", however, it is denoted only as "Begleiter" in the *Ericetum* (TÜXEN). The oceanic *Polygala serpyllacea*, moreover, perhaps finds its greatest development in the *Myrica-Molinia* heaths (B. 1941a).

Nardus stricta is frequently associated with heaths on gently sloping ground with flowing soil water; it may sometimes dominate the boundary between the heath and the entrophic meadows along the rivulets; more rarely, it dominates moderately acidic meadows near spots where the water oozes out of the soil (B. 1941a, pp. 180—181, and the profile p. 23).

[1] ALLORGE (1941, p. 321) considers it (and the var. *depressa*) a subatlantic species.

K. Wet heaths characterized by a mixture of oceanic and northern species (*Empetrum-Vaccinium uliginosum*-group of *Ulicio-Ericion tetralicis*).

In Denmark, most areas of wet and sandy acid soils with stagnant soil water are occupied by *Erica* heath sociations. In western Sweden, *Erica Sphagnum* sociations are abundant in bogs and wet places in the heaths (Osvald, Malmström). Typical *Erica* heaths, on the other hand, were only met with in localities very close to the sea (Loc. 72, 73, 80; Fig. 24) and they are not mentioned by Malmström from the Tönnersjö area. They may be rare at some distance from the coast. Osvald states

Fig. 24. Exposed *Erica-Empetrum* heath at Steninge, Halland, Sweden. (Cf. Table 21, Nos. 11—12). B. photo 1934.

(p. 102) that "auf Moräne oder Sand tritt die flechtenreiche *Erica*-Heide nicht auf, dagegen findet man auf solchen Standorten bisweilen eine nackte *Erica*-Heide". After having studied the Jutland heaths it was very astonishing to observe that *Erica tetralix* was lacking in some places with wet heaths (Loc. 76, Torekov). The same absence of *Erica* was observed in south-easterly Danish heaths (Loc. 66, 69, 70); cf. later, p. 103.

The area of the typical *Erica* heath almost completely dominated by *Erica tetralix* covers Denmark, touches western Sweden and South Norway, and is furthermore found in N.W. Germany and N. France. The areas of the *Erica* bogs are much larger in Sweden, extending to the *Erica-Ledum palustre* boundary described by Granlund (1925). Thus, *Erica tetralix* is able to dominate vegetations within large parts of its area and, consequently, the term "*Erica* heath" (bog) like the "*Calluna* heath" (bog) can only be used to designate a very large group of wet heaths (or bogs) which must be further subdivided. By this division, a northern and a southern group may be separated, but within the Scano-Danish area there hardly exists any western or eastern group, as no important eastern limits of wet heath species run west of the *Erica-Ledum* boundary.

Table 21. Various wet heaths of the *Ulicio-Ericion tetralicis* (Main types J, K, L, M). Method: D.

Analysis No. / Locality No.	Distributional type	1 14	2 14	3 14	4 14	5 2	6 2	7 2	8 2	9 12	10 11	11 12	12 13	13 14	14 2	15 2
1.																
Myrica gale	bso_2(Γ)	—	—	1	1	—	—	—	—	—	—	—	—	2	—	—
Narthecium ossifragum	sbo_1	4	3	4	4	—	—	—	—	—	—	—	—	—	—	—
Molinia coerulea	sbxp	1+	1	2+	2	—	—	—	—	—	1	2	—	—	—	—
Gentiana pneumonanthe	so_3(└)	1	1	+	—	—	—	—	—	—	—	—	—	—	—	—
2.																
Vaccinium uliginosum	bsΓp	—	—	—	1	—	—	2	3	3	5	4	—	—	—	—
— vitis idaea	bs(┐)	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
Empetrum nigrum	bsΓ	—	—	—	—	—	1	—	2	3	—	—	2	—	—	—
Arctostaphylos uva ursi	bsc_3(┐)	—	—	—	—	—	—	—	—	—	—	—	3	1	—	—
Oxycoccus quadripetalus	bsxp	—	—	—	—	+	1	1	1	1+	—	—	—	—	—	—
Habenaria albida	bo_2Mo	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
Juncus balticus	bsΓ(o_3)	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—
Antennaria dioeca	bsx	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
Melampyrum vulgatum	bsx	—	—	—	+	—	—	—	—	—	—	—	—	—	—	—
Pirola rotundifolia	bc_2	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—
Trientalis europaea	b(al)sx	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—
Viola palustris	bso_2	—	—	1	—	+	+	—	—	—	—	—	—	—	—	—
3.																
Erica tetralix	so_1	4	3+	3	3	3	4	4	3	2	2	2	2	2	5	5
Calluna vulgaris	sbo_3	1	1	—	—	—	—	—	—	—	—	—	2	5	1	—
Genista anglica	sdo_1	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—
Carex arenaria	so_2	—	—	—	—	—	—	—	—	1	—	—	—	—	1	2
Scirpus caespitosus	sbo_3	1	2	—	1	—	—	—	—	—	—	—	—	—	—	—
Juncus squarrosus	sbo_2	—	1	—	—	—	1	—	—	—	—	—	—	—	—	—
— bulbosus	sbo_3	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—
— atricapillus	sdo_1	—	—	—	—	2	1	—	2	—	—	—	—	—	—	—
Sieglingia decumbens	sbo_3	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Pedicularis silvatica	so_3	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—
Hydrocotyle vulgaris	so_3	—	—	—	—	—	—	—	—	+	—	—	—	—	—	—
Drosera intermedia	so_3	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—
4.																
Salix repens	sx(└)p	—	1	1	—	3	2	3	2	1	—	—	—	—	3	3
— aurita	sbx	—	—	—	—	1	—	—	1	—	—	—	—	—	—	—
Carex stolonifera	sbx	—	—	—	—	2	3	2	3	1	—	—	—	—	—	1
— panicea	sbx	—	1	—	—	1	1	1	1	+	—	—	—	—	—	1
— echinata	sbx	—	—	—	—	2	1	1	2	—	—	—	—	—	—	—
Eriophorum angustifolium	sbax	—	—	1	—	1	—	1	—	—	—	—	—	—	—	—
Nardus stricta	sbx	—	—	1	—	1	—	—	—	1	1	1	—	—	—	—
Deschampsia flexuosa	sbax	—	—	—	—	—	—	—	—	—	+	—	1	—	—	—
Luzula multiflora	sbxp	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Orchis maculata	sbxp	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
Hieracium pilosella	sbxp	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
Succisa pratensis	sbx	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—
Lotus corniculatus	sbx	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—
Potentilla erecta	sbxp	1	1	2	1	+	1	—	1	—	—	+	—	—	—	—
Comarum palustre	sbx	—	—	—	—	+	—	—	—	—	—	—	—	—	—	—
Drosera rotundifolia	sbx	1	1	—	—	—	—	—	1	—	—	—	—	—	—	—
— anglica	sbx	—	—	—	—	1	1	1	2	—	—	—	—	—	—	—

Table 21 (continued).

Analysis No. / Locality No.	Distributional type	1 / 14	2 / 14	3 / 14	4 / 14	5 / 2	6 / 2	7 / 2	8 / 2	9 / 12	10 / 11	11 / 12	12 / 13	13 / 14	14 / 2	15 / 2
5.																
Hypnum cupressiforme	—	1	1	1	2	—	—	—	—	**3**	1	1	1	**4**	**5**	**5**
Hylocomium schreberi	—	—	—	—	—	—	—	—	—	2	**3**	2	—	+	—	—
Dicranum scoparium	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—
— spurium	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—
Pohlia nutans	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	1
Gymnocybe palustris	—	—	—	—	—	—	1	—	2	—	—	—	—	—	—	1
Acrocladium cuspidatum	—	—	—	—	—	—	1	—	1	—	—	—	—	-	—	—
Mnium hornum and punctatum	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—
Hypnum imponens	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—
Sphagnum subsecundum	—	—	—	—	—	2	1	1	—	—	—	—	—	—	—	—
Riccardia multifida	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—
Cephalozia bicuspidata	—	—	—	—	—	—	—	2	**3**	—	—	—	—	—	—	—
6.																
Cladonia silvatica	—	1+	—	1	—	—	—	—	—	—	**3**	**3**	—	—	1	—
— impexa	—											1	—	—	1	1
— chlorophaea	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—
Peltigera canina	—	—	—	—	—	—	—	—	—	+	—	—	—	—	**3**+	**3**+

Vegetation: Main types J (Nos. 1—4), K (Nos. 5—11), L (Nos. 12—13), M (Nos. 14—15). — Nos. 1—11, 14—15: on wet alluvial sandy soils, Nos. 5—8: in rather moist spots surrounded by typical wet dune heath. Nos. 12—13: rather dry and not typical, see text.

Species groups: 1: Species of main type J. 2: northern species. 3: oceanic-suboceanic rather southern species. 4: indifferent widely ranging, mostly rather southern species. 5: bryophytes. 6: lichens.

The northern group of sociations corresponds to the Scano-Danish dry heath series. For the separation, *Empetrum, Vaccinium uliginosum, Vaccinium vitis idaea, Myrica,* and *Juncus balticus* are employed[1].

In Denmark, *Erica* heaths occur in dune areas or on raised sea floor as well as in diluvial sandy soils. In the alluvial areas, the *Erica* heath may frequently be very mixed, containing particularly a good deal of *Calluna, Salix repens, Vaccinium uliginosum, Empetrum* and, sometimes, *Myrica* and *Genista anglica.* The inland heaths, on the other hand, are more uniform, *Scirpus caespolosus, Calluna,* and *Empetrum* being the most frequent co-dominants.

Tables 21-22 contains a number of analyses of different coast heaths where *Erica* is dominant. Other analyses of Scano-Danish *Erica* heaths have been published chiefly by Raunkiær (1934 a, pp. 267, 275 and 325), Mølholm Hansen (1932), and the writer (1941 a). In Table 23, the constancy and average frequency (within $^1/_{10}$ sq. m.-planes) of 17 important species are given, the data being taken from the material of Table 22 and the works just mentioned. Furthermore, the constancy and the covering

[1] In Steffen's paper (1935, p. 383), *Erica tetralix* is classified as an "Atlantic-subarctic" species, and it is stated that such plants are most frequent in the northern part of the Atlantic area. Considering, however, the abundance of *Erica* in the wet heaths of Germany, Holland and N. France, this can hardly be quite correct, nor does the term "subarctic" fit the range of the species. Hence, we cannot use *Erica tetralix* for the separation of a northern group of sociations and the same is the case with *Scirpus caespitosus* (with the exception of the northern ssp. *austriacus* (cf. below)).

Table 22. Heaths of the *Empetrum-Vaccinium*-group of *Ulicio-Ericion tetralicis* and related heaths. Method: S. (R. in Nos. 8—9, 12).

Analysis No. / Locality No.	Distributional type	1 / 2	2 / 2	3 / 7	4 / 12	5 / 12	6 / 14	7 / 8	8 / 61	9 / 61	10 / 61	11 / 61	12 / 61	13 / 72	14 / 72	15 / 80	Constancy pCt. Nos. 1—5	Constancy pCt. Nos. 8—12
1.																		
Erica tetralix	so_1	10_7	10_5	10_4	6_2	10_7	7_4	8_4	10	10	10_9	10_8	10	10_{10}	10_8	10_{10}	**100**	**100**
Calluna vulgaris	sbo_3	10_9	10_8	+	+	+	10_9	10_{10}	2	8	10_7	5	10	+	9_4	3	**100**	**100**
Genista anglica	sdo_1	—	—	—	—	+	+	—	—	—	—	—	—	—	—	—	20	—
Lycopodium inundatum	so_3	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	20	—
Scirpus caespitosus	sbo_3	+	+	+	—	—	2	—	—	—	6	+	9	—	—	10_2	60	60
Carex arenaria	so_2	3	—	—	6_1	—	1	—	—	—	—	+	—	—	1	—	40	20
— pilulifera	sbo_3	—	—	—	+	—	+	+	—	—	—	—	—	—	—	—	20	—
— pulicaris	sbo_3	—	—	—	—	—	—	—	—	—	—	—	—	9_4	—	—	—	—
Sieglingia decumbens	sbo_3	—	—	+	—	—	—	+	2	+	—	1	—	3	1	—	20	60
Juncus squarrosus	sbo_2	—	—	+	—	3	+	—	—	—	—	—	1	—	—	—	40	20
Pedicularis silvatica	so_3	—	1	—	—	—	—	1	—	—	—	—	—	—	—	—	20	—
Gentiana pneumonanthe	so_3(L)	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—	—	—
2.																		
Myrica gale	bso_2(Γ)	—	—	+	—	—	8_4	6_4	—	—	+	—	4	—	—	—	20	40
Cornus suecica	bso_2	—	—	—	—	10_6	—	—	—	—	—	—	—	—	—	—	20	—
Blechnum spicant	bso_2hy	—	—	—	—	+	—	—	—	—	—	—	—	—	—	—	20	—
Juncus balticus	bsΓ(o_3)	7_2	6	+	—	—	—	—	—	—	—	—	—	—	—	—	60	—
3.																		
Empetrum nigrum	bsΓ	7_2	10_3	10_9	10_{10}	10_6	5	—	—	—	—	10_9	+	4	10_8	—	**100**	40
Vaccinium uliginosum	bsΓp	—	3	10_6	10_8	10_6	3	—	10	1	+	1	—	—	—	—	**80**	**80**
— vitis idaea	bs(¬)	—	—	10_4	—	—	—	—	—	—	—	—	—	—	—	—	20	—
Oxycoccus quadripetalus	bsxp	5	6	—	—	6_5	—	—	—	—	—	—	—	—	—	—	60	—
4.																		
Salix repens	sx(L)p	3	2	4	4	3	2	9_7	9	8	4	6	6	8_3	6	—	**100**	**100**
Lycopodium clavatum	sbx	1	4	—	—	—	—	—	—	—	—	—	—	—	—	—	40	—
Carex stolonifera	sbx	+	5	—	4	10_2	—	—	9	9	8_3	2	3	—	—	—	**80**	**100**
— panicea	sbx	1	6	+	—	—	+	—	3	6	—	—	1	10_9	9_4	10_3	60	60
— echinata	sbx	—	—	—	—	+	—	—	—	—	—	—	—	—	+	—	20	—
Eriophorum angustifolium	sbax	—	—	—	—	9_3	—	—	3	—	—	—	—	1	10_4	—	20	20
Molinia coerulea	sbxp	—	—	+	—	—	—	4	—	—	8_3	3	5	—	—	—	20	60
Agrostis canina	sbxp	—	—	—	—	—	—	—	7	4	—	—	—	—	—	—	—	40
Nardus stricta	sbx	—	—	+	1	2	—	—	7	3	—	—	—	—	—	—	60	40
Luzula multiflora	sbxp	3	—	1	—	—	+	+	—	—	—	—	—	—	+	—	40	—
Platanthera bifolia	sbx	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	20	—
Orchis maculata	sbxp	—	—	—	—	+	—	—	—	—	—	—	—	—	—	—	20	—
Succisa pratensis	sbx	—	—	—	—	—	—	1	+	—	—	—	—	—	—	—	—	20
Lotus corniculatus	sbx	—	—	1	—	—	+	—	—	—	—	—	—	—	—	—	20	—
Potentilla erecta	sbxp	—	1	—	+	9_3	—	3	8	10	+	—	—	6	10_5	—	60	60
Drosera rotundifolia	sbx	2	4	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—
5.																		
Hypnum cupressiforme	—	2	—	9_6	7_1	6_3	8_4	10_7	1	2	10_8	8_3	10	—	3	1	**80**	**100**
— uncinatum	—	9_5	2	—	—	—	—	—	10	9	—	—	—	—	—	—	40	40
Hylocomium schreberi	—	1	2	5	2	2	1	7_3	1	5	10_7	—	4	—	2	—	**100**	**80**
— triquetrum	—	—	—	—	—	1	—	—	—	—	1	—	—	—	—	—	20	20

Table 22 (continued).

Analysis No.	Distri-butional type	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Constancy pCt. Nos. 1—5	Constancy pCt. Nos. 8—12
Locality No.		2	2	7	12	12	14	8	61	61	61	61	61	72	72	80		
Dicranum scoparium	—	1	+	—	—	1	—	3	—	—	1	4	4	—	—	—	60	60
— rugosum	—	—	—	—	—	—	+	1	—	—	—	—	—	—	—	—	—	—
Pohlia nutans	—	5	5	—	—	—	—	—	—	—	—	—	—	—	—	—	40	—
Gymnocybe palustris	—	1	2	—	—	—	+	—	1	5	—	—	—	—	—	—	40	40
Mnium hornum	—	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	40	—
Leucobryum glaucum	—	—	—	—	—	—	—	—	—	—	—	—	3	—	—	—	—	20
Polytrichum commune	—	—	9_9	—	—	—	—	—	—	—	—	—	—	—	—	—	20	—
Sphagnum magellanicum	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	20
— acutifolium	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	20	—
Cephaloziella divaricata	—	1 }	10_5	—	—	—	—	—	—	—	—	—	—	—	—	—	{ 40	—
Cephalozia bicuspidata	—	6 }		—	—	—	—	—	—	—	—	—	—	—	—	—	40	—
Jungermannia inflata	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	20	—
— excectiformis	—	+	1	—	—	—	+	—	—	—	—	—	—	—	—	—	40	—
Frullania tamarisci	—	—	—	—	—	—	—	—	—	—	—	5	—	—	—	—	—	20
Blepharozia ciliaris	—	—	—	—	—	—	1	5	—	—	—	—	—	—	—	—	—	—
6.																		
Cladonia impexa and silvatica	—	6	1	10_{10}	—	9_7	8_3	4	—	1	3	10_8	8	—	—	10_{10}	**80**	**80**
— rangiferina	—	—	—	—	—	—	+	—	—	—	—	6	—	—	—	5	—	20
— uncialis	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	10_2	—	—
— destricta	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—
— chlorophaea	—	—	1	—	—	—	+	2	—	—	—	3	—	—	—	6	20	20
— coccifera	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	20	—
— floerkeana	—	—	1	—	—	—	+	1	—	—	—	—	—	—	—	—	20	—
— gracilis	—	—	—	1	—	—	+	—	—	—	—	—	—	—	—	—	20	—
— strepsilis	—	—	—	—	—	—	+	—	—	—	—	—	—	—	—	—	—	—
Cetraria islandica	—	—	—	—	—	—	+	—	—	—	—	—	—	—	—	7	—	—
— tenuissima	—	1	—	—	—	—	+	1	—	—	—	—	—	—	—	10_7	20	—
— glauca	—	5	3	—	—	—	+	—	—	—	—	—	—	—	—	—	40	—
Parmelia physodes	—	10_8	10_5	4	+	—	+	+	+	—	—	—	—	—	—	—	**80**	20
Usnea hirta coll.	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	20	—
Peltigera canina	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	20	—

Vegetation and localities: No. 1: medium moist. No. 2: moist soil near the lakes of Raabjerg Mile. Nos. 3—4: rather dry soils near the sea coast dunes. No. 5: a large patch covered with *Cornus suecica* in the vicinity of Lild; pH 4.2 Nos. 6—7: medium moist soils, vegetation with much *Myrica*; pH 3.7 in No. 6. Nos. 8—12: near Rørvig. Nos. 9, 10, 12: medium moist. No. 8 moist and No. 11 rather dry soils. Nos. 13—14: rather moist heaths between rocks near the sea; ground layer absent or very poor. No. 14: much exposed to wind. No. 15: rather dry (the analysis has previously been published in B. 1935).

Species groups: 1: oceanic-suboceanic species. 2: northern oceanic species. 3: northern species. 4: widely ranging indifferent species with rather southerly distribution. 5: bryophytes. 6: lichens.

Species not mentioned in the table: Group 4: *Populus tremula* 2 in No. 11, *Betula pubescens* + in No. 2, *Festuca ovina* 4 in No. 7, *F. rubra* + in No. 4, *Desch. flexuosa* + in No. 13, *Agrostis stolonifera* 3 in No. 13, + in No. 14. Group 5: *Hyloc. splendens* 1 in Nos. 7 and 10, *H. squarrosum* 1 in No. 9, *Pellia epiphylla* 1 in No. 1, *Nardia scalaris* + in No. 6. — Fungi: *Lachnea scutellata, Humaria granulata* 1 in No. 2.

of the same species in the *Ericeta* of Germany (after TÜXEN, SCHWICKERATH, and LIBBERT) and France (after LEMÉE) are shown. Nos. I—III and VII come from alluvial soils, while the others are from non-alluvial sandy soils. The abundance of *Vaccinium uliginosum, Salix repens, Potentilla erecta, Siengligia, Nardus,* and *Lotus* in the alluvial heaths is striking; furthermore, *Scirpus caespitosus* perhaps attains the highest values in the non-alluvial heaths. Finally, the occurrence of *Empetrum,*

Table 23. Constancy, Average frequency or covering values of 20 important wet heath species in a number of *Erica tetralix*-heaths.

Author and Locality (Denmark)........	I Raunkiær 1934[1] Loc. 1		II B. Tab. 22 Nos. 1–5		III B Tab. 22 Nos. 8-12		IV Raunkiær 1934[2] Loc. 42		V Mølholm Hansen Loc. 47		VI B. 1941 a Loc. 45		VII Libbert 1939		VIII Schwickerath 1933		IX Tüxen 1937 p. 110 (1 a)		X Tüxen 1937 p. 112 (1 c)		XI Lemée 1937 Tab. 52	
No. of analyses	7		5		5		4		10		10[3]		9		4		20		18		8	
C = Constancy, F = Frequency, D = Covering	C %	F %	C %	F %	C %	F %	C %	F %	C %	F %	C %	F %	C %	D	C %	D	C %	D	C %	D	C %	D
1.																						
Empetrum nigrum...	86	32	100	94	40	20	75	14	100	35	70	21	67	+–2	—		—		—		—	
Vaccinium uliginosum	71	9	80	66	80	24	25	2	—		—		—		—		—		—		—	
— vitis idaea	—		20	20	—		—		—		30	23	—		—		—		—		—	
Myrica gale.........	—		20	+	40	8	—		—		—		—		—		—		—		—	
Juncus balticus	—		30	26	—		—		—		—		67	+–1	—		—		—		—	
2.																						
Erica tetralix	100	99	100	92	100	100	100	90	100	89	100	90	100	2–4	100	2–4	100	1–5	100	1–5	100	2–4
Calluna vulgaris.....	100	100	100	40	100	70	100	88	100	42	100	40	100	1–2	75	+–2	80	+–4	94	1–5	88	1–4
Scirpus caespitosus ..	—		60	+	60	30	100	30	100	32	80	42	11	4	75	+–3	70	+–4	72	+–2	—	
Juncus squarrosus...	—		40	6	20	2	25	1	20	1	60	4	88	+–1	50	+–2	100	+–2	83	+–2	—	
Sieglingia decumbens	57	15	20	+	60	6	—		—		—		—		—		—		—		25	1–2
3.																						
Genista anglica	—		20	+	—		—		—		—		—		100	+–1	—		—		63	+–3
Ulex nanus.........	—		—		—		—		—		—		—		—		—		—		38	+–2
Juncus silvaticus....	—		—		—		—		—		—		—		75	+–1	—		—		38	1–3
4.																						
Salix repens	100	90	100	32	100	66	25	2	—		20	6	100	+–2	100	+–1	30	+–2	—		13	+
Potentilla erecta	71	21	60	20	60	36	—		—		10	1	88	+–1	75	+–2	30	+	—		100	+–2
Molinia coerulea.....	—		20	+	60	31	25	6	50	8	70	23	67	+–2	75	+–3	95	+–3	77	+–2	100	1–4
Nardus stricta	57	23	60	6	40	20	—		—		—		44	+–1	75	+–2	—		—		13	+
Carex panicea.......	86	16	60	14	60	19	100	26	100	49	80	21	67	+–1	(+)		65	+–3	28	+–2	—	
— stolonifera	100	33	80	38	100	61	50	10	90	30	70	40	88	+–1	—		—		—		—	
Lotus corniculatus...	86	65	20	2	—		—		—		—		—		—		—		—		—	

[1] Tab. 7, p. 325. [2] Tab. 34, Nos. 4—7, p. 267. Tab. 52, No. 6, 53 No. 2, 56, 58 No. 8, 63, No. 1, 64 No. 1 and 67 No. 11.

Species groups: 1: northern and northern-oceanic species. 2: oceanic-suboceanic species. 3: southern oceanic-suboceanic species. 4: widely distributed species.

Vaccinium uliginosum, Vaccinium vitis idaea, Juncus balticus, and *Myrica* separates the K-heaths from the more southern M-heaths.

In the alluvial heaths, the number of species is higher than in the diluvial heaths. Undoubtedly, this is to a very large extent due to the greater leaching of the soil in the old inland heaths. *Salix repens, Nardus,* and *Potentilla erecta* are certainly indicators of more fertile soils, the latter species being particularly frequent also on the vigorous *Molinieta* on the Isle of Læsø, the *Myrica-Molinia* heaths of Randbøl Hede, the wet heaths of Ulvshale (B. 1942), and the luxuriant heaths of the Faroes. In the French heath (Table 23, No. XI), it is fairly abundant, but here too the soil is probably relatively fertile.

Thus, within the K-heath, we are able to separate two different ecological types which, furthermore, may be of regional importance. In fact, some of the species of the alluvial coast heaths may be absent or rare inland, partly on account of climatic factors; the same applies to some inland species which are lacking or rare in the coast heaths. Unfortunately, however, it is impossible to detect the cause of this distribution with sufficient certainty; consequently, our two northern *Erica* heath types are neither well defined nor well separated, a number of species being confined to one of them on account of edaphic as well as climatic factors. The species found mainly in the coast heaths are *Vaccinium uliginosum* and *Juncus balticus,* those characteristic of the inland heaths are *Vaccinium vitis idaea* and *Andromeda polifolia.*

Transition types between dry and wet heaths are of frequent occurrence and, sometimes, the boundary is difficult to draw. The writer has endeavoured to collect all heaths with frequent occurrence of wet heath species. A typical transition heath is described in Tab. 24. It is related to the *Calluneto-Genistetum* with *Orchis maculata*

Table 24. Rather moist *Calluna-Empetrum* heath on the slopes at Blegsø (Loc. 13). Gently sloping towards N.W. Sand overlying chalk. Method: R.

1.	
Empetrum nigrum	8
Vaccinium uliginosum	2
Juncus balticus	5
2.	
Erica tetralix	5
Calluna vulgaris	10
Genista anglica	2
Juncus squarrosus	1
Carex arenaria	1
Polygala serpyllacea	+
3.	
Salix repens	6
Potentilla erecta	4
Eriophorum angustifolium	2
Carex panicea	2
Carex stolonifera	5
Molinia coerulea	2
Nardus stricta	1
Deschampsia flexuosa	+
Lotus corniculatus	+
Plantago maritima	1
Pinguicula vulgaris	1
Orchis maculata	+
4.	
Hylocomium schreberi	10
— splendens	3
— triquetrum	3
— squarrosum	1
Hypnum cupressiforme	8
5.	
Cladonia impexa	3
Peltigera canina	2

Species groups: 1: northern-northern-oceanic species. 2: oceanic-suboceanic species. 3: widely distributed species. 4: bryophytes. 5: lichens.

(DIEMONT). Other transitions to dry heaths may be found in B. 1941 a (Table 52, No. 7; Table 53, No. 1; Table 55, No. 4; Skærsø No. 1, p. 171). They come very near to the *Calluneto-Genistetum molinietosum* (TÜXEN). In more fertile localities (Tolne Bakker, Læsø at Østerby, Ulvshale) the transition heaths show an abundance of *Platanthera bifolia, Succisa pratensis, Potentilla erecta,* and others.

Description of guiding species in the K-heaths.

Vaccinium uliginosum is very polymorphous (H. E. PETERSEN) and contains two subspecies with different chromosome numbers (HAGERUP). In Denmark, presumably only the tetraploid var. *genuinum* Herd. occurs, while the arctic-alpine var. *microphyllum* Lge. (or var. *alpinum* Busch) seems to be lacking. In the locality Kaas, extremely small-leaved plants were observed (average leaf length 10.2 mm., leaf breadth 5.0 mm.), but specimens of this kind are perhaps only modifications of the large-leaved type. Both types are circumpolar and var. *genuinum* is subarctic oreophilous.

In Denmark, the area of *Vaccinium uliginosum* (B. 1937a, Fig. 10) is interesting. The plant is very rare in the southern islands, but frequent in the most oceanic regions, particularly along the west coast of Jutland. In the hilly heath areas of central and northern Jutland, it rather frequently dominates small patches on northern slopes (see A-main type, p. 22). The greatest abundance is attained in wet dune heaths and bogs. Following a profile through southern Jutland from west to east, the decrease in this species is striking. There is no doubt that the plant is rare or sporadic in the inland heaths, being absent in the inland heaths of N.-Germany. The dune heath type with much *Vaccinium uliginosum* goes as far south as to the Isle of Sylt in N.-Germany (TÜXEN 1937, p. 113) and reaches northernmost Sealand (Table 22, No. 6).

The sporadic occurrence in level heaths of central Jutland may be explained by the warm and dry climat, and this would agree with the fact that *Vaccinium uliginosum* in the bogs of North Sealand shuns open ground, growing particularly in somewhat shady localities under birch trees (OLSEN, H. E. PETERSEN). The occurrence near the south-eastern parts of the birch trees as described by HELMS and JØRGENSEN is perhaps a local phenomenon.

In many localities, it is quite obvious that the *Vaccinium uliginosum* grows near the margin of the bog, where edaphic conditions are better than in the central parts. The dune heaths are also more fertile than the inland heath and, hence, the distribution in Denmark would seem to be mainly governed by soil factors. This is, however, improbable, since to the north, the species is able to grow in the oligotrophic bogs ranging within NORDHAGEN's *"Oxycocco-Empetrion hermaphroditi"*; furthermore, it ought to grow on a larger scale in the more fertile wet heaths of the Randbøl area; this, however, is not the case. As *Empetrum*, *Vaccinium uliginosum* may be a northern species which to the south prefers oceanic regions or microclimatic damp and cool habitats.

Juncus balticus. According to HULTÉN, this plant is American, transgressing into western Europe and eastern Asia. In Europe it is boreal and suboceanic (MATTHEWS, WIINSTEDT). In Iceland it is widely distributed and not restricted to the sea coast. In Scandinavia and the Baltic states, it is most frequent along the coast and is rare inland. In Denmark, south of 56°40′ N. lat. it is absent from the inland (WIINSTEDT 1937, map Fig. 2).

In the heath, *Juncus balticus* occurs in transition types between wet and dry heaths, where the number of species is high and the soil is relatively rich (Table 24). In the typical wet dune heath, it is frequently abundant, and the same applies to the meadowlike depressions of the heath. The wet heath with *Juncus balticus* reaches the southern shores of the Baltic (LIBBERT 1939, and Table 23, No. 7).

Concerning the other northern species, cf. pp. 41, 49, and later p. 100. On the distribution of *Viola palustris* (Table 21), see B. 1938.

L. Bogs (and wet heaths) characterized by a mixture of oceanic and northern-subcontinental species (*Oxycoccus-Eriophorum vaginatum*-group of *Ulicio-Ericion Tetralicis*).

Heaths belonging to this main type seem to be very rare. Only two examples were found (Table 21, Nos. 12—13), viz. small patches which are rather dry and show affinities to the C-main type.

On the other hand, raised bogs (more particularly dwarf shrub *Sphagnum* communities) characterized by *Erica tetralix* in company with northern species have been described from W.-Sweden (Osvald 1923), from Denmark (Mentz, Mølholm Hansen, Jessen, B. 1941), and from NW.-Germany (Tüxen, Schwickerath). The northern species occurring together with *Erica* are *Andromeda polifolia*, *Oxycoccus quadripetalus*, *Rubus chamaemorus*, *Empetrum*, and *Eriophorum vaginatum*.

With the exception of *Andromeda* and *Oxycoccus*, the boreal element is reduced in many German bogs rich in *Erica* (Tüxen's *Sphagnetum medii subatlanticum*). In northernmost Germany, bogs with patches of *Empetrum* and *Rubus chamaemorus* occur (Libbert 1940), and in Denmark (Jutland) *Empetrum* reaches 100 per cent (constancy) and 73 per cent (average frequency) in the bogs of Nørholm Hede (Mølholm Hansen, Table 7a, Nos. 1—8) and in the large *Sphagnum* bogs Store and Lille Vildmose, all the above-mentioned northern species occur (O. G. Petersen 1896, Jessen 1939). In spite of these differences between Danish and many German bogs, in the present treatise all bogs with frequent occurrence of *Erica*, *Oxycoccus*, and *Andromeda* are referred to the L-type; the German bogs, however, are clearly transitions to the more southern *Erica* bog type almost without boreal plants (M-type).

According to Osvald (1923), a distinct antagonism exists between *Erica tetralix* and the northern species *Empetrum*, *Oxycoccus*, and *Rubus chamaemorus*. This may especially be the case in Sweden near the eastern frequency limit of *Erica tetralix*, where this species is more selective as to its habitat. In Jutland (Store Vildmose, Nørholm Hede, Randbøl Hede), bogs with dominating *Erica tetralix* very frequently contain *Empetrum*, and the bogs dominated by *Empetrum* rarely lack *Erica tetralix*. Furthermore, it may be remembered that *Erica tetralix* and *Empetrum* in the wet heath (cf. p. 50) seem to be related with respect to their ecology.

In Store Vildmose, Nørholm Hede and many other localities in Jutland, the bog sociations contain much *Erica* and northern species and thus they comply with the requirements of the L-type. The same is the case with many West-Swedish bogs. In the Komosse (Osvald 1923), the *Erica* sociations, the *Calluna Sphagnum tenellum* and, to a great extent, the *Calluna-Cladina* and *Calluna-Sphagnum magellanicum* sociations belong to the L-type, while the *Empetrum* sociations and the *Calluna-Sphagnum fuscum* sociations must clearly be excluded from this main type.

In his paper on the bog communities of Europe, Schwickerath (1940) deals with five Atlantic associations (containing *Erica tetralix* and other oceanic plants) and two continental ones, viz. *Sphagnetum medii-rubelli* and *Sphagnetum fusci*. While the latter is obviously a continental bog community, the *Sphagnetum medii-rubelli* must to a great extent be a western European oceanically influenced community, since the *Calluna-Sphagnum rubellum* associations, according to OSVALD, DU RIETZ and others, are characteristic of the most westerly bogs. In the writer's opinion, a boundary between Atlantic and continental bogs should be placed between the *fuscum* and other bogs or, more particularly, between the bogs dominated by true continental species and other bogs (cf. below). Within the "*Ericion*" communities, SCHWICKERATH separates three associations, viz. the *Narthecietum*, the *Juncetum squarrosi*, and the *Scirpetum*. Most probably the sociations of these northern varieties are typical bogs of the J- and L-types. The classification attempted by SCHWICKERATH is made difficult by the distribution of the two character species *Scirpus caespitosus* and *Juncus squarrosus* which both occur far more to the east than does *Erica tetralix*. In fact, *Scirpus caespitosus* dominates the greater part of the Zehlau bog in eastern Prussia (GAMS and RUOFF).

Concerning the floristic composition of the L-bog sociations and their ecological data, the reader is referred to the works mentioned above. A description of the subcontinental northern bog species is deferred to the O-main type (p. 100).

M. Bogs and wet heaths characterized by oceanic species, the northern element reduced or lacking (*Erica tetralix*-group of *Ulicio-Ericion tetralicis*).

The wet heaths of South England and North France are characterized by a number of distinct oceanic ("hyperoceanic") species, viz. *Ulex nanus, Erica ciliaris, Pinguicula lusitanica, Lobelia urens*, and others (*cf.* the "*Tetraliceto Ulicetum nani*" described by LEMÉE 1937). Some of these species reach their northern limit in southern England and are employed for the separation of the "south-western heaths" (cf. TANSLEY 1939, p. 764). Starting from this relatively southern, very oceanic main type (which may be termed *Ulex nanus-Erica ciliaris*-group of *Ulicio-Ericion tetralicis*) we may, to the north and east, reach other regional wet heath types. In more continental regions, the *Ulex-Erica ciliaris* group is followed by the *Erica tetralix* group which may be regarded as a wet heath and bog type corresponding to the D-type of the dry Dutch-German heath series. Analyses illustrating the composition of the M-type communities are found in SCHÜTT (1931), SCHWICKERATH (1933, 1940), JESWIET and DE LEEUW (1933), JONAS (1935), and TÜXEN (1937). It appears from the lists of plants in these papers that no guiding species characteristic of the M-type exists. This latter may, consequently, be separated from the northern K-type by the absence of northern species (cf. Table 23) and from the *Ulex-Erica ciliaris* group by the lack of hyperoceanic species (e. g. *Carex binervis, Carum verticillatum*).

The wet heaths of the M-type are found in Holland and N.W.-Germany and may, moreover, occur in patches along the Baltic coast. LIBBERT's analyses from these regions, however, belong more naturally to the K-type (Table 23). The rapid "Ausklingen" of the *Erica* heaths (and bogs) in a south-easterly direction was mentioned by SCHWICKERATH (1933, p. 108).

The heaths of the M-type may be arranged as follows.

Erica-(Calluna-)Cladonia heath very frequently rich in *Juncus squarrosus* or *Scirpus caespitosus* (Jonas, Tüxen, Jeswiet and de Leeuw). It is the driest type. This type radiates to Denmark (B. 1941 a, Table 56, No. 3) and southernmost Sweden (Table 22, No. 13; not quite typical, containing much *Cetraria islandica*).

A very similar vegetation, but with *Hypnum cupressiforme* and *Hylocomium schreberi* or mixed bryophyte-*Cladonia* union at the ground. It is widely distributed in N.W.-Germany (*Ericetum Tetralicis typicum* described by Tüxen) and is found in Jutland and North Sealand (Table 22, Nos. 7—8) in places where *Empetrum* is missing.

Almost the same phanerogams, but with *Sphagna* at the ground. It is very frequent in N.W.-Germany and extends to Hohe Venn and Schneifel (Schwickerath). In Denmark it occurs in Utoft (Loc. 46 Børgesen and Jensen, Nos. 9—11 with *Sphagnum tenellum, subnitens, subsecundum,* and *compactum,* and of northern species only scattered *Eriophorum vaginatum* in No. 9).

It must be emphasized that no sharp limit exists between the *Empetrum-Vaccinium* and the *Erica* group. In the latter, the northern element counts three species only, viz. *Andromeda, Oxycoccus,* and *Eriophorum vaginatum,* which are very scattered and of low constancy or completely absent. Wet heaths dominated by *Erica tetralix* seem to be rather southern types. In the wet heaths of Rundöy in W.-Norway (Goksöyr 1938, Tables 14, 16 and 17) this dwarf shrub only attains the constancy percentages 0.28 and 46, and the average covering values 1 and 1+.

Bog vegetations without or with very few and scattered boreal plants are found in France where, according to Lemée (Table 50), *Andromeda* is absent and *Oxycoccus* is very rare. In N.W.-Germany, similar vegetations are described by Jonas (1935, pp. 99—100, Nos. 6—11) and by Schmumacher (1932, p. 23). In the vegetation described by Jonas, *Erica* and *Sphagnum compactum* are constant and abundant, *Scirpus caespitosus* and *Calluna* and *Sphagnum molle* are constant, but more scattered, and *Eriophorum vaginatum, Andromeda,* and *Oxycoccus* are absent, although the two latter may occur very scattered in adjacent heathlike *Erica* vegetations. In the *Erica-Calluna-Molinia-Scirpus caespitosus-Sphagnum compactum-molle* vegetation of the "Wahner Heide" (Schumacher), no northern plants occur and, here, the southern *Genista anglica* is scattered. In southernmost Jutland at Gram (Loc. 51), a dry bog was observed (Table 25) which also satisfies the claims of the M-type. Owing, i. a.

Table 25. Small bog in the vicinity of Gram (Loc. 51). Method: D.

1.		
Erica tetralix	3	3–4
Calluna vulgaris	5	5
Molinia coerulea	2	1–2
Eriophorum angustifolium	–	1
Gentiana pneumonanthe	+	+
2.		
Hypnum cupressiforme	2	2
Gymnocybe palustris	–	2
Hylocomium schreberi	1	–
Blepharozia ciliaris	1	1
Jungermannia inflata }	+	1
— ventricosa }		
Scapania nemorosa }		
Cephaloziella divaricata }		
3.		
Cladonia impexa	1	–
— floerkeana	–	1
Parmelia physodes	1	1

to the dryness, the bog is less typical, containing *Molinia* and *Gentiana pneumonanthe* and, outside the area of investigation, *Deschampsia flexuosa, Juncus squarrosus,* and *Scirpus caespitosus. Empetrum* is restricted to the margin on temporarily shaded spots near conifer plantations.

Scirpus caespitosus. The relatively southern-oceanic subspecies *germanicus* can hardly be regarded as a guiding species for the M-type. This subspecies ranges to W.-Norway and the Faroes and is very frequent in Jutland. It may, however, reach its greatest abundance in the vegetations of the M-type. Schwickerath interprets the subspecies *austriacus* (var. *callosus* Bigel.) as boreo-alpine. Its range in America-Greenland shows, however, that this race, too, may at any rate be suboceanic (B. 1938, p. 241). The eurasiatic range is not closed, showing gaps along the arctic sea and in the southern mountain areas. In the Zehlau bog (East Prussia), *Scirpus austriacus* is restricted to constantly wet places on the bog plateau without trees. According to Gams and Ruoff, this fact may be explained by the growth of the plant near its continental limit. This limit has been mapped in Esthonia by Thomson (1924) and has moreover been mentioned by Paasio (1933, p. 169).

The occurrence in the heaths of central Jutland of *Scirpus caespitosus* (mainly its subspecies *germanicus*) has been mentioned in B. 1941a, pp. 172—174. The species prefers sloping ground with slowly moving soil water.

Tüxen mentions *Sphagnum compactum* as a local character species in his *Ericetum*. In fact, this oceanic plant is very frequent in heaths and bogs of the M-type (cf. also Jonas and Schumacher); it extends, however, far to the north and east (Osvald 1925a, Paasio 1933), but is absent from the Zehlau bog.

2. Subatlantic-subcontinental series. Wet heaths and bogs east of the *Erica tetralix-Ledum palustre* boundary containing suboceanic-subcontinental species.

This series includes two groups (alliances), viz. a northern one almost exclusively containing bogs (termed *Oxycocco-Andromedion*) and a southern one containing heaths and bogs (*Callunio-Juncion squarrosi*). Several main types may be separated within the northern group. In the present treatise, however, only Danish and closely related types will be considered more thoroughly.

The course of the *Erica-Ledum* boundary in Sweden appears from the maps in Granlund (l. c.) and du Rietz (1925c). In Denmark, the course of this boundary was discussed in B. 1937a (p. 30). The map (B. l. c., p. 3) shows that a frequency limit runs from north to south through eastern Jutland. Notably, however, this limit will follow edaphic, not climatic changes. Another, less marked frequency limit runs from NE (Helsingør) to SW, perhaps corresponding to that in Sweden. Unfortunately, the dots indicate only presence, not frequency, and it must be emphasized that *Erica* in the bogs of North Sealand is very rare (Olsen 1914), occurring e. g. in small patches under trees in the bog Sortemose. The writer no longer assumes that the absence of *Erica* in these bogs is due to conditions during the immigration. Consequently, he is inclined to place the *Erica-Ledum* boundary west of these bogs. This view is substantiated by the course of the absolute eastern limit for *Narthecium ossifragum* (cf. the map in HOLMBOE 1937) which in Sweden almost coincides with the *Erica-Ledum* boundary and in Denmark bends to the north of Sealand and runs southward through East Jutland and Funen. The *Narthecium* limit is also used by SCHWICKERATH (1933, Fig. 8).

According to DU RIETZ (1925, p. 22), the limit between the westerly (mainly *Sphagnum magellanicum* union) and the easterly bog type (mainly *Sphagnum fuscum* union) coincides fairly well with the *Erica-Narthecium-Ledum* boundary. Most Danish bogs by far belong to the *magellanicum-rubellum* type. In North Sealand, however, *Sphagnum fuscum* may dominate very locally in company with *Sphagnum magellanicum* (OLSEN 1914). The distribution of *Sphagnum fuscum* ought to be studied in greater detail. For the present, we may say, to summarize, that this species is northern-subcontinental; to the north reaching the Atlantic where it is rare on the Faroes, to the south having a western limit at some distance from the coast (cf. the map in SCHUMACHER 1937). In Jutland it is rather scattered and not found dominating.

N. Bogs characterized by northern, northern-subcontinental, and suboceanic species (*Scirpus caespitosus*-group of *Oxycocco-Andromedion*).

To this main type only such *Scirpus caespitosus* bogs are referred which lack *Erica tetralix* or other oceanic species. Such vegetations are found in northern West Norway (OSVALD 1925a, pp. 47—48), Finnland (PAASIO 1933, p. 28), Esthonia (THOMSON), East Prussia (GAMS and RUOFF), and in the Black Forest (SCHUMACHER 1937, pp. 238—240). In Denmark (North Sealand, cf. Table 26), this bog type occurs, although rarely. It is almost exactly the same vegetation as was investigated fom East Prussia by GAMS and RUOFF (p. 151), being dominated by *Scirpus*, *Calluna*, and *Sphagnum rubellum*. The vegetation from the Zehlau bog differs only by a greater admixture of northern or continental species (*Rubus chamaemorus*, *Sphagnum fuscum*, *Cladonia alpestris*) which, however, are all scattered and less constant. In both vegetations, *Eriophorum vaginatum* occurs, yet it rarely attains high covering values. This statement is in accordance with the fact that *Scirpus* and *Eriophorum vaginatum* bogs are in a sense alternative communities (cf. TANSLEY 1939, p. 707; GOKSÖYR 1938, p. 40). The ecological contrast is explained by SCHUMACHER (1937) who writes that *Scirpus* "sich in einer Gesellschaft wohl zu fühlen scheint, die eine wesentlich stärkere Wasserbewegung und damit auch eine bessere Ernährung und Durchlüftung hat als die Hochmoore sie ausserhalb der Laggs und Rüllen anscheinend bieten können. Während das Scheidenwollgras (*Eriophorum vaginatum*) unbekümmert im Wachstumsgebiet der Moorhochfläche gedeiht, zieht die Rasensimse (*Scirpus*) entschieden die Stillstands- und Abschwemmungsflächen vor." This mode of occurrence of *Scirpus* in bogs thus corresponds entirely to its occurrence in the heath (cf. B. 1941 a and above p. 96).

Concerning the occurrence of *Scirpus* in alpine or arctic heathlike meadows in places, where water oozes out of the soil, cf. B. 1933, Schumacher (l. c.), and Kalela (1937). When occurring in relatively continental regions, the typical *Scirpus* bogs seem to be comparatively rich in oceanic *Sphagna* (*Sphagnum papillosum*, cf. Paasio) and poor in true continental species.

Table 26. *Scirpus caespitosus* bog in North Sealand. Buremose. According to C. Olsen 1914, Tab. 1, No. 5. Method: R.

1.		4.	
Scirpus caespitosus	10	Hylocomium schreberi	3
Calluna vulgaris	10	Hypnum cupressiforme	+
		Gymnocybe palustris	7
2.		Sphagnum rubellum	10
Andromeda polifolia	3	— magellanicum	1
Oxycoccus quadripetalus	10	— recurvum	2
Eriophorum vaginatum	8	— acutifolium	1
3.			
Eriophorum angustifolium	1	5.	
Drosera rotundifolia	1	Cladonia rangiferina coll.	2

Species groups: 1: suboceanic species. 2: northern species. 3: widely distributed species. 4: bryophytes. 5: lichens.

O. Bogs characterized by northern and northern-subcontinental species (*Empetrum nigrum-Oxycoccus*-group of *Oxycocco-Andromedion*).

The position of the alliance *Oxycocco-Andromedion* is intermediate between the oceanic *Ulicio-Ericion tetralicis* and the continental *Ledio-Chamaedaphnion*. In addition to the N-type where suboceanic plants play a part, the *Oxycocco-Andromedion* contains a number of sociations which are dominated by northern and subcontinental species. This vegetation is called main type O. There are many transitions between O and N as well as between O and the more arctic alpine bogs which have been termed by Nordhagen (1936) "*Oxycocco-Empetrion hermaphroditi*", but which, within the writer's system of geographical main types and alliances, should be called the *Betula nana* group of *Oxycocco-Andromedion*. The transition is made by O-bogs containing much *Rubus chamaemorus*, *Sphagnum fuscum*, and *rusowii*.

In North Sealand, bogs of the O-main type have been described by Olsen (1914) and by H. E. Petersen and his collaborators in the investigations of Maglemose in the wood Gribskov. Maglemose is undoubtedly the most representative bog in North Sealand. Other large bogs mainly belonging to the O-type are found in central Sealand (Aamosen, cf. Fig. 25), where large areas are occupied by *Calluna-Empetrum* or *Vaccinium vitis idaea-Empetrum-Eriophorum vaginatum-Sphagnum* sociations with *Oxycoccus* and *Andromeda*. In the more northern *Betula nana* group, the ground

Table 27. Bogs of the *Oxycocco-Andromedion* (O main type). Nos. 1—9 according to C. Olsen 1914. Method: R (S in No. 10).

Analysis No. / Locality in North Sealand[1]	Distributional type	1 a	2 b	3 c	4 c	5 d	6 e	7 e	8 f	9 g	10 g	Constancy pCt.
1.												
Empetrum nigrum	bsΓ	—	10	10	10	8	7	10	2	10	10_7	**90**
Vaccinium uliginosum	bsΓp	—	+	+	5	—	+	2	—	—	—	50
— vitis idaea	bs(˥)	—	—	—	6	—	—	1	—	—	—	20
Oxycoccus quadripetalus	bsxp	10	10	10	10	10	10	7	—	6	10_5	**90**
Andromeda polifolia	bsc_3	+	—	—	—	—	+	3	—	—	—	30
Eriophorum vaginatum	bsx	10	9	5	8	8	8	7	8	10	10_4	**100**
2.												
Calluna vulgaris	sbo_3	10	10	10	10	10	9	10	10	10	10_8	**100**
Scirpus caespitosus	sbo_3	4	—	—	—	—	—	—	—	—	—	10
3.												
Eriophorum angustifolium	sbax	—	—	—	—	—	—	—	+	—	—	10
Drosera rotundifolia	sbx	—	+	—	—	+	—	+	+	+	2	60
4.												
Hylocomium schreberi	—	10	—	—	—	3	6	8	6	7	4	70
— triquetrum	—	—	—	+	—	+	—	—	—	—	—	20
— splendens	—	—	1	3	6	—	—	4	—	1	—	50
Hypnum cupressiforme	—	—	—	7	5	—	2	8	3	—	—	50
Gymnocybe palustris	—	4	4	3	2	7	4	3	4	3	10_7	**100**
Polytrichum strictum	—	—	4	—	—	+	—	—	1	1	8_5	50
Leucobryum glaucum	—	—	—	+	—	—	—	—	—	—	—	10
Dicranum scoparium	—	—	—	1	—	—	+	2	—	—	—	30
— rugosum	—	—	1	—	—	—	+	1	—	—	—	30
Plagiothecium denticulatum	—	—	—	—	—	—	—	—	+	—	—	10
5.												
Sphagnum magellanicum	—	+	4	2	1	9	1	+	5	1	10_5	**100**
— rubellum	—	5	5	5	2	5	1	2	—	4		**90**
— acutifolium	—	2	1	+	+	—	—	—	—	1		60
— recurvum	—	—	7	2	6	10	—	—	—	6		60
— fuscum	—	—	4	—	—	—	—	—	—	—	—	10
— angustifolium	—	—	—	—	—	—	7	2	—	—	—	20
— cuspidatum	—	—	—	—	—	—	+	—	—	—	—	10
— russowii	—	—	—	—	—	—	—	+	—	—	—	10
— apiculatum	—	—	—	—	—	—	—	—	9	—	—	10
6.												
Bazzania trilobata	—	—	—	4	2	—	+	—	—	—	—	30
Kantia trichomanis	—	—	1	1	+	+	—	+	3	1	—	70
Cephalozia media	—	—	1	—	+	+	—	+	—	—	—	40
— connivens	—	—	—	—	—	—	—	—	1	—	—	10
Jungermannia ventricosa	—	—	—	+	—	—	—	—	—	—	—	10
Odontoschisma sphagni	—	—	—	—	—	—	—	+	—	—	—	10
7.												
Cladonia rangiferina coll.	—	—	2	4	1	7	5	2	1	—	—	70
— pyxidata coll.	—	—	—	+	+	—	+	—	1	—	—	40
Parmelia physodes	—	—	—	—	5	3	1	4	—	—	—	40

[1] Localities: a: Buremose. b: Vandmosen. c: Maglemose. d: Lille Grib-Sø. e: Horserød Hegn. f: bog in Teglstrup Hegn. g: Lyngby Mose.
Species groups: 1: northern species. 2: suboceanic species. 3: widely distributed species. 4—6: bryophytes. 7: lichens.

is dominated by *Sphagnum fuscum* and *rusowii*. In one case only, Olsen (l. c., Table 2, No. 4) describes a North Sealand bog dominated by *Sphagnum magellanicum* and *fuscum*. As compared with the other typical O-bogs (cf. Table 27), this sociation seems to be more wet, containing *Drosera rotundifolia* with F $^0/_0$ 92. Of more continental bog sociations related to those of North Sealand we may mention the *Calluna-Sphagnum rubellum magellanicum* sociation of the Zehlau bog (Gams and Ruoff, p. 148) and some of the sociations of the Ryggmosse and Stigsbo Rødmosse (du Rietz and Nannfeldt) which, however, are transitions to the *Betula nana* group or to *Ledio-Chamaedaphnion*, containing *Rubus*, *Sphagnum fuscum*, and sometimes *Ledum*.

On the sketch map "Die Moorprovinzen Europas" by v. Bülow (1929, Fig. 56) a limit between typical raised bogs and wood bogs (Waldhochmoore) crosses Denmark from NE to SW. The map in Gams and Ruoff divides Denmark into three areas, viz. "den friesisch-jütischen Bezirk der *Erica tetralix*-Hochmoore", "den südbaltischen Bezirk der *Erica*-Moore" and "die mittelbaltischen Kalk- und Vorseegebiete". The latter includes North Sealand. None of these two divisions is quite successful; this may partly be due to the lacking knowledge of Olsen's paper. Undoubtedly, it is correct to place the Jutland bogs in the same section as the West-Swedish-Northwest-German bogs and it may be correct, furthermore, to place some East-Danish bogs with *Erica tetralix* in the same group together with German bogs at the Baltic. However, in the writer's opinion, the Sealand bogs mentioned above must be looked upon as a separate subcontinental bog type which is a southern variety of Swedish bogs without *Erica* and *Ledum*. The O-type is not a wood bog. It should, however, be emphasized here that a distinct inclination towards a "Bewaldung" is very frequently observed (Helms and Jørgensen, 1924; Gram, 1936, p. 380; and Fig. 25). The succession leads to *Betula* bogs, (frequently with much *Picea excelsa*) not to typical wood bogs dominated by *Pinus silvestris*.

In the hollows of the Sealand bogs, two boreal subcontinental species, viz. *Scheuchzeria palustris* and *Carex limosa*, occur. They are both rare in W.-Norway and are classified among the northern-continental plants by Matthews. *Scheuchzeria* is rare in Jutland, and *Carex limosa* does not occur in the bog hollows of Randbøl Hede and it is rare in Store Vildmose. In company with *Scheuchzeria*, it occurs, however, in the Lille Øxsø bog (near Loc. 17; cf. Mentz, 1912) and, in company with *Carex lasiocarpa*, in bogs at Loc. 21. All these plants of wet hollows or in *Sphagnum* filling lakelets belong to the "*Scheuchzerietalia palustris*" (Nordhagen) which recently have been described by Paul and Lutz (1941) and which also include a *Carex chordorrhiza* association. They do not seem to be extremely oligotrophic and this fact combined with their continental tendencies may explain their absence from the hollows of most West Jutland bogs, where sociations belonging to the *Rhyncosporetum sphagnetosum cuspidati* (Diemont and Tüxen) dominate. *Rhyncospora alba* hollows are very rare in Sealand (Bure Mose) and may frequently be characterized by oceanic species (*Rhyncorpora fusca*, *Drosera intermedia*, *Lycopodium inundatum*, *Erica tetralix*). Thus, the "Schlenken" vegetation of bogs also can be divided by making use of distributional types. This division may largely coincide with that obtained by the aid of character species.

Andromeda polifolia seems to be the most representative flowering plant of the O-type. According to B. (1937a, p. 9), it is perhaps a boreal plant, to the south showing continental tendencies. In Denmark it is mainly absent near the West coast (Fig. 26), where, however, true *Sphagnum* bogs hardly occur. In very oceanic regions, *Andromeda* is sometimes lacking (Faroes, Utsire) or rare (Rundöy, Goksöyr). Matthews (map 11, p. 57) counts *Andromeda* among the northern continental species. In wet heaths it is scattered or rare (cf. Mølholm

Fig. 25. Sandelyng Mose in Central Sealand. The bog (hummock) formation has ceased. *Betula* colonized in the heather (frequently *Calluna-Empetrum* soc.). After B. 1943 a.

Hansen 1932, Table 6a, Nos. 6 and 8; B. 1941a, Table 64, Nos. 2—3; B. 1940, Table 1, No. 5) and it has never been found in the wet dune heaths.

The different subspecies of *Oxycoccus* also show at any rate weak continental affinities (cf. Matthews) and the same is the case with *Vaccinium vitis idaea* (cf. p. 41), but hardly with *Eriophorum vaginatum*. The latter plays a comparatively small part in the vegetation of the oceanic West-Norwegian bogs (Osvald 1925 a), but it is very abundant in many areas of the British Islands.

Rubus chamaemorus is low-arctic-subarctic and subcontinental. From the detailed treatise by Th. Resvoll (1925) we may mention that the plant is rare or missing in N.W.-Europe and that it is rare in Norway in the coast land south of the Trondhjem Fjord. In Denmark, it is much rarer than in the same latitudes in Lithuania (cf. the map in Hryniewicki 1932). Here, its claims to continentality and habitat are presumably best fulfilled in North

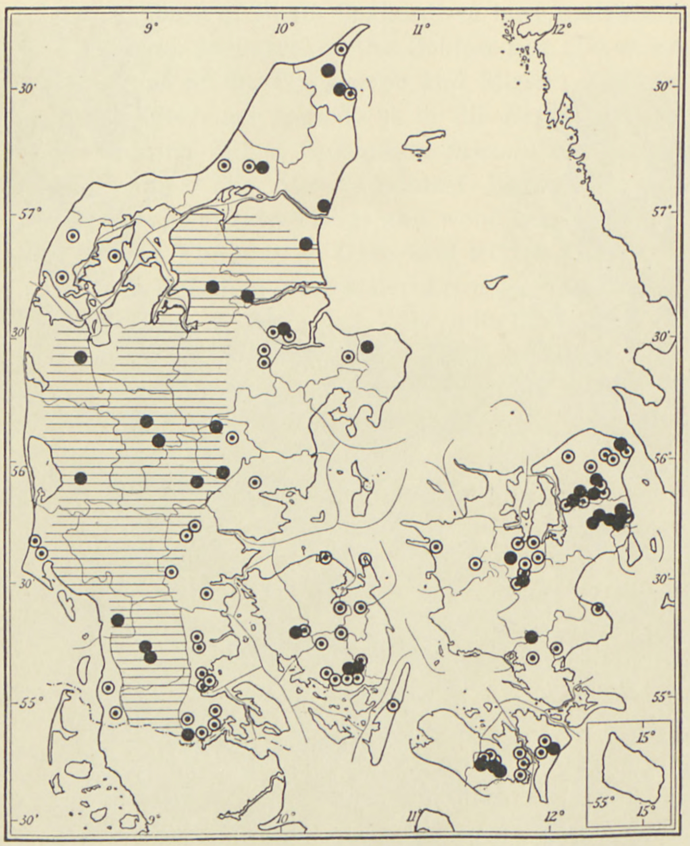


Fig. 26. Danish range of *Andromeda polifolia*. After B. 1937 a.

Sealand and North Jutland. *Betula nana*, the guiding species of the northernmost bog type within *Oxycocco-Andromedion*, has also a low-arctic-subarctic and subcontinental range (for further details, cf. B. 1938).

The bogs which mainly occur east of those belonging to *Oxycocco-Andromedion* are characterized by true northern-continental species, viz. *Ledum palustre*, and *Chamaedaphne* (*Cassandra*) *calyculata*. Concerning the distribution of *Ledum*, cf. Granlund (1925), for that of *Chamaedaphne*, see the maps in Thomson (1924), Hryniewicki (1932, p. 325), and Paasio (1933, Fig. 1). Most of these bogs are wood bogs and the vegetation has very little in common with atlantic dwarf shrub vegetations. For the sake of completeness, some important points respecting these bog types (called *Ledio-Chamaedaphnion*) may nevertheless be mentioned.

Descriptions of very typical bogs of this kind are found in the papers by KATZ (1926, 1929), SOKOLOWA (1937), LEONTJEV (1937), and from Scandinavia, in the papers by OSVALD (1923, p. 298), DU RIETZ and NANNFELDT (1925), WARÉN (1926), PAASIO (1933), and NORDHAGEN (1937). These bogs are mostly wood bogs dominated by *Pinus silvestris* (cf. photo in WALTER 1927, p. 257; OSVALD 1925b). Two main types may be separated, one of which is relatively westerly with *Ledum* (without *Chamaedaphne*) and occurring in Sweden, North Norway, West Finland, West Esthonia, and East Prussia. Some of the bogs of this main type are open, others woody; another one is more easterly and contains *Ledum* and *Chamaedaphne*. From the data in LEONTJEV's paper (pp. 137—138) we may cite the following analysis: Under the trees (*Pinus silvestris, Picea obovata, Betula pubescens*) comes a layer with much *Betula nana*, then a dwarf shrub layer composed of *Chamaedaphne* (5—6;5[1]), *Vaccinium uliginosum* (4;4—5), *Empetrum* (4; 4—5), *Ledum* (3;3), *Vaccinium vitis idaea* (3;4) *Eriophorum vaginatum* (4;3), *Andromeda* (3—4;3), *Carex pauciflora* (4;4), *Oxycoccus* (3—4;4), *Rubus chamaemorus* (3—4;4), *Vaccinium myrtillus* (—;3), *Carex globularis* (—;4), In the moss layer, *Sphagnum fuscum* and *parvifolium* dominates; *Polytrichum strictum, Cladonia alpestris, mitis* and *rangiferina* are frequent.

P. Wet heaths (and bogs) with reduced oceanic and boreal elements (*Callunio-Juncion squarrosi*).

This main type may also be defined as an alliance. Undoubtedly, a northern and a southern subtype exist, but they do not seem to be so different as to deserve the rank of main types. The northern subtype is attached to the G-main type of the Baltic-submontane dry heath series; the southern subtype may be attached to the E-F-types of the dry Dutch-German series. Important guiding species are the suboceanic *Juncus squarrosus* and *Sieglingia decumbens*[2]. The total range of the former is shown in Fig. 132 of B. 1938.

Northern subtype. Wet heaths almost without northern, southern or euoceanic species were found in the peninsula Ulvshale (Loc. 66). Analyses from this locality are published in B. 1942 (Table 4). The most important type is the *Calluna-Juncus squarrosus* heath. In other places, the wet heaths are dominated by *Calluna* in company with widely distributed species, particularly *Molinia, Nardus, Potentilla erecta, or* the suboceanic *Sieglingia*, while *Platanthera bifolia* and the suboceanic *Pedicularis silvatica* are more scattered. In Southeast-Jutland too, a *Calluna-Molinia* soc. without *Erica tetralix* was observed in a single locality on relatively fertile soil.

On the Isle of Bornholm, the wet places in the heath have a vegetation which also belongs to the P-type. In depressions in the dune heaths at Boderne *Sieglingia* (!), *Nardus* (!), *Potentilla erecta*, and *anserina* occur. In somewhat moist patches at Gudhjem, mainly *Molinia, Sieglingia, Potentilla erecta, Succisa pratensis* were observed and, furthermore, *Serratula tinctoria* occurs occasionally. From wet patches in the central heaths, WARMING (1914) mentions *Juncus squarrosus, Scirpus caespitosus, Sieglingia, Nardus, Leucobryum glaucum*, and *Sphagna*. From the south-east point of the islands, WARMING gives the following zonation. Near a pond between two heath-

[1] Figures showing the degree of abundance in two different localities.
[2] Cf. HÅRD 1935.

covered alluvial ridges ("fulls"), a *Salix repens-Carex stolonifera-Sphagnum squarrosum* soc. with *Hydrocotyle, Comarum, Pirola minor* and a few more. It borders on a *Calluna* heath with *Alnus glutinosa* scrubs and plenty of *Lycopodium clavatum*. The *Salix* soc. is not a true wet heath, however, it houses one of the suboceanic wet heath plants, viz. *Hydrocotyle vulgaris*. This zonation indicates that the wet heath, when going to more continental regions, is depauperated or made less typical much more rapidly than is the dry heath. This is presumably due mainly to soil factors. In continental regions, only dry soils without influence of the ground water are sufficiently acid and infertile for a heath vegetation.

Southern subtype. In the literature, one description only was found. Unfortunately, it is a rather dry transition heath (p. 91), found in Württemberg (Waldenburger Berge) by Libbert (1939) and it contains the suboceanic *Calluna, Juncus squarrosus, Sieglingia, Pedicularis silvatica, Holcus lanatus, Polygala serpyllacea, Leucobryum*, and the montane suboceanic *Centaurea nigra* and *Arnica montana* (abundantly). As continental plants, *Genista sagittalis, Genista tinctoria*, and *Scorzonera humilis* may be mentioned.

It is not impossible that certain bog sociations (*Calluna-Sphagnum* soc.) without or with very scattered boreal species should exist. If so, they would belong to the P-main type.

VII. Survey of the dwarf shrub communities of Europe and the employment of spectra of distributional types.

Dry and wet heaths as well as dwarf shrub bogs may be looked upon as one very large vegetational unit. The great number of small vegetational types within this large unit are never separated by sharp boundaries. All attempts to classify and divide vegetations are, consequently, of somewhat limited value but, nevertheless, classification is a very important link in vegetational research, since it renders comparisons possible and facilitates the descriptions. The principles advanced in the present treatise lead to a geographical division, at the same time separating ecologically different types. The vegetation is divided by limits which almost coincide with northern limits or continental-oceanic limits (including frequency limits) of certain species. The system of geographical series and main types is based upon floristic details and, consequently, rather far-reaching accordances between this system and that of the school of Braun-Blanquet prevail. The differences between the two systems being comparatively small, the writer has decided to use a nomenclature of the larger units (alliances) which may be easily comprehensible for most ecologists and phytogeographers and which, in some cases, may even be employed by botanists who make use of the system of character species. In naming the unities, the most important geographical guiding species have been used. Oceanic species characterize the most westerly vegetations and suboceanic-subcontinental ones the more easterly vegetations. Thus, *Calluna* which is a widely distributed suboceanic species is only used in the suboceanic alliances, viz. *Callunion balticum* and *Callunio-Juncion squarrosi*. In some cases, older terms (e. g. *Ulicio-Ericion tetralicis*) have been maintained, although their meaning has been altered.

In the following survey the dwarf shrub vegetation of northern Europe is reviewed. Not considered are the true continental or Mediterranean *Helianthemum* or *Cistus* dwarf shrub vegetations. The main types mentioned above are included. In most cases, they represent suballiances ("Unterverbände"), more rarely alliances.

I. Dry heath communities.

Arctic-alpine series.

Phyllodoco-Myrtillion (cf. text, p. 12).

Rhacomitrium group. Oceanic. (cf. e. g. B. 1937b, Table 6, Nos. 3—5).

Phyllodoce coerulea-group. Suboceanic-subcontinental and widely ranging arctic alpine species mixed (cf. Table in Nordhagen 1936, 1943 and Table 1, Nos. 12—16).

Myrtillus-group. Subcontinental and widely distributed, arctic alpine species (e. g. *Betula nana-Empetrum-Vaccinium-Hylocomium splendens* soc.).

Loiseleurieto-Arctostaphylion (cf. text, p. 13).

Loiseleuria-Juncus trifidus-group. Among the flowering plants, suboceanic and subcontinental species, ground layer frequently with continental lichens (*Alectoria ochroleuca*) (cf. Nordhagen 1936, p. 66, Nos. 1 and 3).

Arctostaphylos uva ursi-group. Subcontinental-widely distributed flowering plants, continental lichens. Suboceanic-arctic element much reduced (cf. Nordhagen, l. c., p. 66, Nos. 5—7).

Cassiope tetragona-group. Continental, subcontinental (*Cassiope tetragona, Calamagrostis lapponica*), and widely distributed plants. Suboceanic element reduced. Examples, cf. B. 1933, Nos. 61 and 65; Nordhagen, l. c., p. 66, No. 2.

Kobresieto-Dryadion (cf. p. 18).

Continental element very prominent. Perhaps subtypes with many widely distributed and rather few continental plants or with a large number of frequent continental plants (*Cassiope tetragona-*, *Rhododendron lapponicum-*, *Arctostaphylos uva ursi-*, and *Dryas*-sociations (cf. Nordhagen l. c., pp. 38—39)).

The *Empetrum-Vaccinium* heath rich in *Dryas* from the Faroes (B. 1937b, Table 16) is ecologically clearly related to *Dryadion*. It belongs, however, to another group or to another related oceanic alliance which may further occur in Ireland and Iceland ("Mo" vegetation, cf. Mølholm Hansen 1930, pp. 81 and 104).

Scano-Danish (Scotch) series (cf. p. 18).

Myrtillion boreale.

Cornus-Blechnum-Hylocomium loreum-group, cf. main type A and Table 2, Nos. 6—9, Table 3, Nos. 1—20 and see, furthermore, B. 1940, Table 1 and Table 2, Nos. 1 and 4 as well as Nordhagen 1917, pp. 87—88.

Myrtillus-Hylocomium splendens-triquetrum-group. Oceanic and northern oceanic element reduced. A-type. Examples in Tables 2—3.

Empetrion boreale.

Empetrum-Vaccinium vitis idaea-group. Suboceanic-subcontinental, cf. main type B, p. 35.

Empetrum type, cf. Tables 6, 7, and 8.
Vaccinium vitis idaea type, cf. Tables 5 and 6, No. 7.
Arctostaphylos uva ursi-group. Subcontinental. Cf. main type C, p. 50 and examples in Table 9.

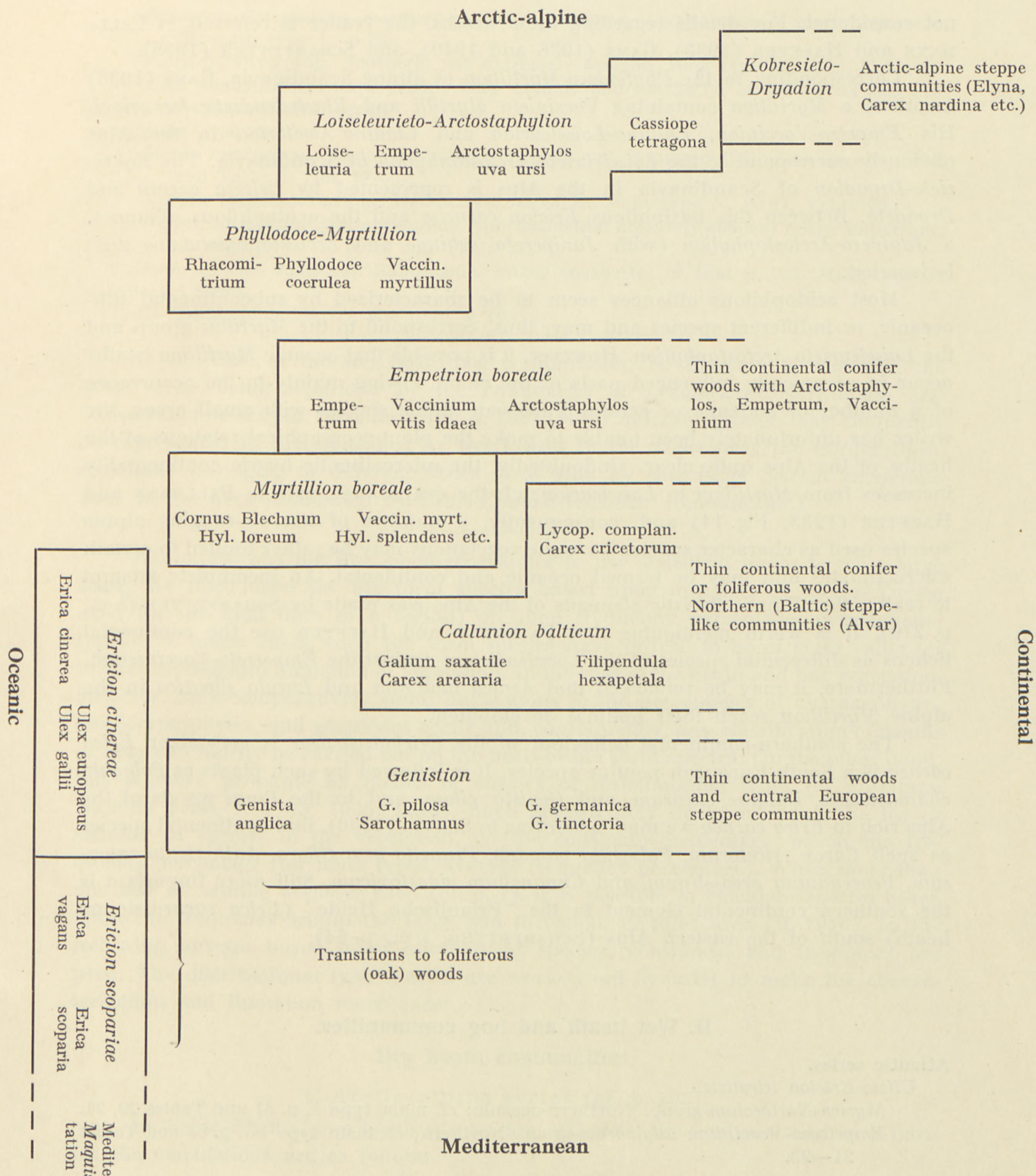
Dutch-German series (cf. p. 55).
Genistion.
Genista anglica-group. Oceanic. Main type D, p. 57; cf., moreover, the *Calluneto-Genistetum* of Tüxen and others.
Genista pilosa-Sarothamnus-group. Suboceanic. Cf. main type E, p. 58 and Tables 11—12.
Genista germanica-tinctoria-group. Subcontinental. Cf. main type F, p. 61.
Genista sagittalis-group. Suboceanic montane; cf. Bartsch 1940.

Baltic-submontane German series (cf. p. 62).
Callunion balticum.
Galium saxatile-Carex arenaria-group. Suboceanic; cf. main type G, p. 62 and Tables 13—15.
Lycopodium complanatum-Carex ericetorum-group. Subcontinental northerly. Main type H, p. 67 and Table 16.
Filipendula hexapetala-group. Subcontinental southerly; cf. main type I, p. 72 and Table 18.

Euoceanic series (cf. B. 1940, p. 45).
Ericion cinereae, a rather northerly alliance including heaths of the Faroes, West Norway, the British Islands, and northern France.
Erica cinerea-group. Northernmost main type, cf. Nordhagen 1921; B. 1940, Table 2 (excl. Nos. 1 and 4).
Ulex gallii-europaeus-group. More southerly type; examples in Pethybridge and Praeger 1905, Tüxen and Diemont, and Lemée l. c.
Ericion scopariae, the southernmost heath alliance occurring in France (Les Landes), Spain and Portugal. Transitions to Mediterranean *Maquis* are numerous.
Erica vagans-group. Rather northerly type, extending to Cornwall and North-France (cf. Rübel 1930).
Erica scoparia-group; cf. Mentz 1911, Weevers 1938, and Allorge, 1941.

In order to make clear the distribution of the main types and alliances, we may arrange them in a diagram (p. 107). Here, the series are separated by wide intervals, while the alliances in each series are separated by lines, only. Transitions between the different series, alliances, and main types occur mainly in such cases where they border on each other or are placed close to one another. The diagram shows only the main distribution; thus, *Genistion* heaths may occur locally in the areas otherwise occupied by *Empetrion boreale,* and rather continental heath types may sometimes find suitable habitats within areas dominated by the euoceanic series. In most cases, all main types of the same series may occur in the same heath area and, sometimes also, heaths from different series are intermingled in the same locality. The diagram, consequently, is only a survey and shows the climatic relations of the different types. Owing to many differences in microclimate and soil, several heath types are able to grow side by side within all larger heath areas.

In the survey, the central European, alpine-subalpine dwarf shrub heaths are



Survey of dry heath communities of Europe

excluding central and south European alpine heaths.
The transitions to more continental communities indicated.

not considered. For details regarding these heaths, the reader is referred to Pallmann and Haffter (1933), Gams (1936 and 1940), and Scharfetter (1938).

Corresponding to the *Phyllodoco-Myrtillion* of alpine Scandinavia, Gams (1936) mentions a *Myrtillion* containing *Vaccinieta Myrtilli* and *Rhododendreta ferruginei*. His *Empetro-Vaccinion, Calluna-Loiseleurion* and *Cladina-Alectorion* in the Alps obviously correspond to the *Loiseleurieto-Arctostaphylion* of Scandinavia. The *Kobresieto-Dryadion* of Scandinavia in the Alps is represented by *Ericeta carnea* and *Dryadeta*. Between this basiphilous *Ericion carneae* and the acidophilous alliances, a *Junipero-Arctostaphylion* (with *Junipereta sabinae* and *Arctostaphyleta uva ursi*) is inserted.

Most acidophilous alliances seem to be characterized by subcontinental suboceanic, or indifferent species and may, thus, correspond to the *Myrtillus* group and the *Loiseleurieto-Arctostaphylion*. However, it is possible that oceanic *Myrtillion* heaths occur in oceanically influenced parts of the chain. Owing mainly to the occurrence of a number of endemic or central European alpine species with small areas, the writer has unfortunately been unable to make the plant-geographical relations of the heaths of the Alps quite clear. Undoubtedly, the microclimatic hygric continentality increases from *Myrtillion* to *Loiseleurion*; cf. the evaporation data in Pallmann and Haffter (1933, Fig. 14) and, consequently, a number of narrow-ranging alpine species used as character species for some vegetations may be rather limited to certain microclimates and may be termed oceanic and continental. An incomplete attempt to realize the climatic floristic elements of the Alps was made by Scharfetter (l. c., p. 270). It is worth mentioning that Pallmann and Haffter use the continental lichens as differential species of the *Loiseleurietum* against the *Empetreto-Vaccinietum*. Furthermore, it may be remarked that *Arnica montana* and *Luzula silvatica* in the alpine *Myrtillion* reach their optimal development.

The southern-continental behaviour of the *Ericion carneae* is very clear. *Erica carnea* is a South European pontine species. It is followed by such plants as *Polygala chamaebuxus, Daphne cneorum,* and *Genista pilosa,* and in the *Pinus* woods of the Alps rich in *Erica carnea* we may, according to Schmid (1936), find continental species as such *Carex ericetorum, Pulsatilla vulgaris, Prunella grandiflora, Anthericum ramosum, Peucedanum oreoselinum,* and *Cynanchum vincetoxicum*. Still more important is the southern continental element in the "Friaulische Heide" (*Erica carnea*-steppe heath) south of the eastern Alps (Scharfetter, l. c., p. 54).

II. Wet heath and bog communities.

Atlantic series.

Ulicio-Ericion tetralicis.

Myrica-Narthecium-group. Northern-oceanic; cf. main type J, p. 81 and Tables 20, 21.

Empetrum-Vaccinium uliginosum-group. Northern; cf. main type K., p. 85 and Tables 21—23.

Oxycoccus-Eriophorum vaginatum-group. Northern-subcontinental species present. Cf. main type L, p. 95.

Erica tetralix-group. Southern, not extremely oceanic. Main type M, p. 94, Table 25.

Ulex nanus-Erica ciliaris-group. Very oceanic and southerly; cf. text p. 94 and 116.

Subatlantic-subcontinental series.

Oxycocco-Andromedion.

Betula nana-group. Alpine-subalpine; cf. p. 98 and Booberg 1930, Nordhagen 1936, and Table 1, Nos. 17—18.

Scirpus caespitosus-group. Northerly-suboceanic. Main type N, p. 97, Table 26.

Empetrum nigrum-Oxycoccus-group. Subcontinental northerly element rather important; cf. main type O, p. 97 and Table 27.

Callunio-Juncion squarrosi. Suboceanic, rather southerly; cf. text p. 103. Main type P.

Continental series.

Ledio-Chamaedaphnion; cf. the text, p. 103.

In the case of the wet heath-bog communities, no diagram is required, the three series being separated by the boundaries of *Ledum-Erica-Narthecium* and *Chamaedaphne-Scirpus caespitosus* (cf. p. 102). More different groups may frequently be represented in the same bog or wet heath. In the areas near the border lines, sociations belonging to different series grow side by side (e. g. *Scirpus caespitosus* bogs in the area dominated by *Ledio-Chamaedaphnion* communities.)

Raunkiær was the first plant-geographer to use statistical methods on a large scale. He introduced the life form spectra based upon numbers of species (when used for the total flora of a region) or upon frequency percentages (vegetational types). In many cases, such life form spectra have proved to be of great value for the description and limitation of vegetation. In the case of the heath and bog vegetation, however, only comparatively small fluctuations in the percentages of chamaephytes, hemicryptophytes, and geophytes occur and, consequently, any classification of heaths or bogs can hardly be carried out on the basis of life form spectra. On the other hand, this is more probable by means of spectra of distributional types (cf. Mølholm Hansen 1930, B. 1933, 1938, 1940). Such spectra may be based upon the list or number of species in the vegetation, on the constancy percentage, or on the frequency percentage (for main types, average frequency percentage). When more than one size of sample areas is used (cf. p. 7), it is possible to calculate spectra based upon the frequency within the large and the small circular area (B. 1940). In the following, spectra based upon numbers of species, constancy, and frequency are used. The distributional type spectra are worked out in order to make the characterization and limitation more exact.

Dry heath communities.

1. Arctic-alpine series (cf. p. 105).

In Table 28, 9 alpine heath spectra are collected; the analyses used as a basis for the calculations are as follows.

Table 28. Arctic-alpine series.

	Constancy pCt.								
	1	2	3	4	5	6	7	8	9
Arctic alpine suboceanic (a, o)	16	15	8	10	30	26	10	4	—
Subarctic subalpine-temperate suboceanic (b, s, o)	16	7	—	2	—	—	6	5	—
Total suboceanic	**32**	22	8	12	30	26	16	9	0
Arctic alpine continental (a, c_1)	—	—	—	—	—	—	1	8	9
Arctic alpine subcontinental (a, c_2)	—	5	18	11	10	2	18	17	33
Subarctic subalpine subcontinental (b, c_2)	—	2	—	2	—	—	—	1	—
Total continental	0	7	18	13	10	2	19	**26**	**42**
Arctic alpine indifferent (a, x)	30	43	50	54	60	70	49	54	51
Total Arctic alpine	46	63	76	75	**100**	**98**	78	**83**	**93**
Subarctic subalpine-temperate indifferent (b, s, x)	38	27	24	20	—	2	16	10	7
Total subarctic subalpine-temperate	**54**	**36**	**24**	**24**	0	2	**22**	16	7
Indeterminable	—	—	—	—	—	—	—	1	—
Continental arctic alpine lichens	—	—	—	—	—	!	!	—	—
	Rhacomi-tr. group	Phyllodoco-Myrtillion			Loiseleurieto-Arcto-staphylion		Kobresieto-Dryadion		

1. B. 1937b, Table 6, Nos. 3—5. *Empetrum-Vaccinium myrtillus-Rhacomitrium hypnoides* soc. Faroes. Frequent occurrence of *Galium saxatile, Thymus serpyllum, Festuca vivipara, Alchemilla alpina.*
2. This paper, Table 1, Nos. 9—16.
3. Nordhagen, 1936, pp. 72—73, No. 5. *Empetrum-Cladonia silvatica* soc. Sikkilsdal, Norway.
4. Nordhagen, l. c., pp. 72—73, No. 1. *Vaccinium myrtillus-Betula nana-Cladonia silvatica-Jungermannia lycopodiodides* soc. Sylene, Norway.
5. Nordhagen, l. c., pp. 66—67, No. 1. *Loiseleuria-Diapensia-Cesia-Ochrolechia* soc. Northern Scandinavia.
6. Nordhagen, l. c., pp. 66—67, No. 3. *Loiseleuria-Vaccinium uliginosum-Arctostaphylos alpina-Alectoria ochroleuca* soc. Sikkilsdal, Norway.
7. Nordhagen, l. c., pp. 38—39, No. VII. *Rhododendron lapponicum-Alectoria ochroleuca* soc. pH 5.3. Central southern Norway. Not typical; on rather acidic soil.
8. Nordhagen, l. c., pp. 38—39, No. VIII. *Cassiope tetragona-Dryas-Hylocomium splendens* soc. pH 6.1—5.6. Northern Scandinavia.
9. Nordhagen, l. c., pp. 38—39, No. X. *Arctostaphylos uva ursi-Dryas* soc. pH. 7.8. Northern Norway.

The spectrum reveals that a classification by means of distributional types of the arctic-alpine heath types mentioned by Nordhagen and du Rietz is evidently justified. As a whole, *Myrtillion* is more subarctic than the two other alliances. In the case of the Faroe heath, it is clearly very oceanic. The percentages of oceanic plants are also high in the *Loiseleurieto-Arctostaphylion*; here, however, a number of important continental lichens occur. The transition heath No. 7 is separated from the typical *Dryadion* heaths by low percentages of continental plants. It is otherwise not separated from the *Myrtillion* heaths with regard to the percentages of distributional types of flowering plants. If, however, spectra considering the distribution of mosses and lichens were at hand, they would be clearly different, No. 7 having a comparatively high value for continental lichens. As regards the distribution of arctic and alpine plants, cf. the papers by BLYTT and other Scandinavian authors, and B. 1938.

Table 29. Scano-Danish (Scotch) series.

	Constancy pCt.							Average frequency pCt.					
	1a	2	3a	4a	5a	6a	7a	1b	3b	4b	5b	6b	7b
Oceanic (o_1) ... } s	3	—	—	4	3	4	8	(1)	—	4	+	—	1
Suboceanic (o_2) ... } s	4	4	8	15	9	6	11	2	8	26	7	(1)	5
Suboceanic widely distrib. (o_3) ... } s	7	8	13	15	37	20	16	6	16	22	39	41	20
North. (montane) oceanic (b, o)	**6**	**15**	2	1	—	2	1	**9**	3	2	—	—	—
Southern oceanic-suboceanic calculated separately (sdo)	—	—	—	3	—	6	**15**	—	—	4	—	—	5
Total oceanic ...	20	27	23	35	49	32	36	18	27	**54**	**46**	**42**	26
Continental-subcontinental (s, c)	—	—	3	2	—	—	3	—	1	—	—	—	1
Northern cont.-subcont. (b, c).	2	—	2	—	—	9	12	2	1	—	—	1	31
Total continental ...	2	0	5	2	0	9	**15**	2	2	0	0	1	**32**
Northern indifferent (b, x)....	24	37	21	16	18	24	15	42	28	31	44	38	24
Total northern ...	32	**52**	25	17	18	35	28	**53**	32	33	44	39	**55**
Widely distrib. central European, indifferent (s, x) ...	54	36	50	47	33	35	33	**38**	**42**	14	10	19	18
Oceanic bryophytes ...	!	!	(!)	—	—	—	—	!	(!)	—	—	—	—
	Cornus Blechnum-group		*Myrtillus*-group	*Empetrum Vacc. vitis idaea*-group			*Arctostaphylos uva ursi*-group	*Cornus Blechnum*-group	*Myrtillus*-group	*Empetrum Vacc. vitis idaea*-group			*Arctostaphylos uva ursi*-group
	A-type *Myrtillion*			B-type *Empetrion*			C-type *Empetrion*	A-type *Myrtillion*		B-type *Empetrion*			C-type *Empetrion*

2. Scano-Danish (Scotch) series.

The distributional type spectra (Table 29) are based upon analyses mainly published in this paper. The figures refer to the following heaths.

1. *Empetrum-Vaccinium-(Cornus)-Hylocomium loreum* soc. and related sociations, B. 1940, Table 1, Nos. 1—5 (constancy values), Nos. 3—5 (average frequency values), and NORDHAGEN 1917, pp. 87—88, Nos. I—IV.
2. Table 3, Nos. 1—20.
3. Table 2, Nos. 6—14, and 16.
4. Table 8a, Nos. 1—10.
5. Table 6, Nos. 1—6.
6. Table 5.
7. Table 9.

In this case too, the spectrum gives a valuable characterization of the different alliances with their subtypes. There are rather large differences between the constancy and the average frequency values. Mostly, the differentiation of the various types is more distinct if frequency is used. The low values of oceanic and southern (Dutch-German) oceanic plants are noteworthy. Only in the dry *Arctostaphylos* heath exposed to the south, are the southern species able to reach rather high constancy values. The *Empetrum-Vaccinium vitis idaea* heaths (type B) have larger frequency values for oceanic plants than the other heaths. This may be significant in the case of separation of the B-type from other types. The A-type in the same manner as the *Phyllodoco-Myrtillion*, contains rather oceanic heath types which, however, mainly show their oceanic behaviour by a large content of oceanic bryophytes (cf. p. 27).

3. Dutch-German and Baltic submontane series.

Table 30, Nos. 1—4 (Dutch-German series), Nos. 5—9 (Baltic submontane series).

1. *Genista anglica*-group. "*Calluneto-Genistetum typicum*", 22 analyses made by TÜXEN 1937 (p. 117). Not considered are *Pinus*, *Quercus*, and *Betula*.
2. *Calluna-Deschampsia flexuosa* heath of Randbøl Hede, cf. B. 1941a, Table 37, Nos. 1—4. This vegetation forms a transition between the *Genista anglica* and the *Genista pilosa-Sarothamnus*-groups.
3. *Calluna-Genista pilosa* heath. "*Genisteto-Callunetum*", 9 analyses made by LIBBERT 1936 (Table IV).
4. *Calluna-Antennaria* heath. 9 analyses made by TÜXEN 1937 (p. 121).
5. *Calluna-Deschampsia-Carex arenaria* (or *Galium saxatile*) sociations, cf. Table 13 (main type G).
6. *Calluna* heaths of the I-main type. Table 18.
7. *Calluna-Lycopodium complanatum* heath. Main type H. Table 16, Nos. 1—5.
8. "*Xerocallunetum typicum*". 6 analyses made by JURASZEK 1928 (Table 5a).
9. *Calluna-Cladina* heath of Tunåsen at Upsala. 11 analyses made by DU RIETZ 1930 (Table 6). Continental, arctic alpine lichens are very important in the ground layer.

The table shows decreasing values for the oceanic plants from left to right. No. 4, the *Calluna-Antennaria* heath, forms a transition between the two series; it ought perhaps to have been placed in the *Callunion*, but it contains scattered *Genista pilosa* and not rarely *Genista germanica* (cf., moreover, p. 65). The three main types belonging to *Callunion* are separated by the content of continental and northern

Table 30. Dutch-German and Baltic submontane series.

	Constancy pCt.				Constancy pCt.				
	1	2	3	4	5	6	7	8	9
Oceanic (o_1) } s	**16**	3	—	—	—	—	—	—	—
Suboceanic (o_2) } s	11	12	10	1	9	4	3	—	—
Suboceanic widely distrib. (o_3) } s	32	28	22	34	17	12	17	29	16
Northern oceanic (b, o)	—	3	—	—	—	—	—	—	—
Southern oceanic-suboceanic calculated separately (sdo)	**20**	**15**	8	1	—	—	3	14	—
Total oceanic	**59**	**46**	**32**	**35**	26	16	20	29	16
Continental (c_1) } s	—	—	—	—	3	6	—	8	—
Subcontinental (c_2) } s	—	—	—	3	3	19	7	2	10
Subcontinental widely distrib. (c_3) } s	1	2	—	—	2	14	—	—	—
Northern continental-subcont. (b, c)	—	—	—	—	—	—	**21**	**12**	**14**
Southern continental-subcontinental calculated separately (sdc)	—	—	—	3	1	4	—	9	10
Total continental	1	2	0	3	8	**39**	**28**	**22**	**24**
Northern and submontane indifferent (b, x)	1	9	7	10	8	—	28	—	11
Total northern	1	9	7	10	8	0	**49**	**12**	**25**
Southern indifferent (sdx)	4	—	—	—	—	—	—	—	—
Total southern	**24**	15	8	4	1	4	3	**23**	10
Widely distrib. centr. Europ., indifferent (sx, sbx)	36	43	64	52	57	46	24	50	39
Indeterminable	—	—	—	—	—	—	—	—	10[1]
	Genistion (typical only Nos. 1—3)				Callunion balticum				

[1]) "Breitblättriges Gras".

species. The heaths from Poland and Sweden are peculiar, having both northern and southern continental plants (cf. p. 70) and lacking suboceanic plants. The latter are difficult to separate from the *Arctostaphylos* group of the *Empetrion* (Table 29, No. 7 a) and this fact also appears from the values in the spectra.

4. Euoceanic series.

Table 31, Nos. 2—9. The heaths are arranged from south to north. For comparison, the oceanic group of the *Myrtillion* is placed to the right in the table (Nos. 10—11).

1. *Erica scoparia-Lavandula stoechas* vegetation with much *Calluna*. Département de l'Hérault. Analyses made by Braun-Blanquet 1926. *Erica scoparia* dominant, *Calluna* and *Cistus salvifolius* very frequent.

Table 31. Euoceanic series (Nos. 2—9).

	Number of species pCt.											Constancy pCt.						
	1	2	3a	4	5	6a	7a	8a	9a	10a	11a	3b	6b	7b	8b	9b	10b	11b
Oceanic (o_1) …… } s	3	**27**	**29**	**29**	18	8	9	14	11	9	4	**32**	18	13	16	13	3	3
Suboceanic (o_2) … } s	3	15	—	—	18	17	14	11	9	9	5	—	11	16	17	11	9	4
Suboceanic-widely distrib. (o_3) …. } s	11	8	6	4	18	8	12	14	13	7	5	12	14	14	16	15	7	7
Northern oceanic (b, o)	—	—	—	—	—	—	2	3	1	7	5	—	—	1	3	2	8	6
Southern oc.-suboc. calcul. separately (sdo).	3	**25**	18	**22**	18	8	4	3	—	—	—	18	12	6	3	—	—	—
Mediterranean-oceanic (oL) ……………	8	**17**	**18**	**13**	—	—	—	—	—	—	—	**21**	—	—	—	—	—	—
West Mediterranean (WMe)………….	8	6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Total oceanic ……	30	**73**	**53**	46	**54**	33	37	42	34	32	19	**65**	43	44	52	41	27	20
Continental (c_1) .. } s	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Subcontinental (c_2) } s	—	1	—	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Subcont.-widely distrib. (c_3) …. } s	5	—	—	—	5	—	2	—	—	—	—	—	—	1	—	—	—	—
Northern subcont. (b, c)	—	—	—	—	—	—	—	—	2	2	4	—	—	—	—	1	1	2
Total continental ..	8	1	0	4	5	0	2	0	2	2	4	0	0	1	0	1	1	2
Northern indiff. (b, x).	—	—	—	—	0	2	2	11	7	9	16	—	1	3	18	3	15	24
Total northern…..	0	0	0	0	0	2	4	14	8	**18**	**21**	0	1	4	**21**	0	**24**	**32**
Southern centr. Europ., indifferent (sd, x) …	8	3	—	25	—	3	—	—	—	—	—	—	2	—	—	—	—	—
Mediterranean (Me) …	**36**	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Total southern…..	**53**	**54**	**36**	**60**	18	11	4	3	0	0	0	**39**	14	6	3	0	0	0
Widely distrib. central. Europ., indiff. (sx, sbx)	0	20	47	25	36	62	59	47	56	56	61	35	54	52	30	55	57	54
	Transition to Maquis	Ericion scopariae			Ericion cinereae					Myrtillion boreale oceanic group		Ericion scopariae	Ericion cinereae				Myrtillion boreale oceanic group	

2. *Ulex-Erica* heath, very rich in species. Northern Spain, "Lande a Ajoncs, Bruyères et Graminées euatlantiques", cf. Allorge 1941 b, pp. 321—322. In the list of plants occur, e. g., *Dabeocia polifolia, Erica scoparia, vagans, arborea*, and *Cistus salvifolius.*
3. *Calluna-Erica cinerea-Ulex europaeus* and *Erica scoparia-Molinia*-sociations 8 analyses from "Les Landes" made by Weevers 1938 (p. 116).
4. *Erica vagans-Ulex* heath. Lizard Point Cornwall. 1 analysis, cf. Rübel 1930 (p. 123).
5. *Ulex europaeus* heath. West France, massif de Multonne. Allorge 1926 (pp. 10—11).
6. *Calluna-Erica cinerea-Ulex europaeus* heath. Perche, North France. 10 analyses made by Lemée 1937 (pp. 550—551).
7. *Ulex gallii* heath. Eire, so. o. Dublin. 7 analyses. Pethybridge and Praeger 1905 (p. 154).
8. *Calluna* heath. Eire, so. o. Dublin. 9 analyses by Pethybridge and Praeger l. c. (pp. 161—162). The vegetation is montane and a typical, rather wet moor, containing *Juncus squarrosus* and other plants of wet soil.

9. *Calluna-Erica cinerea* heath. The Faroes. B. 1940 (Table 2, Nos. 2—3, 5—8) and W. Norway, NORDHAGEN 1921 (p. 100).
10. *Calluna* heath rich in *Juniperus communis; Erica cinerea* very scattered. 7 analyses from Rundöy in West Norway, GOKSÖYR 1938 (p. 161).
11. Oceanic variety of *Myrtillion boreale*. 9 analyses taken from B. 1940 (Table 1, Nos. 1—5), NORDHAGEN 1917 (pp. 87—88).

Although this series is placed along the Atlantic coast, the percentages of total oceanic species do not lie at the same level. A decrease from south to north is noticeable and, if we continue north of or above the true oceanic regions (Nos. 10—11), this decrease is evident. A similar decrease is found where the heaths merge into Mediterranean scrub vegetation (No. 1). The two alliances belonging to the euoceanic series are clearly separated by the high values for total southern, oceanic, and Mediterranean oceanic, and the absence of northern species. In spite of the rather high percentage of northern species, the montane *Callunetum* from Eire (No. 8) may belong to *Ericion cinereae*. It contains a good deal of *Erica cinerea* and scattered *Ulex gallii*, but is otherwise a heath which seems to be intermediate between wet and dry heaths.

The *Erica scoparia-Lavandula* vegetation (No. 1) cannot be classified as a heath; it is rather a Mediterranean shrub vegetation with much *Calluna*. In this as well as in several other cases, it is, however, extremely difficult to establish a limit for the heath vegetation (cf. p. 49). We may take into consideration the large continent of Mediterranean species and resolve that such vegetations are not heaths; we are unable to state how many Mediterranean plants are required to justify the denotation of Mediterranean shrub vegetation. Undoubtedly, a vegetation containing so many southern plants must grow on rather fertile soil and, probably, we should be able to classify heaths and Mediterranean shrubs by studying the soil. However, this would hardly lead to any clear separation, since gradual transitions from podsolated heath soils to other soils occur.

In the same manner, it is very difficult to place the *Ulex europaeus* shrubs which occur in western Europe. From the data in PETHYBRIDGE and PRAEGER (l. c., p. 151), it is doubtful whether the *Ulex europaeus* vegetation should have anything to do with heath vegetations. It contains about 80 species, 12 of which are common heath plants. The vegetation is very rough, 5—10 feet in height, with small trees and climbing shrubs, and with lanes and patches of grass. The flora comprises *Ilex aquifolium* and shade plants such as *Primula vulgaris* and *Arum maculatum*. A similar picture is obtained from a study of the plant list of the *Ulex europaeus* vegetation from Belle-Ile-en-Mer (cf. GADECEAU 1903, pp. 320—321) although this vegetation approaches true heaths. The latter contains many heath plants (*Pteridium, Erica vagans, Erica cinerea, Sarothamnus, Genista tinctoria, Hypericum pulchrum, Polygala serpyllacea, Sieglingia, Veronica officinalis*) and, furthermore, e. g. *Betonica officinalis* (also heaths in Cornwall and S. France), *Filipendula hexapetala, Digitalis pupurea*, the euoceanic *Hypericum linarifolium*, and the Atlantic Mediterranean *Gladiolus illyricus*. In both cases, the *Ulex gallii* vegetation are more typical heaths and must be classified as heaths. According to Pettybridge and Praeger, the upper limit of *Ulex europaeus,* where it is succeeded by *Ulex gallii,* is often climatic and a result of exposure. Elsewhere, it is an edaphic phenomenon caused by the appearance of peat. The *Ulex gallii* vegetation of Belle-Ile-en-Mer contains e. g. *Erica cinerea, vagans, Helianthemum guttatum* (mediterranean oceanic), and *Simethis bicolor* (submediterranean oceanic).

Wet heath and bog communities.

In Table 32, the constancy values of 19 different wet heaths or bogs are tabulated. The figures refer to the following vegetations.

1. A number of *Molinia-, Schoenus nigricans-* or *Juncus silvaticus* vegetations from Les Landes (Weevers 1938, Relevé D—G). The vegetations are closely related or belong to the *Ulex nanus-Erica ciliaris* wet heath group containing much *Carum verticillatum, Wahlenbergia hederacea,* and others.
2. *"Tetraliceto-Ulicetum nani".* 8 wet heath analyses from Perche made by Lemée (1937, Table 52). It contains i. a. *Erica ciliaris* and *Lobelia urens.*
3. *"Tetraliceto-Sphagnetum".* 15 bog analyses by Lemée (1937, Table 50), containing e. g. *Carex binervis, Erica ciliaris, Circium anglicum, Juncus silvaticus* (constancy per cent 93), *Ulex nanus,* and *Schoenus nigricans.*
4. *Scirpus caspitosus-Erica tetralix-Sphagnum* bog. Wahner Heide. 10 analyses made by A. Schumacher (1932, p. 23).
5. *"Ericetum tetralicis cladonietosum".* 18 analyses from N.W.-Germany made by Tüxen (1937, p. 112).
6. *"Ericetum tetralicis typicum".* 20 analyses by Tüxen (l. c., pp. 110—111).
7. *Erica tetralix* heaths. This paper, Table 22, Nos. 1—10.
8. *Erica-tetralix* heath. Nørholm Hede in Denmark. 10 analyses by Mølholm Hansen (1932, Table 6a).
9. *Erica tetralix* heath. Randbøl Hede in Denmark. 10 analyses. B. 1941a.
10. *"Sphagnetum medii subatlanticum"* (with *Erica tetralix*). 9 analyses by Tüxen (l. c., pp. 113—114).
11. Bogs with *Erica tetralix.* Denmark. 3 analyses from Nørholm Hede by Mølholm Hansen (l. c., Table 7a, Nos. 6—8) and 2 from Store Vildmose by K. Jessen (1939, p. 661).
12. *Erica-Cladina* soc. of Komosse in Sweden. 22 analyses by Osvald (1923, pp. 96—97).
13. *Calluna-Sphagnum magellanicum* soc. Komosse. 40 analyses by Osvald (l. c., pp. 120—121).
14. Wet heath from W.-Norway. 20 analyses made by Goksöyr (1938, Table 14).
15. *Myrica-Narthecium* heath or bog. This paper, Table 20, Nos. 1—3, and Mølholm Hansen (l. c., Table 7a, Nos. 9—10).
16. Wet heath from S.E.-Denmark (Ulvshale). 9 analyses by B. (1942, Table 4, Nos. 1—7, 20—21).
17. Bog vegetation from North Sealand (C. Olsen), cf. Table 27.
18. *"Oxycocco-Empetrion hermaphroditi".* 8 constancy investigations from Norway (Sylene, Sikkilsdal). Nordhagen (1936, pp. 80—81).
19. *Ledum palustre* bog from Bosekop in Alta. Nordhagen (l. c., p. 78).

The different groups of the Atlantic series are characterized by southern oceanic and oceanic species (*Ulex-Erica ciliaris*-group), oceanic and widely distributed species (*Erica tetralix*-group), oceanic and northern species (*Empetrum-Vaccinium uliginosum*-group), northern oceanic and northern (*Myrica-Narthecium*-group), oceanic, sub-

Table 32. Wet heath and bog communities.

	Constancy pCt.																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Oceanic (o_1) } s	**43**	**30**	**26**	13	18	13	9	13	12	15	12	20	7	2	8	—	—	—	—
Suboceanic (o_2) } s	10	11	12	13	15	13	5	3	7	—	—	—	—	1	—	12	—	—	—
Suboceanic-widely distrib. (o_3) } s	8	10	8	**27**	**30**	19	20	**27**	19	10	19	**27**	**24**	12	8	20	20	7	—
Northern oceanic (a and b, o)	—	—	3	—	2	1	7	—	1	—	—	—	1	—	**17**	—	—	3	—
Southern oceanic calculated separately (sd,o)	**33**	**28**	**24**	4	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
Mediterranean oceanic (oL)	5	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Total oceanic	**66**	**51**	**50**	**53**	**65**	46	41	43	39	25	31	47	32	15	33	32	20	10	0
Subcontinental-central European (s, c_{2-3})	3	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Continental northern (a and b, c_1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	**10**
Subcontinental northern (a and b, c_{2-3})	—	—	—	—	—	(1)	—	4	—	19	12	28	25	3	—	—	5	26	31
Total continental	3	2	1	0	0	(1)	0	4	0	19	12	**28**	**25**	3	0	0	5	**28**	**41**
Northern indifferent (a and b, x)	—	—	1	—	2	1	15	13	12	17	31	22	28	20	20	1	62	57	53
Total northern	0	0	4	0	4	2	22	17	13	**36**	**43**	**50**	**53**	23	37	1	**67**	**85**	**94**
Southern indifferent (sdx, Me)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Total southern	**38**	**28**	**25**	4	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
Widely distrib. centr. Europ. indiff. (sx, cbx)	28	47	48	46	33	53	45	40	47	39	26	2	15	**61**	47	**67**	13	4	6
Indeterminable	3[1]	—	—	1[2]	—	—	-	—	—	—	—	—	—	—	—	—	—	—	—
	Ulex nanus-Erica ciliaris-group			Erica tetralix-group			Empetrum-Vaccinum uliginosum-group			Oxycoccus-Erioph. vaginatum-group				cf. text	Myrica-Narthec.-group	Callunio-Juncion squarrosi	Empetrum Oxycoccus-group	Betula nana-group	Ledio-Chamaedaphnion
	Ulicio-Ericion tetralicis																Oxycocco-Andromedion		
	Atlantic series															Subatl. Subcont. series			Continent. series

[1] *Carex* sp.
[2] "*Orchis sphagnicolus*".

continental and northern species (*Oxycoccus-Eriophorum*-group). For comparison, a West-Norwegian wet heath community is included (No. 14). Here, the number and percentage of oceanic species is low and the percentage of northern species is rather high. This fact indicates that from south to north the oceanity and the importance of the oceanic element decrease in spite of the close vicinity of the ocean.

The different groups of the subatlantic-subcontinental series are characterized by suboceanic and no continental, suboceanic and northern, and subcontinental, northern, and suboceanic species. Finally, the continental series shows an isolated position, having no oceanic and 10 per cent very continental species.

Table 33. Comparison of dry heath with wet heath and acidic heathlike meadow. Material from Denmark and S. Sweden.

	Average frequency per cent						
	Tab. 29, 6 b	Tab. 29, 5 b	Tab. 29, 4 b	Tab. 32, 7	Tab. 32, 8	Tab. 22 13—15	4 Analyses
Oceanic (o_1) ... } s	—	+	4	**17**	**28**	**18**	**25**
Suboceanic (o_2) ... } s	(1)	7	26	2	(0.4)	1	7
Suboceanic widely distrib. (o_3) } s	41	39	22	14	24	23	21
Northern oceanic (b, o) ...	—	—	2	5	—	—	2
Total oceanic ...	42	46	54	38	52	42	55
Northern subcontinental (b, c) ..	1	—	—	—	2	—	—
Northern indifferent (b, x) ...	38	44	31	23	11	9	—
Total northern ...	**39**	**44**	**33**	28	13	9	2
Widely distrib. central European indifferent (s, x) ...	19	10	14	**38**	**35**	**49**	**45**
	Dry heath			Wet heath			*Deschampsia setacea-* or *Lycopodium inundatum-* soc.

Comparisons of the Tables 29—32 indicate that no general separation of wet and dry heaths is possible when applying the distributional type spectra. On the other hand, a very distinct difference is observed in most cases when wet and dry heaths inhabiting the same region are compared. Thus, the percentages of oceanic (euoceanic, not total oceanic) species increases on passing from dry to wet heaths. In particular, this is evident from the average frequency values of Table 33. Here, the dry heath is characterized by northern, the wet heath and the acidic meadows by oceanic and widely distributed plants. A close relationship between wet heaths and meadows is furthermore found, these communities being separated only by the values for northern species. The very same increase in oceanic species from dry to wet heaths is observed on comparing constancy percentages for euoceanic and Scano-Danish heaths. In "Les Landes", France, the difference between the percentages of oceanic species in dry and wet heaths amounts to 14 %, in northern France (Perche) it is 18—22 %, and in Denmark it is on an average 7 %. If frequency values were at hand, the same difference would undoubtedly be demonstrable also in the case of the north-west German heaths. The constancy spectra here show no difference with regard to the oceanic species but, at the same time, they exhibit a distinct difference in the values for southern oceanic plants, reaching 20 % in dry heath and 0 % in wet heaths.

VIII. Index of species and communities mentioned in parts I and II of Studies on the Plant-Geography of the North-Atlantic Heath Formation.

NB. Only important or typical elements of heaths, bogs or related communities included. As a rule, the names of plants in the tables are not indexed. Exceptions are made, however, for some of the more important species which are not mentioned in the accompanying text. I: B. 1940; II: the present paper.

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