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

I. THE HEATHS OF THE FAROES

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1. Introduction.

A journey to the Faroes in 1935 gave me an opportunity to study the heath vegetation[1] more closely, and later (1938) I saw allied heaths in Norway. The material collected forms the basis of a number of comparisons of heath vegetation at the northern Atlantic, followed by an attempt to compare heath vegetation in various localities along the whole of the Atlantic Coast of Europe, especially within the area of distribution of *Erica cinerea*. Finally, the ecology and plant geography of some heath plants from the Faroes and western Norway will be subjected to a more detailed investigation.

2. Analyses of Heaths "heathermoors" in the Faroes.

OSTENFELD (1907) was the first to deal with the heath of the Faroes. He pointed out some of its essential features: "The appearance and occurrence of the heath absolutely

[1] TANSLEY (1939) makes a distinction between heath and heather-moor. The latter is distinguished by a "marked preponderance of species of non-vascular plants which depends closely on damp air"; it is most frequent at higher altitudes on deep acid peat, whereas the heath is developed on sandy or gravelly soil with a minimum of peaty humus. However, it seems difficult to maintain a definite distinction between heath and heather-moor, as according to TANSLEY there is a very "substantial community" between them. The Faroes heath is undoubtedly rather of the character of heather-moor, but nevertheless we will in the following only use the one designation, *viz.* heath, which thus also will be made to include heather-moor.

makes the impression on the spectator that it is a formation which does not thrive particularly well in the Faroes, and in consequence it must be considered exacting and particular. It requires a fairly dry soil and sun, both of which are rare commodities." These requirements can be satisfied on south-facing slopes in the lowlands. At heights of less than 300 m above the sea the vegetation is locally characterized by the heath or by related grass-communities (*Nardeta*, *Agrostideta*) full of oceanic species (cf. Böcher 1937 b).

In the Faroes it is in particular possible to distinguish between two kinds of heath: a type rich in *Empetrum* or *Vaccinium* with relatively few oceanic species (see later) and a type with many of these species.

A. The Heath rich in *Empetrum-Vaccinium*.

This type was examined in an area west of Ejde on Østerø, where there is a rather level undulating stretch surrounding a large lake. The greater part of this area was covered by grass-vegetation, most frequently dominated by *Nardus* (cf. Ostenfeld's "Hedekær" (acidic grassland)). On small slopes there were heath-sociations rich in mosses, especially *Calluna*- or *Empetrum* heath; more rarely the *Vaccinium* species were met with in larger quantities. The whole of the area was very moist, and with the exception of the drier heath-covered knolls it all presented the appearance of a large, greatly variegated heath bog. The variation was due to the inhomogeneity of the substratum. *Eriphorum polystachyum* and *Sphagnaceae* occurred in the most moist localities (e.g. turf pits); however, *Eriophorum* could also grow in the mosses on tops of low, flat hills. It is peculiar that *Eriphorum vaginatum* does not play any great part in such vegetation, seeing that this species dominates the vegetation in large parts, for instance of the British Isles ("Cotton-grass Moor", see Moss 1913).

Time did not permit to make a thorough investigation of the distribution of all sociations. The exposition seemed to exercise a rather considerable influence. Ostenfeld (l. c. p. 77) mentions how the various heath shrubs can be closely associated with southern slopes. In table 1 there is an example of the difference which can exist between a heath-covered north and south side of a low wall in that locality. The bottom layer of the heath mainly consisted of thick moss; *Cladonia*-species only occurred as extremely scattered individuals. The moss chiefly consisted of *Hylocomium* (*Rhytidiadelphus*) species, locally also with *Rhacomitrium hypnoides* as a dominant. In some cases the tops of the flat rocky knolls were covered by a cap consisting of *Empetrum-Rhacomitrium hypnoides*-soc., whereas the sides where the peat and the soil were much thicker, were covered by *Calluna-Hylocomium*-soc.

The north-facing wall (No. 3, Table 1) was particularly rich in bilberries and marsh wortleberries, the latter and *Cornus suecica* were almost only to be found here; bilberries were extremely dense (100.100.4)[1] whereas on the southern slope (No. 4, Table 1) they were scattered (90.60.0)[1] in the heather. A peculiar feature of the south-facing slope examined was the great density of *Juncus squarrosus*; I have very rarely seen this species so dense. The cause of this density is probably due to the exposition combined with favorable edaphic conditions (a thick raw humus layer and a higher degree of humidity in the soil) than in the steeper south-facing slopes, where the other type of heath occurs (cf. Table 2). The Faroes are situated at

[1] See explanation p. 38, footnote.

the northern limit of the species (fig. 132 in Böcher 1938); it hardly ever enters into the alpine vegetation, but has a pronouncedly vertical limit of frequency in the islands, at the same time as the heath decreases in frequency. The examined vegetation lay at about 200 m. above the level of the sea, in the very part where the heath disappeared as a dominant formation.

From the list of species and the spectrum (pp. 40—41) it appears that the vegetation is rather rich in boreal species. This Faroes heath type agrees very well with the English and Scotch "heathermore" rich in *Vaccinium*, as well as with the humid heath types in western Norway (see Nordhagen 1917, Goksøyr 1938), but also farther north and south there are allied types of vegetation. A subalpine *Empetrum-Vaccinium* heath, rich in mosses with *Dryas* and many temperate and arctic species (Kodlur at Ejde), forms a transition to the *Empetrum-Vaccinium* heath of south-eastern Greenland (Böcher 1937b, p. 190). There is also some resemblance with Norwegian subalpine-oceanic *Empetrum-Vaccinium* heaths; an analysis of a heath of this kind is to be found in Table 1, No. 5. It is distinguished from the Faroes-heath by being richer in lichens and boreal-arctic species. There is a rather considerable similarity with many mossy heaths in more temperate regions e. g. Denmark and western Sweden. Here such heaths, however, are closely connected with northern slopes. We find them on the heather-covered hills in central and eastern Jutland, where *Hylocomium* species (however, with the exception of *H. loreum*) and in certain regions *Cornus suecica* dominates *Calluna*-heaths rich in *Vaccinium*. The vegetation which in Danish latitudes approaches most nearly to the one mentioned above from the Faroes, is the heath on the north-facing rocky slopes of the Halland Ridge towards the Kattegat (Hovs Hallar). Here also *Hylocomium loreum* enters as a dominant in the heath. These Danish and Swedish heaths will be mentioned in a later treatise.

B. The heath rich in *Erica cinerea.*

This type of heath was especially examined on the south-western slopes at Bordö Vig, south of Klaksvig (Plate 1) and also in the area behind Thorshavn. It is most typically developed (with *Erica cinerea* dominating) in the driest and warmest localities; with increasing humidity the vegetation merges into a *Calluna*-heath without *Erica cinerea*, and this vegetation again approaches the type rich in *Empetrum-Vaccinium* (No. 4, Table 1). The six analyses from the Faroes (Table 2) are arranged in such a manner that partly at Thorshavn (1—3), partly at Klaksvig (4—6) they form the transition from *Calluna* to *Calluna-Erica cinerea* heath; Nos. 1 and 4 are *Calluna* heaths, Nos. 3 and 6 *Calluna-Erica cinerea* heaths and Nos. 2 and 5 transition heaths.

The driest and warmest places in the Faroes are the lower parts of the south-facing slopes, where inclination and exposition cause better drainage (and so less humidity and greater warmth in the soil) and a stronger influence of the rays of the sun. In the Faroes literature I have only found one indication of *Erica cinerea* outside the southern lowland heath and this (Ostenfeld 1908, p. 955) in faintly sloping acidic grassland, where it was of rare occurrence, probably in some slightly drier spot.

The *Calluna-Erica cinerea* heath is nowhere on the Faroes so luxuriously developed as e. g. at Kvala in western Norway (p. 20); this is presumably due both to climatic

Table 1. The heath rich in *Empetrum-Vaccinium*.

	The Faroes				Norway
Analysis No.	1	2	3	4	5
Method (see p. 38)	D.	—	S.	S.	S.
Height above the sea	220	230	200	200	500
Exposition	N.	SW.	N.	S.	NW.
Inclination	15—20°	rather strong	30°	10—15°	20°
Northern species:					
Empetrum nigrum (+ hermaphroditum)	5	!	100.90.3	90.30.0	100.100.4
Vaccinium myrtillus	1	!	100.100.4	90.60.0	40.10.0
— uliginosum	1	!	90.20.0	—	100.60.2
— vitis idaea	—	—	—	—	50.20.0
Arctostaphylos alpina	—	—	—	—	100.60.2
Cornus suecica (O.)	—	!	80.50.0	—	100.40.1
Carex rigida	—	—	—	—	70.20.0
Andromeda polifolia	—	—	—	—	50.30.0
Alchemilla alpina (O.)	1	—	—	—	—
Trientalis europaea	—	—	—	—	10.0.0
Temperate oceanic species:					
Calluna vulgaris	—	!	30.10.0	100.90.3	20.10.0
Juncus squarrosus	—	!	+	100.70.3	—
Narthecium ossifragum	—	!	+	20.0.0	—
Galium saxatile	1	+	—	—	—
Polygala serpyllacea	—	+	—	—	—
Blechnum spicant	+	+	—	—	—
Carex binervis	—	—	—	+	—
Temperate species:					
Potentilla erecta (O.?)	1	!	100.30.1	100.30.1	—
Nardus stricta	—	!	90.40.0	70.20.0	—
Deschampsia flexuosa	1	+	—	20.10.0	80.30.0
Molinia coerulea var. (O.?)	1	—	—	70.20.0	—
Carex stellulata	—	—	60.20.0	—	—
— panicea	—	+	—	—	—
— Goodenoughii	—	+	—	—	—
Luzula multiflora	1	+	20.0.0	10.0.0	—

Table 1 (continued).

	The Faroes				Norway
Analysis No.	1	2	3	4	5
Method (see p. 38)	D.	—	S.	S.	S.
Height above the sea	220	230	200	200	500
Exposition	N.	SW.	N.	S.	NW.
Inclination	15—20°	rather strong	30°	10—15°	20°
Festuca ovina vivipara (O.?)	—	—	40.20.0	+	—
Anthoxantum odoratum (O.?)	—	!	10.0.0	—	—
Agrostis canina var. mutica	—	—	20.0.0	—	—
Scirpus caespitosus (O.?)	—	!	—	30.10.0	+
Eriophorum polystachyum	—	!	30.0.0	10.0.0	—
Orchis maculatus	1	—	10.0.0	60.0.0	—
Rumex acetosa	—	!	+	—	—
Thymus serpyllum var. (O.?)	1	—	—	—	—
Plantago maritima (O.?)	1	—	—	—	—
Lycopodium clavatum	—	—	—	—	20.10.0
Solidago virgaurea	—	—	—	—	+
Mosses and lichens:					
Hylocomium loreum (O.)	4	!	100.100.5	100.70.1	10.0.0
— parietinum	1	!	50.10.0	80.50.1	90.50.0
— proliferum	3	!	80.50.0	50.20.0	—
Plagiothecium undulatum (O.)	—	!	60.20.0	70.50.0	—
Rhacomitrium hypnoides (O.?)	+	!	—	—	100.80.2
Polytrichum commune	—	!	100.50.1	—	60.20.0
— alpinum	—	!	—	—	—
Dicranum scoparium	1	!	30.10.0	—	40.10.0
Stereodon cupressiformis	1	—	—	30.0.0	—
Andraea petrophila	—	—	—	—	40.10.0
Frullania tamarisci (O.)	1	!	—	—	—
Blepharozia ciliaris	—	—	—	—	80.50.0

Table 1 (continued).

	The Faroes				Norway
Analysis No.	1	2	3	4	5
Method (see p. 38)	D.	—	S.	S.	S.
Height above the sea	220	230	200	200	500
Exposition	N.	SW.	N.	S.	NW.
Inclination	15—20°	rather strong	30°	10-15°	20°
Cephalozia divaricata	—	!	—	—	—
Diplophyllum albicans (O.)	—	!	—	—	—
Jungermannia quinquedentata	—	!	60.30.0	—	—
Jungermannia Floerkei	—	—	—	40.10.0	50.10.0
— ventricosa	—	—	50.20.0	—	—
Martinellia gracilis (O.)	—	!	—	—	—
Mylia Taylori (O.)	—	—	—	—	40.10.0
Kantia trichomanis	—	—	—	40.20.0	—
Cetraria islandica	—	—	—	—	100.80.2
Cladonia silvatica	1	—	—	—	90.30.0
— uncialis	—	—	—	—	30.20.0
— cf. chlorophaea	—	—	—	—	10.0.0
— rangiferina	—	—	—	—	+

No. 1: Heath at Ejde (at the lake) on Østerø. No. 2: Western side of Skaalefjordsdalen, Østerø (Jensen 1897, page 208). Nos. 3—4: Ejde (at the lake). No. 5: Blåmannen at Bergen; vegetation in a strongly exposed place with rocky ground below a thin layer of soil. In more sheltered places *Calluna* heath was found here with very nearly the same species, in more humid soil on the transition between meadow and heath: *Erica tetralix*, *Molinia*, *Nardus* and *Scirpus caespitosus*.

(O.) = Oceanic species.

(O.?) i. e. possibly represented by a special oceanic race.

and biotic conditions. In the summer the climate is cooler in the Faroes as compared with that of western Norway; add to this, that the heaths e. g. at Kvala are hardly so

Table 2. The heath rich in *Erica cinerea*.

	The Faroes						Norway	
Analysis No.	1	2	3	4	5	6	7	8
Method (see pag. 38)	D.	D.	D.	S.	S.	S.	S.	S.
Height above the sea	200	50	50	150	200	150	ca. 50	ca. 50
Exposition	SE.	S.	S.	SW.	WSW.	S.	SW.	S.
Inclination	30°	20°	20°	30°	40°	35—40°	10—15°	30—40°
Northern species:								
Alchemilla alpina (O.)	—	—	—	30.10.0	+	—	—	—
Thalictrum alpinum	—	—	—	30.10.0	—	10.0.0	—	—
Selaginella selaginoides	+	—	—	10.0.0	—	—	—	—
Empetrum nigrum	1	1	1	+	—	—	—	—
Arctostaphylos uva ursi	—	—	—	—	—	—	—	30.10.0
Vaccinium myrtillus	—	—	—	—	—	—	10.10.0	—
Silene acaulis	—	—	—	+	—	—	—	—
Temperate oceanic species:								
Erica cinerea	—	4	5	—	20.20.0	100.100.4	90.50.0	100.100.4
Calluna vulgaris	4	3	1	100.100.4	100.100.4	100.80.3	100.100.4	70.30.0
Polygala serpyllacea	1	1	+	30.10.0	30.10.0	40.20.0	30.0.0	+
Hypericum pulchrum *)	1	1	1	50.0.0	30.0.0	40.10.0	40.10.0	50.20.0
Carex binervis	—	—	—	—	10.0.0	20.0.0	+	—
Narthecium ossifragum	1	—	1	+	—	10.10.0	—	—
Juncus squarrosus	1	1	—	—	30.10.0	—	—	—
Galium saxatile	1	1	1	—	—	—	30.0.0	+
Blechnum spicant	1	—	—	—	10.0.0	—	—	10.0.0
Erica tetralix	—	—	—	—	—	—	—	40.0.0
Temperate species:								
Potentilla erecta (O.?)	3	1	1	100.50.2	80.20.0	90.20.0	100.70.2	100.30.1
Agrostis canina (incl. var. mutica)	2	1	1	80.30.0	90.50.0	90.60.0	—	—
Deschampsia flexuosa	—	—	—	—	10.0.0	—	90.40.0	—
Scirpus caespitosus (O.?)	—	—	—	40.20.0	50.10.0	70.20.0	—	+
Carex pulicaris (O.*)	—	—	—	40.10.0	—	30.10.0	—	70.10.0
Viola Riviniana (O.?)	1	1	—	80.10.0	—	30.0.0	—	40.10.0
Thymus serpyllum (O.?)	1	2	1	60.0.0	—	50.10.0	—	—
Nardus stricta	1	1	1+	20.10.0	10.10.0	40.0.0	10.0.0	—
Carex pilulifera (O.*)	1	1	1	20.0.0	20.0.0	30.10.0	10.0.0	20.0.0
Carex panicea	1+	—	—	20.0.0	—	20.10.0	—	10.0.0

Table 2 (continued).

	The Faroes						Norway	
Analysis No.	1	2	3	4	5	6	7	8
Method (see pag. 38)	D.	D.	D.	S.	S.	S.	S.	S.
Height above the sea	200	50	50	150	200	150	ca. 50	ca. 50
Exposition	SE.	S.	S.	SW.	WSW.	S.	SW.	S.
Inclination	30°	20°	20°	30°	40°	35—40°	10—15°	30—40°
Festuca ovina vivipara (O.?)	1+	1	1	50.20.0	40.10.0	40.20.0	10.0.0	+
Anthoxanthum odoratum (O.?)	1+	1	1	20.10.0	30.10.0	40.20.0	+	—
Orchis maculatus	—	—	—	—	20.0.0	10.0.0	30.0.0	+
Pinguicula vulgaris	—	—	1	20.0.0	10.0.0	+	—	—
Plantago lanceolata (O.?)	+	—	—	—	—	10.0.0	—	—
Euphrasia cfr. scotica	1	1	1	20.0.0	+	—	—	—
Luzula multiflora	—	—	—	+	+	—	—	—
Agrostis tenuis	2	1	1	—	—	—	20.0.0	—
Juniperus communis	—	—	—	—	—	—	10.0.0	50.10.0
Agrostis alba	—	—	—	—	—	—	50.0.0	—
Campanula rotundifolia	—	—	—	—	—	—	40.0.0	20.0.0
Sieglingia procumbens (O.*)	—	—	—	—	—	—	50.0.0	20.10.0
Antennaria dioeca	—	—	—	—	—	—	30.0.0	20.0.0
Molinia coerulea (O.?)	—	—	—	—	—	—	—	40.10.0
Sanguisorba officinalis	—	—	—	—	—	—	20.0.0	—
Succisa pratensis	—	—	—	—	—	—	50.10.0	—
Solidago virgaurea	—	—	—	—	—	—	30.0.0	—
Plantago maritima (O.?)	—	—	—	—	—	—	50.0.0	+
Brunella vulgaris (O.?)	+	—	—	—	—	—	—	+
Lotus corniculatus	—	—	—	—	—	—	10.0.0	—
Mosses and lichens:								
Hylocomium loreum (O.)	4	2	1	**100**.50.1	60.60.0	60.40.0	10.0.0	—
— parietinum	—	1	1	40.20.0	20.0.0	**70**.30.0	**100**.50.2	—
— proliferum	2	1	1	60.50.0	30.10.0	—	40.10.0	—
— triquetrum	—	—	—	10.0.0	—	—	—	—
— squarrosum	—	+	1	—	—	—	40.20.0	—
Stereodon cupressiformis	—	1	1	40.30.0	**80**.60.0	60.20.0	**100**.80.3	**80**.50.0
Thuidium tamariscifol. (O.)	—	—	—	**70**.60.0	—	20.10.0	**90**.20.0	20.0.0

Table 2 (continued).

	The Faroes						Norway	
Analysis No.	1	2	3	4	5	6	7	8
Method (see pag. 38)	D.	D.	D.	S.	S.	S.	S.	S.
Height above the sea	200	50	50	150	200	150	ca. 50	ca. 50
Exposition	SE.	S.	S.	SW.	WSW.	S.	SW.	S.
Inclination	30°	20°	20°	30°	40°	35—40°	10—15°	30—40°
Dicranum scoparium	—	—	—	20.20.0	—	40.0.0	50.0.0	—
Rhacomitrium hypnoid.	—	—	—	20.10.0	20.10.0	10.10.0	—	10.0.0
Leucobryum glaucum (O.)	—	—	—	—	—	—	20.0.0	—
Polytrichum juniperinum	—	—	—	—	—	—	10.0.0	—
Blepharozia ciliaris	+	1	—	60.10.0	30.10.0	50.20.0	—	—
Frullania tamarisci (O.)	+	—	+	70.30.0	40.20.0	20.0.0	80.20.0	30.10.0
Diplophyllum albicans (O.)	+	1	+	50.20.0	40.40.0	20.0.0	—	—
Nardia scalaris (O.)	—	1	—	—	—	—	—	—
Mylia Taylori (O.)	—	—	—	—	} 40.10.0	—	—	—
Martinellia gracilis (O.)	—	—	—	—		—	—	—
Scleropod. purum (O.)	—	—	—	10.10.0	—	—	10.0.0	—
Cladonia silvatica	—	—	—	—	—	—	+	+
— uncialis	—	—	—	—	10.0.0	—	—	—
— fimbriata	—	—	—	—	—	—	—	10.0.0
Bæomyces roseus	—	—	—	—	—	—	—	+

No. 1: At Thorshavn very heavily grazed. Nos. 2—3: At Thorshavn (Husaraun). Nos. 4 and 6: Bordø Vig, Torvadalsá. No. 5: Heath at Anir, Bordø. No. 7: Heath at Skudenæshavn in Karmø. The place lay near a vertical rocky wall and had, as its downward limit, a heath with *Narthecium*, *Carex pulicaris*, *stellulata*, *binervis*, *Erica tetralix*. The upper part of the soil below the heath was very rich in humus, perhaps rather of the character of peat. No. 8: Kvala at Haugesund (Plate 2). At the foot of the scree *E. tetralix* and also *Carex viridula* and *Pinguicula* were very frequent. Below the heath there was only very little humus (12,6 %), the soil was brownish down to a depth of 25—30 cm. No distinct podsolation. P_H see page 27).

O.? = possibly represented by a specially oceanic race.

O.* = slightly oceanic (suboceanic) according to Hård av Segerstad (1935).

*) = var. *procumbens* in Nos. 1—6.

heavily grazed as those of the Faroes. The extensive *Nardeta* which form a kind of mosaic with the heath patches in the Faroes, dominates entirely when the grazing becomes particularly intensive (cf. Scarth (1911), Nordhagen (1921, pp. 61—62)). That there is no heath near the villages may be due to the human exploitation of the heather plants. Thus Hornemann (1821, p. 431) writes: "In the Faroes they are used for the smoking of the meat of sheep"; more particularly, however, the heath was used as winter fodder for sheep.

A characteristic feature of the transition from *Calluna* to *Calluna-Erica cinerea* heath is the great decrease of the mosses, which fact presumably has some bearing upon the increasing desiccation, and recurs in western Norway (Table 2, Nos. 7—8) and in alpine English heaths (see p. 21).

The abundance of species in the heaths of the Faroes is striking when comparing it with the greater number of those of western Jutland, both moraine sands and fluvio-glacial plains. This undoubtedly first and foremost has some bearing upon edaphic conditions. Investigations of the hydrogenion concentration in the soil of Faroes heaths (Table 3) shows that both *Empetrum-Vaccinium* and *Calluna-Erica* heaths, have p_H values which compared with Danish heaths (Weis 1933, and my own unpublished analyses) is rather high. Whereas the raw humus layer in the heaths of Jutland on an average is situated at p_H 3.8—4.5, we find that the upper soil layers of the Faroes heath has p_H 4.6—5.3 (6.5). The cause of the high value must be looked for in the greater base-content of the Faroes soils. The basalt contains rather large quantities of calcium which in spite of the heavy precipitation are not totally

Table 3. Hydrogenion concentration and organic content in some Faroes heath-soils.

Sample No.		p_H	Humus (loss on ignition) percentage
1.	Empetrum-Vaccinium uliginosum-Soc. (subalpine with Dryas, Böcher 1937 b p. 191)............................	6.5	
2.	Empetrum-Vaccinum-Soc.(Table 1, No.3)	4.6	high value
3.	Empetrum-Soc. (rich in mosses: Hylocom. loreum, Stereodon, Polytrichum alpinum) Thorshavn................	4.9	51.4 (28.2[1])
4.	Vaccinium Myrtillus-Soc. (rich in mosses: Nardia scalaris, Diplophyllum albicans, Dicranella heteromalla, Pogonatum polytrichoides, Polytrichum alpinum) Thorshavn................	4.6	71.7
5.	Calluna-Juncus squarrosus-Soc. (Table 1, No. 4)............................	4.7	high value
6.	Calluna-Soc. (with Nardus, Agrostis tenuis and mosses, particularly Dicranum). Thorshavn	5.3	67.5
7.	Calluna-Soc. (with Erica cinerea, Table 2, No. 5)............................	5.1	very high value
8.	Calluna-Erica cinerea-Soc. (Table 2, No. 6)	5.2	rather high value
9.	Erica cinerea-Calluna-Rhacomitrium hypnoides-Soc. (with Potentilla erecta, Nardus, Carex Oederi, Agrostis tenuis, Stereodon, Dicranum Starckei, Polytrichum alpinum, Diplophyllum albicans, Nardia scalaris) Thorshavn. Upper 2—5 cm of the soil	5.2	67.0
10.	In the same place, but 7—10 cm. further down in the soil......................	4.9	60.3
11.	Calluna-Erica cinerea-Soc. (rich in mosses) Thorshavn. Upper 2—5 cm of the soil	4.7	81.1
12.	In the same place, but 10—13 cm. further down in the soil................	5.2	80.2

[1] 4 greater particles of gravel included.

washed away. Even though the organic content of the soil can rise to considerable values, the p_H figures are not so low as those quoted for Danish heaths. This is presumably partly due to the fact that the vegetation does not make quite such acid humus as the Danish one, partly to the presence of earth worms (observed in sample 9—12). Besides well-water in the soil may lead to an admixture of basic substances from the underground, and finally particles of gravel due to the weathering of the rocks (as observed in samples 3—4) can add mineral components of basic influence to the soil.

It is a well-known fact, however, to what an extent the volcanic rocks in Iceland form basic compounds during their weathering so that only extremely few soils here have a very acid reaction. Besides the investigations of Weis (1933) reference may here be made to Steenbjerg & Gunnarsson's exhaustive analyses (1938). The latter on p. 82 makes the following mention of the Icelandic heaths: "These heather vegetations are extremely mixed and do not bear the slightest resemblance to Scandinavian heaths with their often entirely unmixed heather vegetation; besides, it was not possible with the naked eye to prove any podsolation or destruction of the upper layer of earth which, when viewed in connection with the above-mentioned reaction of the soil, is probably due to the fact that the Icelandic soils, so rich in minerals, and more particularly calcium and magnium, counteracts the formation of humic acid sol which presupposes the comprehensive destruction of the upper layer, resulting in the formation of distinct podsol-profiles." After this are mentioned two measurings of p_H in Icelandic *Calluna* heaths, being situated in p_H 5.7 and 6.4. Also Weis states that podsolation is extremely rare on Iceland. Nor have I on the Faroes, even under a thick layer of raw humus, seen anything, in the line of a bleached podsol layer.

Finally, it must be borne in mind that the great abundance of species is probably not merely due to the high p_H values and the resulting greater Ca-contents (cf. TOVBORG JENSEN 1936). There is every probability that a greater quantity of other nutritive substances will be present in the heaths of the Faroes than in those of Denmark (cf. the large kali-content of Icelandic uncultivated "mo" soils (STEENBJERG & GUNNARSSON l. c.)).

As opposed to the greater part of Danish, South-Swedish and North-German heaths the Faroes heath (both type A and B) can in the main be regarded as a natural type of vegetation; perhaps it is even a climax vegetation in great parts of the lowland (particularly on south-facing slopes), but here it has to a very large extent been replaced by *Nardeta* (p. 14) and possibly further reduced by the humid climate of present days. In all probability the heath had a greater distribution in the Faroes during the warmer and drier subboreal period (JESSEN & RASMUSSEN 1922, JESSEN 1925).

3. Types of Vegetation rich in *Erica cinerea* outside the Faroes.

Before making a plant-geographical comparison of vegetations containing *Erica cinerea*, we will first of all have to orientate ourselves as regards the distribution of the species. The distribution in Europe appears from fig. 1. Outside the closed area it is said to exist in western Germany (further details see GREVELLIUS & KIRCHNER 1923, p. 162), the western Alps and the Ligurian Appenines (BRAUN-

Blanquet 1923, p. 121). It is absent in low-lying regions in the Mediterranean area. Outside Europe it is according to Allorge (1927, p. 204) to be found in Algiers, and besides it is represented by a special subspecies on Madeira (*Erica maderensis* Bornm. = *E. cinerea* var. *maderensis* D.C.). As shown on fig. 1 the eastern limit of the species coincides with the January isotherm of 2° (cf. *Ilex* and other species mentioned in Holmboe's works). At the southern limit in Spain the winter temperature may also possibly exercise a certain influence, but here—as in many localities in the Mediterranean (and in Madeira), where the species is rare or entirely absent in the lowland—the summer heat, together with edaphic conditions, is the factor which more than any other helps to limit the area. We are surely justified in defining the species as temperate-thermic-oceanic (see further p. 23) as opposed to northern-oceanic (e. g. *Lobelia dortmanna*) and southern-oceanic species (*Rubia peregrina*) cf. Matthews (1937).

After this we will examine in detail the occurrence of *Erica cinerea* in the most important parts of its area:

Norway. The plant-geography and vegetation of the westernmost part of Norway has in particular been examined by Nordhagen (1917, 1921), Holmboe (1926, 1927), Degelius (1935) and Goksøyr (1938).

The plant-geographic zonation on the western coast of Norway is exceptionally definite. During a few hours it is possible, when travelling in a motorbus from the interior to Haugesund out at the sea, to pass at any rate two important plant-geographical boundaries; there is an *Erica tetralix* zone and an *Erica cinerea* zone. Already at Kyrping (50 km. from the sea) one enters the coast land, where the lowland is characterized by foliferous trees (ash, elm) and where *Digitalis purpurea* grows as weeds along the road or is scattered in grass plots in open shrubs. Close west of Ølen (35 km. from the sea) the heaths begin to appear; *Erica tetralix* and *Myrica* occur in great quantities in wet heath, rich in mosses and frequently tussocky. At Etne the country is still rich in foliferous trees (small woods with grass plots). These glades become greater and greater towards west and are gradually replaced by heaths. At Skjold (20 km. from

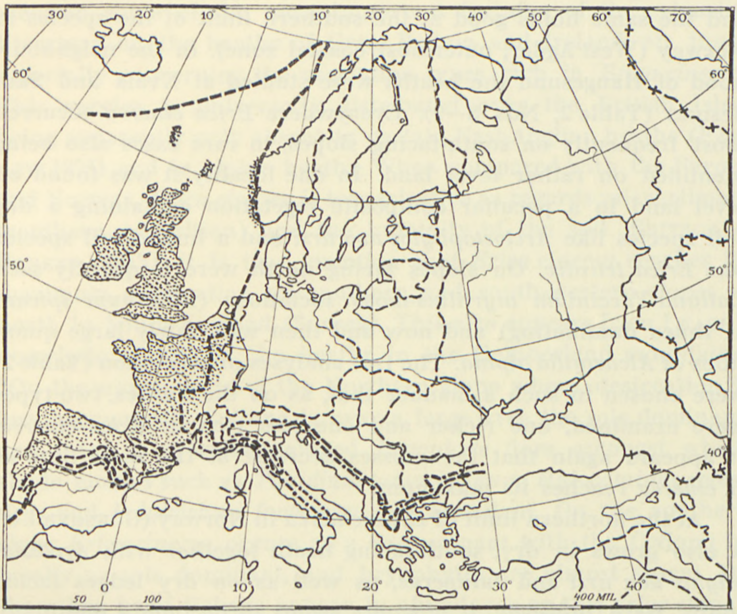


Fig. 1. The distribution in Europe of *Erica cinerea* L. (dotted area; the arrow north of Corsica indicates the localities in the Ligurian Appenines). The stippled line = January isotherm of 2° (Celsius). The line with dots and dashes interchanging = July isotherm of 22° (according to ALT (1932) and BIRKELAND and FØYN (1932)).

the sea) the heath begins to predominate, though frequently with a good deal of birches and junipers. At the most westerly branch of Skjold's Fjord (10 km. from the sea) *Erica cinerea* suddenly occurs together with *Calluna* in firm soil on the southwestern slopes, being raised above the moist heath with *Erica tetralix, Narthecium, Orchis maculatus* etc. At Haugesund the region is pronouncedly oceanic; the vegetation bears a considerable resemblance to that of the Faroes, though with a far more southerly character (*Vicia orobus, Sanguisorba).* In the gardens *Sarothamnus* *scoparius, Picea sitkensis* and *Araucaria araucana* flourish. Immediately east of Haugesund the January isotherm of 2° is passed (Skudesnæs and Utsire have the January mean temperature of 2.2°) and at the northern limit of *Erica cinerea* in Norway (Rundøy) the January mean temperature is 3.1°; on the islands northeast of Rundøy the January mean temperature quickly approches 1°, and the same holds good at the southern limit of the species in Norway (West Agder, outermost coastal zone). In the neighbourhood of Haugesund the heaths were studied at Kvala and Skudesnæs (Table 2, Nos. 8—9). Everywhere *Erica cinerea* occurred most frequently on south-facing slopes, in rare cases also being identified on rather level land. In one locality it was found on level land in a peculiar composite vegetation containing a dry soil species like *Arctostaphylos uva ursi* and a humid-soil species like *Erica tetralix*. On slopes facing north were frequently seen *Calluna-Vaccinium myrtillus*-moss sociations (*Blechnum spicant* at times dominating) and now and then with fairly large quantities of *Alchemilla alpina*. The two analyses of vegetation (Table 2) were chosen in such a manner that, as on the Faroes, two types were examined, one richer and one less rich in *Erica cinerea*. It appears again that the mosses decrease at the same time as *E. cinerea* reaches its maximum.

At the northern limit of *Erica cinerea* in Norway (Goksøyr l.c.) it also grows in dry, south-facing heath together with *Arctostaphylos uva ursi* and *Juniperus*, as well as on dry ledges facing south. Here, however, it nowhere seems to become a dominant. The small patch of heath at Utsire, which the sheep have not been able to exterminate (Nordhagen 1921) is also very like the Faroes vegetation, and we see again that the mosses decrease considerably with the appearance of *Erica cinerea*.

Vierhapper (1927, p. 156) mentions from the island Tysnes south of Bergen an interesting "Laubmischwald", the character of which is Atlantic. In drier localities with *Pinus silvestris* and *Juniperus* he found *Erica cinerea, Hyperichum pulchrum* and *Galium saxatile*. There is much evidence of a number of heaths in western Norway (like those in Denmark) having arisen after destruction of such woodlands (sheep-grazing, the cutting down of trees); see Holmboe 1926, p. 63. On Karmø where there are many *Erica cinerea* heaths, it is still possible to find scattered oak trees and a few hazels; in the 16th century there were still forests here (Norske Rigsregistranter II 565, see TROELS LUND: Dagligt Liv i Norden vol. I). FÆGRI (1935, page 32) proves that Jæren was partly covered with heath during the late glacial period, and it is not excluded that certain heaths in western Norway (the most exposed coast heaths) are natural.

The British Isles[1]. In this place it is only possible to mention some of the most important features of the extensive literature on the heaths of Great Britain and Ireland, *viz.* those especially concerning the vegetation types rich in *Erica cinerea.* This species is universally distributed over the British Isles, being apparently only absent in certain East-Anglian heaths (FARROW 1925) and in alpine heaths. When compared with the Faroes and Norway, *Erica cinerea* is less selective as regards microclimate (southern exposition) and the humidity of the soil. FRITSCH & PARKER (1913), it is true, mention that *Erica cinerea* reaches its maximum domination on southern and south-western slopes in heath in South-England (Surrey). This also appears from LEACH's description (1925) of the heaths in the Cumberland mountains: "On the upper parts of the Northern slope where desiccation is less pronounced, *Calluna* is over a large area the sole dominant, and there is a well-developed *Bryophyte* flora amongst which shade mosses such as *Thuidium tamariscinum, Hylocomium splendens* and *Polytrichum formosum* are abundant. On the southern slope *Erica cinerea* occurs as a co-dominant with the *Calluna* or locally as sole dominant, and bryophytes are almost absent. On the other hand lichens appear in abundance on this drier slope". It appears, however, from numerous descriptions of the heath in other regions that *Erica cinerea* does not require a southern exposition. Even though it is beyond a doubt most frequent in dry soil, it may occur scattered in moist heaths (WATSON 1931) or in *Molinia* or *Scipus cæspitosus*-sociations together with *E. tetralix* and *Drosera rotundifolia* (ARMSTRONG, INGOLD & VEAR). *Erica tetralix* may for that matter exist locally without being associated with humid soil (FRITSCH & PARKER l. c. p. 155).

The heaths rich in *Erica cinerea* sometimes floristically very much resemble those of the Faroes; most frequently, however, they contain a good deal of *Ulex* (*U. Gallii, minor, europæus*). In Ireland *Dabeocia polifolia* (see fig. 7) may furthermore enter into

[1] A summary of English heaths and heather moors is to be found in TANSLEY (1939).

the vegetation (Praeger 1934). A special heath type is to be found on sand dunes and raised beach (Moore 1931, Good 1935). In such localities *Erica cinerea* occurs as a pioneer of the heath during the succession from dune or shore field to dune-heath. The floristic composition of the dune heath corresponds very well with that of the Danish dune-heath; only, in the Danish the *Ulex*-species, and *Erica cinerea* and in the English *Empetrum* are lacking; on the other hand there is hardly any resemblance between these English dune-heaths and the Faroes heaths.

Many heaths have arisen by the cutting down or burning of trees (e. g. Scotch pine forests with an undergrowth of *Calluna* and scattered *E. cinerea,* see Wyllie Fenton 1935). Where owing to the structure of the ground grazing animals are kept away, there is in Ireland instead of heath a copse wood in which *Taxus* frequently dominates, and in which *Erica cinerea* is to be found among *Ilex, Hedera, Calluna, Juniperus, Arctostaphylos uva ursi, Hymenophyllum* etc. (Praeger l. c.).

France. *Erica cinerea* enters as a dominant in the heaths of northern France (*Calluneto-Ericetum cinereae*). These comparatively dry heaths (Lemée 1937, p. 162) largely resemble the heaths of the Faroes (*Polygala serpyllacea, Hypericum pulchrum, Sieglingia, Nardus, Potentilla erecta, Galium saxatile*) but like most of the English ones, they are distinguished from them by dominating *Ulex* (*europæus*). Tüxen & Diemont (1936 analysis 1—3, p. 175) calls this vegetation the "*Erica-cinera Ulex europæus*-Assoziation".

South of Gironde the character of the heath vegetation (according to Mentz (1911) and Allorge) changes; the heaths of les Landes contain many Mediterranean plants (*Erica scoparia, vagans, Helianthemum alyssoides* and *Quercus Tozza*) but lack e. g. *Galium saxatile* and *Genista pilosa.* (cf. Weevers' analyses (1938) and of older investigations see those of Mentz (1911)). Both the heaths of northern France and les Landes have arisen after the destruction of foliferous woods (*Quercion roboris sessilifloræ,* see Tüxen & Diemont, Lemée and Weevers).

Near the eastern limit of *Erica cinerea* in the southernmost part of France the latter, according to Braun-Blanquet (1915), appears as a constant together with *Calluna* in the undergrowth of the *Quercetum Ilicis* which has been almost destroyed by the agency of man. In advanced stages of destruction a heath of the character of a macki arises, with *Erica arborea, cinerea, Calluna,* *Sarothamnus* and *Cistus*-species, *Buxus Teucrium scorodonia, Helianthemum* etc. a vegetation which out of above fifty species has only four in common with that of the heaths of the Faroes.

Spain and Portugal. In the north-western corner of the Pyrenees *Erica cinerea* occurs in great quantities in mountain heaths; together with *E. vagans* and *scoparia* it dominates the mountain heaths of the Cantabrian-Asturian mountains; ALLORGE (1927) has made an analysis from Lugo in north-western Spain, and here it i.a. occurs together with *E. umbellata* as also in the mountains of northern Portugal (WILLKOMM). Somewhat south of the northern range it appears in the upper part of the *Quercus Tozza* Wood on Sierra de Moncayo (WILLKOMM) and towards east RIKLI (1907) mentions it from a macki at a height of 900—1200 m. at Barcelona. (Here *Quercus ilex, Buxus* and *Viburnum tinus* were dominants.) According to WILLKOMM it dominates in mountain heaths in Portugal between a height of 750 and 1450 metres; it may, however, also occur in the lowland near the ocean, *viz.* in the undergrowth of the great pine forest Pinhal del Meiria, where it is i. a. found together with the Azorian *Myrica Faya*. It most frequently seems to be absent in the heaths of the eastern Pyrenees (the French part); here it may, however, be found in an open beech wood (GAUSSEN 1926, p. 357).

Madeira. VAHL (1904) mentions *Erica cinerea maderensis* from the upper shrub region (12—1800 m.) among a sparse rock-vegetation (cf. LOWE's (1868) statement: "The craggy summits of the highest central peaks"). The vegetation is here Mediterranean in character, and the Climate, from a thermic point of view, reminds of that of south-western Europe.

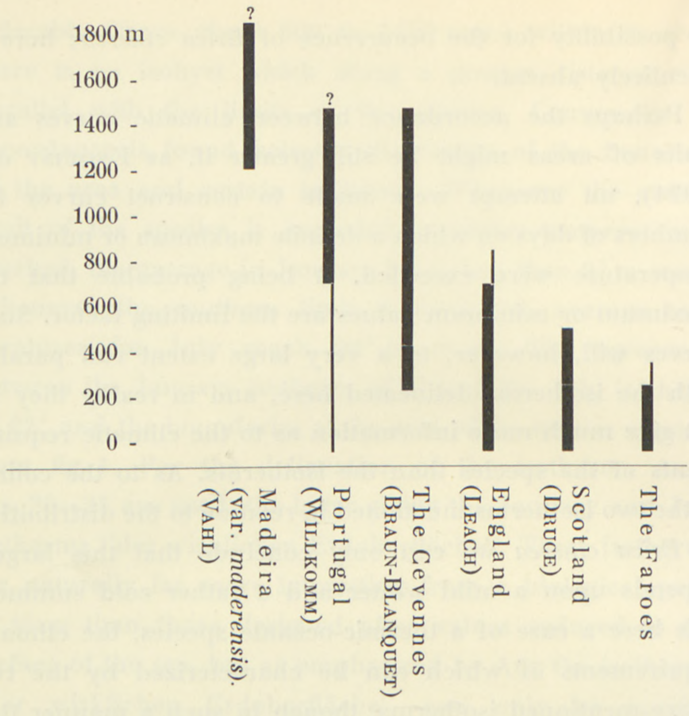
4. Contributions to the Aut-ecology of *Erica cinerea*.

A number of important features regarding the aut-ecology of *Erica cinerea* can be extracted from the preceding summary. The distribution of the species was designated as temperate-thermic-oceanic. As to this a further explanation is required. When going over measurings from climatologic stations within the area of the species and along its limits it appears that the yearly precipitation may vary considerably (from about 600 to 1450 mm.) within its area; there is no isohyet which along a greater distance runs parallel with the limits of the species. Conversely, an accordance is found between the course of the boundary of the area and certain isotherms. Whenever the eastern limit of the species is exceeded, a winter temperature is reached, the average in January being less than 2° or more. Whenever the southern limit is exceeded, average temperatures for July reach 22° or more. The agreement between the January isotherm of 2° and the July isotherm of 22° and the boundaries of the area of the species appears from fig. 1. For the delineation of the isotherms Alt's figs. 30—31 are used, the latter giving the January and July isotherms "der wirklichen Erdoberfläche". These isotherms are naturally far more interesting from a biological point of view than those designed after values reduced to the surface of the sea, but as emphasized by Alt the isotherms "der wirklichen Erdoberfläche" can only be roughly drawn, seeing that they are to a very large extent dependent upon the height curves of the land; both local and certain regional details can often not be rendered in the small scale. The agreement between isotherms and boundaries of area is rather remarkable, when taking into account how difficult it is to make the small scale comprise details. In certain localities in the Ligurian coastal mountains the species has been regarded as a kind of Atlantic relic (Braun-Blanquet 1923, p. 133); it appears, however, that this area is cut off from the occurrences in Dauphine by an inflection in the January isotherm of 2°. Where the two said isotherms deflect from each other, the species begins to be common; where the two isotherms in Italy and on the Balkans, as it were, lie on top of each other, there is no possibility for the occurrence of *Erica cinerea*; here it is entirely absent.

Perhaps the accordance between climatic curves and limits of areas might be still greater if, as Enquist did (1924), an attempt were made to construct curves for numbers of days on which a definite maximum or minimum temperature were exceeded, it being probable that the maximum or minimum values are the limiting factor. Such curves will, however, to a very large extent run parallel with the isotherms delineated here, and in reality they do not give much more information as to the climatic requirements of the species than the isotherms. As to the course of the two isotherms mentioned in relation to the distribution of *Erica cinerea* we can only conclude that this largely depends upon a mild winter and a rather cold summer; it is here a case of a thermic-oceanic species, the climatic requirements of which can be characterized by the two above-mentioned isotherms, though in such a manner that the limiting effect is not thought to be excercised by the mean temperatures themselves but by certain climatic conditions, or edaphic conditions dependent upon the climate (see later), which run parallel with the isotherms (cf. Fægri 1937).

As the northern limit of the species seems to be controlled by the winter temperature, it is probable that this also applies to its vertical limits. The graphic production given p. 26 shows the vertical distribution of the species from south to north within its area; a thin line indicates a rare occurrence. Both in Madeira and in Portugal the plant reaches the mountain tops for which reason the upward limit of growth is here uncertain.

Apart from the climate, *Erica cinerea* makes certain



edaphic requirements. In the first place it seems to be associated with relatively dry localities, as e. g. in the Faroes the south-western slopes. It is here worth mentioning that another thermic-oceanic species, *Carex binervis,* in the Faroes is not particularly associated with the southern slopes; this plant, however, can stand a much greater humidity of the soil. It is to be found in the heaths (see the tables) and furthermore in acidic grass land (Ostenfeld's *Carex binervis—Luzula silvatica*-Soc. Nordhagen's *Macroluzuletum*) and in *Nardeta* and bogs. In France it is a character plant of the moist heath series (Allorge, Lemée). It must, however, be borne in mind that the localities where *Erica cinerea* grows are frequently rather moist; in the thick peat which is a frequent habitat for it on the Faroes the water capacity is very high. However, the soil under *E. cinerea* is only temporarily quite soaped, and the water does not stagnate in its habitats; this agrees with the fact that e. g. in England it thrives on the tops of tussocks in mosses and on brinks along watercourses running through the bogs where there is also a good drainage.

In this context it should also be borne in mind that *Erica cinerea* may occur in particularly dry dune-vegetation and e. g. in France in *Corynephoreta* (LEMÉE p. 38).

All authors are agreed to classify the species as a plant belonging to acid soil. We have the following measurings of the hydrogenion concentration in its habitats:

	p_H	
The Faroes	4.7—5.2 (Table 3)	(T. B.)
Western Norway	4.5—5.1 (Table 2, Nos. 7—8)	(T. B.)
Isle of Man (dune-heaths)	5.8—6.6	(MOORE 1939 p. 126)
England (Herefordshire)	4.8—6.2	(DE SILVA 1934 p. 539)
Northern France (Perche)	4.4—5.0	(LEMÉE 1937 p. 191)
Southern France (Heath plantation) ..	4.4—5.8	(WEEVERS 1938)

All in all, it seems that the species is able to stand p_H values from 4.4 to 6.6; in proportion to *E. tetralix* the values are high; *E. tetralix* is most frequently found in soil with p_H round 4.0. *E. cinerea* both thrives in podsolated soil (France according to TÜXEN & DIETMONT (pp. 176—179) and LEMÉE (p. 183)) and in non-podsolated soil (the Faroes). In southern regions it looks as if the species is associated with montane soils and avoids the Mediterranean neutral-basic ones[1]. A glance at the maps figs. 115a and b in Braun-Blanquet (1928) gives one the impression that the southern limit of the species is very largely conditioned by climatic-edaphic factors. The boundary of the Mediterranean soils and the course of the lines with the same N—S quotient[2] in southern France practically coincides with the July isotherm of 22°. It also appears that the absence of the species in the upper Rhône Valley practically falls within an area of "brown earth" on the transition to Mediterranean soil, whereas to the west in the Cevennes and to the east in the westernmost Alps it occurs in montane soils.

5. Some studies of the other species of the *Calluna-Erica cinerea*-heath.

After this summary of the ecology of *Erica cinerea* we will, in greater detail, go over the list of plants in Table 2 and try to give an account of the biological distributional type to which the various species belong. We may divide the species into three groups: the northern, the temperate and the temperate-oceanic; among the northern there are a few which may be called northern-oceanic (see the table). The justification for these terms will appear from the literature regarding the distribution of the species. The groups might naturally be further subdivided: among the temperate-oceanic ones it was possible to separate a northern sub-group (*Calluna, Erica tetralix, Hypericum pulchrum*, var. *procumbens, Narthecium*) and a southern one (*E. cinerea, Carex binervis*). One of the principal difficulties in the

[1] p_H 6.8—7.4 (Braun-Blanquet 1928, p. 149). As to p_H measurings in similar (North-African) soils see Lüdi (1939).

[2] Niederschlag: Sättigungsdefizit.

way of a proper classification of species in a system of distributional types is the variation of the species, *viz.* their contents of races with a different ecology (see BÖCHER 1938). It is, however, a very interesting task to try to conquer this difficulty. Beyond a doubt, many species occur in the Faroes in races which in various ways are adapted to an oceanic climate. Such species should then on the Faroes also be termed oceanic, seeing that biologically they belong to the species which may upon the whole be termed oceanic (*Erica cinerea*). In the table I have for the time being elected to mark with an O? the species which I think occur in oceanic races, while O is used in the sense of oceanic.

Below a list will be given of some of the species which in various ways have caused difficulties with regard to classification of the biological distributional types to which they belonged. Mention is partly made of studies of their variation, partly of their distribution.

1. *Anthoxantum odoratum* L. Eurasiatic species which towards west reaches Greenland, the Azores and Madeira. Material from two localities in the Faroes was transplanted to Denmark. As compared with Danish and Norwegian races the Faroes plants flower 2—3 weeks later and has fewer panicles.

2. *Molinia coerulea* (L.) MOENCH. occurs on the Faroes in small individuals. TURESSON (1930, p. 124) has shown that the progeny of Faroes plants in culture attain an average height of 61 cm., whereas plants from Scotland on an average reached 96 cm. Also *Succisa pratensis* occurs on the Faroes in a genetypically low growing race (TURESSON l. c.).

3. *Carex pilulifera* L. The Faroes plant deviate from the normal one by not being cæspitose; it has up to 10 cm. long rhizomelike stems, hidden in the peat (fig. 12 A in BÖCHER 1937 b). Besides the individuals collected by myself on Klakken similar individuals were identified by OSTENFELD (Trangisvaag) and C. JENSEN (Strømø). No really cæspitose individuals exist. It is

evidently the same plant which Beeby (1887) found on the Shetlands. Beeby's collection (No. 757 west slopes of Saxa North Hill Unst) is in full accordance with the material from the Faroes; in his paper it is mentioned as "a form with slightly creeping and rooting stems, not at all cæspitose". After having seen Beeby's material I dare not deny that we are dealing with a special race, not a modification. Cultivation experiments are here greatly needed. The type mentioned above from the Faroes and the Shetlands bear a considerable resemblance to *Carex azorica* Gay (Gay Annales des Scienc. Nat. II Series, Vol. 11 1839 p. 185, and illustration in Trelease 1897, plate 48). This species also sometimes has a rhizome-like subterranean stem, but is clearly distinguished from the rest by having more closely joined spikes, two styles and in consequence flatter fruits.

4. *Potentilla erecta* (L.) Hampe. This species is particularly polymorphous, special studies on the polymorphy of Danish individuals being found in H. E. Petersen (1926). It is an Eurasiatic, widely distributed plant, which towards west reaches the Faroes, the Azores and Madeira. In the Faroes it is of particularly common occurrence. The Faroes plants resemble Danish types, but are on an average smaller (modifications?). Plants from western Norway, Lizard Point, the Hebrides and the Shetlands entirely resemble the Faroes individuals. Large, robust, and large types with narrow leaves I have seen from the region of Oslo, from Finland, Russia and France. Cultivation experiments with different types have been commenced.

5. *Hypericum pulchrum* L. As to the distribution see in particular Braun-Blanquet (1923) and Køie (1939). A map of the most northerly localities along the coast of Norway is found in Nordhagen (1917, fig. 12).

The typical plant particularly belongs to the oak region of western Europe; it grows in oak forests, oak shrubs and in hilly, mossed heaths in Jutland. In the Faroes it is rather rare, being f. inst. found in the lowland at Thorshavn. It may be defined as a temperate-suboceanic species.

As opposed to the principal type, *H. pulchrum* var. *procumbens* Rostr. is of common occurrence in the Faroes, particularly in the lowland in heaths (Table 2), in *Nardus* and *Anthoxanthum* sociations (Jensen 1897, p. 183, Ostenfeld 1907, p. 79) and more rarely in the mountains; here it may be met with in south-facing herb-fields rich in species, at a height of 500 m. above the sea (Böcher 1937 b, p. 178). The distribution of this variety is rather peculiar; besides in the Faroes it is to be found in the Shetlands, where Beeby (1887) mentions it as frequently occurring on "serpentine hills about Baltasound"; later (1888) he also mentions a find of the upright main type from "a deep and sheltered ravine". In the Orkneys it is known from three localities (Bennett 1915, Johnston 1921). In Scotland var. *procumbens* according to Williams (1901—12, p. 558) occurs near Holburn Head, Caithness and, according to G. Cl. Druce (1929) on a mountain 743 m. high at West Ross immediately at the sea. Wilmott states that it occurs on the outer Hebrides (communication by letter from Dr. H. G. Pugsley). In Ireland it occurs, according to Praeger (1934), in two of the westernmost localities, on Clare Island (in the highest point together with several Alpine species) and on Achill Island (on the promontory Croaghan). The variety ought to be looked for in western Norway where it is not known (Dr. K. Fægri, communication by letter). It consequently looks, as if var. *procumbens* has an extremely narrow area of distribution, which is pronouncedly oceanic and relatively northern (fig. 7).

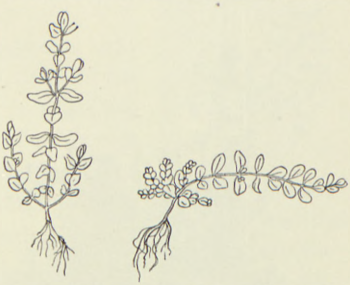


Fig. 2. 11 weeks-old individuals of *Hypericum pulchrum* var. *procumbens* Rostr. (to the right) and a typical *Hypericum pulchrum* (to the left). Both figures × 1/2.

Beeby (1887) writes: "The var. *procumbens* remains unaltered in cultivation; entirely maintaining its prostrate habit and three-flowered cyme." In spite of this observation Brown (1891) regards var. *procumbens* as a modification, but my investigations agree with those of Beeby. Plants which were transplanted from the Faroes in 1935 have still kept their characteristic appearance. Comparative investigations of progeny individuals of typical plants from Denmark (two localities) and from the Faroes (var. *procumbens* from two localities) yielded the same result; already quite small, three months-old individuals of the Faroes type prove to be prostrate, and as compared with the main type they have a far greater number of small basal shoots (figs. 2 and 3). The growth takes place somewhat more slowly in var. *procumbens* than in the main type. In the autumn a characteristic difference appears, in that the Danish type at the beginning of September dies down to the perennial parts in the surface of the soil, whereas var. *procumbens* remains green until November and, in a green-house free from frost, for the greater part of the winter. Both types have the same chromosome number (2 n = 18, material from the Faroes, see fig. 4, and from Randbøl Heath in Jutland). The number

Fig. 3. Progeny individuals (cultivated under the same conditions and sowed at the same time) of *Hypericum pulchrum* var. *procumbens* Rostr. from Husaraun at Thorshavn (T. B. 110) and a typical *H. pulchrum* from Kaas in Jutland (T. B. 48). The plants are three years old, No. 48 is 10—15 cm. high.

corresponds with former countings of *H. pulchrum* (Chattaway 1926, in Brit. Jl. Exp. Biol. 3, p. 141).

6. *Arctostaphylos uva ursi* (L.) Spr. In the Finmark and several other localities this species has a continental character (see Böcher 1937 a); it is, however, frequently found in dry localities along the southern part of the west coast of Norway, frequently on southern slopes, i. e. in similar localities as *Erica cinerea*. I saw great quantities of this species at Haugesund and Mandal, and it also occurs in Scotland and Ireland and in several localities along the western coast of Europe. The fact that it avoids the coast of northern Norway may perhaps be due to its requiring a relatively high summer heat. The species may be regarded

as a boreal dry-soil plant, without any connection neither with oceanity nor with continentality.

7. *Calluna vulgaris* (L.) Salisb. The species, it is true, penetrates far towards east, but occurs most frequently in north-western Europe. Towards east it is particularly selective as regards the microclimate of the habitat. Its eastern boundary (Mattfeld 1929, Beijerinck 1936) runs parallel with the oceanic coast of Europe from northeast to southwest. The species is northerly-temperate and suboceanic.

8. *Brunella vulgaris* (L.). This species may be found scattered in the oceanic heaths of the Faroes and in western Norway, but is most frequent in different types of meadow. The Faroes plant is a genotypically low, early-flowering race (Böcher 1940), the closer relationship of which with other races is to be examined in detail, but which shows certain points of similarity with Mediterranean plants.

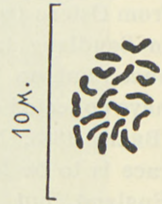


Fig. 4. Mitosis from the root-tips of *Hypericum pulchrum* var. *procumbens* Rostr. 2 n = 18.

9. *Plantago maritima* L. Very strongly polymorphous (Literature in Böcher 1938, p. 180). A number of transplantings of Faroes plants to Denmark shows thats the many Faroes types very largely maintain their characteristic appearance. In the Faroes the species enters into heaths, fell-fields and snow-patches; besides it is found on the beach and in meadows in the lowland. The investigation of the geographical and ecological conditions of the many Faroes types is still so defectively examined that I only dare to consider it probable that a number of the many races are oceanic and western-European.

10. *Plantago lanceolata* L. This species occurs in the Faroes in several varieties, some of which resemble Danish types. Particularly deviating from the Danish material is a nearly lanuginous type. Cultivation and transplant-experiments show that this race is particularly different both from Danish and Faroes races belonging to var. *dubia* (L.) Wahlenb. (cf. figs. 5—6). All the races examined have the same chromosome number (n = 6). When dealing with *Plantaginaceae* (in »das Pflanzenreich«) Pilger (1937) has subdivided *P. lanceolata* into a number of varieties; the hairy Faroes variety must be classed with var. *dubia* subvar. *eriophora* Pilger. Var. *dubia* is as a rule regarded as a southern group of races, and subvar. *eriophora* is said to belong in Middle France

and in the Mediterranean area. The most important difference between my *eriophora*-race from the Faroes and my cultures of var. *dubia* subvar. *eudubia* (= *eriophylla*) lies in the much greater hairiness and the thicker and stiffer leaves of the Faroes plant[1].

The herbarium of the Botanical Museum of Copenhagen contains plants of the above-mentioned hairy Faroes type from four localities (Strømø and Bordø), to which I may i.a. add a locality from Østerø (see below). Only one plant, collected by STEENSTRUP in Saudlaugsdalur on Iceland, seems to approach it in appearance; but on Vestmannaeyjar HELGI JÓNSSON and OVE PAULSEN have collected entirely corresponding plants. Also in the Shetlands (BEEBY 1886, Nos. 661—662) and in Scotland (DRUCE 1929) this race is to be found, and Dr. PUGSLEY suspects "that it grows in England, but has not been distinguished" (communication by letter). As to southwestern Europe I have seen it from Les Sables d'Olonne in France and from Coruña and Pontevedra in Galizia. In the Azores the subvar. *eriophora* is widely distributed; the material from there at one time led to the setting up of a new species, *Plantago azorica* HOCHST, which entirely corresponds with the Faroes plant (see Plate VII, fig. 2 in SEUBERT (1844)); according to DE CANDOLLE (Prodromus Pars XIII, p. 715) types corresponding with *P. azorica* are to be found "in arenosis Europæ mediæ", in sand-dunes in western France, on the top of the 900 m. high mountain Foia in Algarve, Portugal, and in the Azores, Madeira and the Canaries. If we limit ourselves to the plants which distinctly resemble those of the Faroes[2], it looks as though we face a pronouncedly Atlantic distribution; when considering PILGER's distribution of subvar. *eriophora* (and DE CANDOLLE's central-European material, in all probability from France) the race rather becomes Mediterranean-Atlantic. The Danish material of var. *dubia* only slightly approaches the Faroes type from the point of view of hairiness and must thus be referred to "*eudubia*". No Norwegian individuals are so longhaired as subvar. *eriophora* (FÆGRI, communication by letter).

Ecologically there is some resemblance between *eudubia* and *eriophora*. In Denmark the former is often found in dry fields and on hills, whereas the large, smooth-leaved upright races belong near roads and in inhabited places. Smooth-leaved races are

[1] See further PILGERS Diagnoses (pp. 322—23) of subvar. *eudubia* and *eriophora*.

[2] Black dots without signs of interrogation on fig. 7.

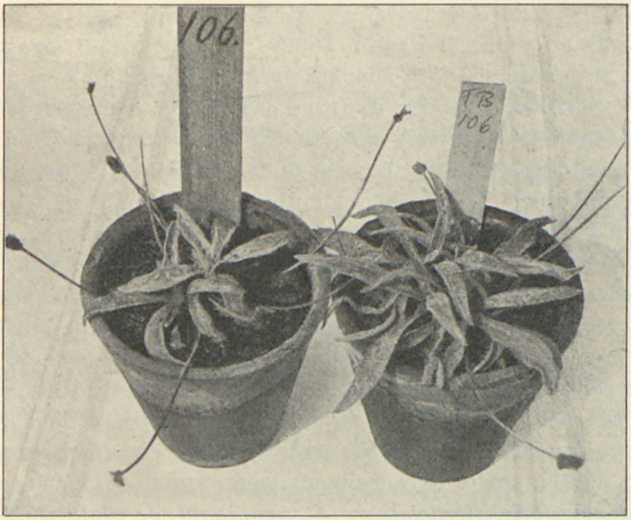


Fig. 5. *Plantago lanceolata* subvar. *eriophora* Pilger from the Faroes (Kodlur) transplanted to Copenhagen. The upper diameter of the flower-pots: 10 cm.

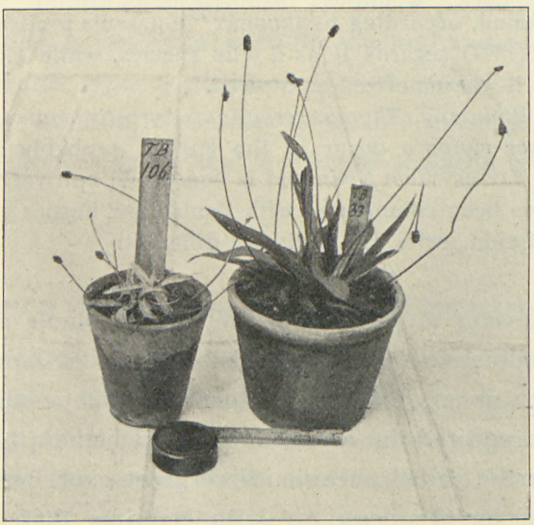


Fig. 6. *Plantago lanceolata* subvar. *eriophora* Pilger (to the left) and *Pl. lanceolata* subvar. *eudubia* Pilger (to the right); both from the Faroes and cultivated in Copenhagen. The tape measure stretched to about 10 cm.

found in cultivated grass-land and near villages on the Faroes, while var. *eriophora* live in the south-facing *Calluna-Erica cinerea*-heaths, in subalpine south-facing *Empetrum-Vaccinium* heaths, rich in species (*Dryas!*), and in dry grass-vegetation. A grass-vegetation of this kind is extremely rare in the Faroes; it occurred on a slope inclining 40° towards west in the direction of the sea, on the promontory Kodlur at Ejde the local climate of which is relatively dry. The vegetation was almost entirely closed. There were hardly any mosses, and the soil was here and there visible among the plants. Dominants were *Holcus lanatus* and *Vicia cracca* (in a peculiar race, which reminds of the one to be found in our sand-dunes). Common were: *Succisa pratensis, Polygonum viviparum, Thymus serpyllum, Ranunculus acer, Empetrum, Angelica silvestris, Armeria vulgaris, Festuca ovina* and *rubra, Plantago lanceolata* (*eriophora*) and *maritima* and *Botrychium lunaria*; finally, scattered specimens were found of *Silene acaulis, Brunella vulgaris, Hieracium* sp., *Athoxanthum odoratum, Habenaria viridis, Trifolium repens, Rumex acetosa, Euphrasia* sp. and *Equisetum arvense*. This vegetation was not very much influenced by the sheep, which in this place are kept off during the whole of the summer season. In the Azores *Plantago lanceolata* var. *eriophora* is found, according to Seubert "in pascuis pratisque siccis" Trelease (1897) regards it as a wild species, while *P. lanceolata* (*genuina*) is characterized as a weed.

Viola Riviniana, Thymus serpyllum, Agrostis tenuis and *canina* and *Festuca vivipara* occur in the Faroes, probably in special races; as far as *Viola Riviniana* is concerned cultivation experiments have been commenced with Danish and Faroes plants. The transplantation series are distinctly different.

If we want to prove that the Faroes plants are genotypically different from the Danish ones, is the work before us, as it appears, rather considerable; but a still greater work is required in order to prove whether the Faroes races can be called oceanic. Here great experiments must be made, for who can say with certainty that a race is oceanic, before he has cultivated it from numerous both oceanic and continental habitats, and perhaps besides has made various physiological experiments with the races found?

When using the biological types of distribution in the following, we must consequently bear in mind that the percentage of temperate species is undoubtedly too high, while the percentage of the oceanic ones is too low. In particular the percentage of the oceanic ones will rise, if *Potentilla erecta*, which occurs with $F^0/_0$ 80—100, is included in the oceanic species.

Among the above-mentioned distributional types of the Faroes heath-plants there is one, the relatively southern temperate-oceanic type which demands particular attention. It is represented by quite few species, *viz. Erica cinerea*, which forms a transition between the oceanic and the Mediterranean-Atlantic species (*Ilex*); besides there is *Carex binervis* and, in so far as may be seen from the information at hand, *Plantago lanceolata eriophora*. Also *Anagallis tenella* which grows by lakes in the lowland and *Scilla verna* belong to this type of distribution, but *Anagallis tenella* is according to Lüdi (see fig. 7) almost entirely Mediterranean-Atlantic, seeing that it extends towards east as far as Crete.

6. Biological Distributional Types and Character-Species.

On a former occasion (1938, pp. 289—290) mention was made of the agreement which sometimes exists between the geographical distributional types and the character species (in the sense of Braun-Blanquet), particularly such as were based upon the climatic demands of the species. Outside the Scandinavian literature Lemée in his monograph on Perche also makes use of types of distribution.

As to his *Corynephoretum occidentale* he says e. g. that it contains "11 espèces atlantiques (dont 4 caractéristiques) soit 14 $^0/_0$ de l'ensemble, et 6 sub-méditerranéennes (dont 5 caractéristiques) soit 6.6 $^0/_0$. C'est une association d'aire atlantique à affinités méridionales". As basis for the classification of the vegetation Lemée, however, as usual makes use of the character species.

Meusel quite lately (1939) has attempted to create a foundation for the investigation of vegetation, which largely builds on the total distribution of the species. In the case of each plant community its "pflanzengeographischer Charakter" is mentioned, and special weight is attached to an examination of the area of the "Leitarten" of the plant community (i. e. species which within his area of examination are more or less closely connected with a special community).

In the following an attempt will be made to divide the Faroes heaths on the foundation of the biological distributional types (which term may appropriately be abbreviated to B. D. types). In the same manner in which Raunkiær calculates his biological spectrum of life forms, it is possible to calculate the biological spectrum of distributional types. This material of figures is in the case of the vegetation analyses here published grouped in Table 4. The B. D. percentage is partly based on the list of species partly on the frequency percentage within $^1/_{10}$ m^2 large circular planes (cf. Raunkiær), partly within small (0.006 m^2), the method followed being the modified Raunkiær method (Böcher 1935)[1].

[1] This method can briefly be described as follows: The frequency of the species is examined, not only within a number (here only 10) of circular planes of $^1/_{10}$ m^2, but at the same time within circular planes

From the spectrum of biological distributional types the following facts appear:—

1) In the material from Table 1 a considerable oscillation from dominance of northern to dominance of oceanic species, at the transition from a northern to a southern slope.
2) In the material from Table 2 a rise in the oceanic phanerogams at the transition from the more humid, mossy *Calluna*-heaths, to the drier *Calluna-Erica cinerea* heaths, somewhat poorer in mosses. This fact is interesting, because it reflects the different ecology of the two groups, the phanerogams and the mosses. The former are highly thermic-oceanic, whereas the mosses are highly hygric-oceanic.
3) The characteristic differences between the vegetations examined appear most distinctly when using the figures

of 0.056, 0.025 and 0.006 m^2, the one overlapping the other; the four different sizes of circles are designated 1 (0.1 m^2), 2, 3 and 4 (0.006 m^2). Besides the frequency is examined within a plane of about the size of a halfpenny (the "centre" of the circles); this very small circle which almost corresponds with a point in the New Zealand point method is termed 5. The densest species naturally obtain the highest frequency percentage within the very small circles; the species which almost entirely cover the soil become dominants, even when the size of the circle is as small as a half-penny. For each of the species in the tables (1—2) are indicated: 1) the frequency percentage within circle 1 (0.1 m^2); 2) the frequency percentage within circle 4 (0.006 m^2), and 3) the minimum area (i. e. the one of the 5 sizes of circles which must be used, in order that the species may get the frequency percentage 100). The figures **100**.50.2 thus mean: The species is a dominant within circle 1, gets 50 % within circle 4 and will not be a 100-percent-dominant, if the size of the circle becomes less than that of circle 2 (0.056 m^2). The average density of its shoots is then about 20 cm.

Analyses made by means of this modified RAUNKIÆR method is in the tables marked *S*, while determinations of degree of covering (HULT-SERNANDER) are marked *D*.

Table 4. Spectrum of

Analysis		Northern species %	Oceanic species %	Temperate species %
Table 1, No. 1...	Number of species	30.8	23.1*	53.8
Table 1, No. 2...	Number of species	20.0	35.0*	50.0
Table 1, No. 3...	Number of species	23.5	23.5*	58.8
	Frequency: Circle 1	47.4	14.1*	48.7
	Frequency: Circle 4	**68.4**	15.8*	28.9
Table 1, No. 4...	Number of species	13.3	26.7	60.0
	Frequency: Circle 1	23.4	28.6	48.0
	Frequency: Circle 4	26.5	**47.0**	26.5
Table 1, No. 5...	Number of species	64.3	14.3*	28.6
	Frequency: Circle 1	83.7	16.2*	13.5
	Frequency: Circle 4	**87.2**	12.8*	10.3
Table 2, No. 1...	Number of species	9.5	33.3	57.2
Table 2, No. 2...	Number of species	5.9	35.3	58.8
Table 2, No. 3...	Number of species	5.9	35.3	58.8
Table 2, No. 4...	Number of species	21.7	21.7*	60.9
	Frequency: Circle 1	8.5	25.6*	69.1
	Frequency: Circle 4	6.9	**41.4***	**55.2**
Table 2, No. 5...	Number of species	5.0	40.0*	60.0
	Frequency: Circle 1	0.0	38.9	61.1
	Frequency: Circle 4	0.0	**56.0**	44.0
Table 2, No. 6...	Number of species	4.8	28.6	66.6
	Frequency: Circle 1	1.2	35.6	63.2
	Frequency: Circle 4	0.0	**55.0**	45.0
Table 2, No. 7...	Number of species	4.0	24.0	72.0
	Frequency: Circle 1	1.1	31.9	67.0
	Frequency: Circle 4	3.4	**55.2**	41.4
Table 2, No. 8...	Number of species	4.4	30.4	65.2
	Frequency: Circle 1	4.3	39.1	56.5
	Frequency: Circle 4	4.2	**62.5**	33.3

* In the calculation the northern-oceanic species are included.

The percentage of lichens and mosses is calculated on the base of the percentage is a great help towards the classification of heaths. In this case mosses are of far greater importance in the vegetation than the lichens. The continental heaths, where the lichen percentage increases. If with regard to the percentage for northern (*Jungerm. Floerkei, J. qvinqvedentata, Polytrichum* to be a difference in the occurrence of these two types within heaths rich the former contains more northern species than the latter and this in its mosses are marked with an O.

Mosses %	Lichens %	Number of species		Points	
		Phanerogames	Mosses + Lichens	Phanerogames	Mosses + Lichens
92.3	7.7	13	8	—	—
100.0	0.0	20	13	—	—
100.0	0.0	17	8	—	—
100.0	0.0	—	—	780	530
100.0	0.0	—	—	380	300
100.0	0.0	15	7	—	—
100.0	0.0	—	—	770	410
100.0	0.0	—	—	340	220
64.3	35.7	14	14	—	—
68.9	31.1	—	—	740	740
64.9	35.1	—	—	390	370
100.0	0.0	21	5	—	—
100.0	0.0	17	8	—	—
100.0	0.0	17	7	—	—
100.0	0.0	23	12	—	—
100.0	0.0	—	—	820	550
100.0	0.0	—	—	290	310
90.9	9.1	20	11	—	—
97.3	2.7	—	—	590	370
100.0	0.0	—	—	250	220
100.0	0.0	21	9	—	—
100.0	0.0	—	—	870	350
100.0	0.0	—	—	400	130
91.7	8.3	25	12	—	—
100.0	0.0	—	—	910	550
100.0	0.0	—	—	290	200
57.1	42.9	23	7	—	—
93.3	6.7	—	—	690	150
100.0	0.0	—	—	240	60

number of species and points for mosses and lichens. This lichens-mosses it had naturally not been necessary to calculate it, as it is evident that the calculation has been undertaken to provide values for comparison with more the mosses the percentage is calculated for oceanic (Western-European) and *alpinum*, *Andræa petrophila*, *Mylia* cf. C. Jensen 1901) there will also prove in *Empetrum-Vaccinium* and *Calluna-Erica cinerea* respectively, seeing that turn more oceanic species than the former. The oceanic western-european computed on the strength of the frequency within circle 4, and it must be remembered that only the very densest species can attain greater values, when this small circular plane is used. On the other hand, dominants and scattered species have the same numerical value in the computation of the figures, which are based upon the number of species. The value of Raunkiær's method, and more particularly its modified form, is clearly very great, and too little attention has been paid to it. The usual life-form percentages based on numbers of species, which are contained in numerous works[1] written by foreign scientists, ought to be supplied with life-form percentages based on frequency figures.

4) By means of the biological types of distribution it is possible to distinguish between 3 types for the here examined heaths: 1. The heaths rich in *Empetrum-Vaccinium* (Nos. 3 and 5, Table 1) characterized through a percentage for northern species of 68 and 87. 2. *Calluna*-heaths (No. 4, Tables 1—2) with 47 and 41 per cent. of oceanic species, and 3. *Calluna Erica cinerea*-heaths (Nos. 5—8, Table 2) with 56, 55, 55 and 62 per cent. of oceanic species. If the oceanic species were divided into relatively northern and relatively southern ones, a clearer distinction of type 3 in proportion to type 2 would be obtained, seeing that *Erica cinerea* would cause the southern species to obtain a relatively high value in type 3, as distinguished from type 2, where the southern species would hardly obtain any values worth mentioning.

[1] Cf. e. g. the critical remarks of Diemont (1938, p. 42) to the effect that the proportion of quantity of the species is not expressed in life-form spectra, as the latter are computed on the strength of the number of species. The original life-form spectra of Raunkiær at any rate do not suffer from this deficiency! (cf. Raunkiær 1934).

It should not always be a dominans of a given distributional type which is to make the foundation of the division; only a constant occurrence of a certain type of distribution in a series of analyses should be used to divide these into a special type of vegetation. It will, however, then be evident that there is no very great difference between the use of distributional types and the use of character species in the division. It therefore also appears that the character species, which are used for the division of heaths in different countries, very often belong to the same type of distribution (oceanic character species in western European heaths, continental in "Pontic" etc.).

However, in spite of the similarities, this is not merely an argument about words i. e. whether one wants to use the one or the other term in a division of vegetation. There is a great difference in the degree of objectivity obtained. Many character species are classified in the following manner: first the plant community is examined and the species found, which are supposed to be more or less closely connected with it; some species of the community are selected, which seem to have an ecologically narrow amplitude within the given area; finally, the community (association) is characterized by means of these species. Here it is not possible to a certain extent to avoid circular conclusions, and besides many character species can only be used within a limited area, "regional character species". Conclusively the choice of character species is naturally more or less subjective, being e. g. dependent upon the experience of the individual botanist. If on the other hand B. D. types, which are based on the total distribution of the species, are used in the division, this will be more objective, and at any rate one does not commit any offence to way of circular conclusions. It is a different matter that the B.D. types are sometimes difficult to cope with, because the work required in the geographic-racebiological investigation of the species is so very great. However, I am of the opinion that all plant-geography and ecology in a greater or lesser degree suffers from the drawback that the unities used for the investigations (i. e. the species) are far too little known. It may thus be said with perfect justice that the road is long and arduous, but on the other hand I think that it is necessary to go on, in order to attain a greater exactitude and stringency of the problems bearing upon biologic plant-geography. For that matter, the character species used are surely only serviceable within a given area, because they here occur in comparatively few biotypes (races). The race-biological studies are likewise very valuable for the further substantiation of character species; often the best character species are found among the microspecies and races of the species (ecotypes).

The classification principles by means of B.D. types, which have been sketched above, apparently suffer from the drawback that the B.D. type of the species, in a way, is apt to be relative: a northern type in the flora of the Faroes will become southern in Greenland. Still, the oceanic and the continental requirements of the species will be determined once for all. If one only always knows the exact total distribution of the species (the variety), it is easy to say whether it is northern, southern etc.

7. The Faroes heath in relation to other heath-types.

It appears from the preceding studies that the Faroes heath types may recur in western Norway and in the British

Isles (particularly in the north or montane). How then does the heath-vegetation change when starting from the Faroes-West-Norwegian heaths, we pass to 1) more northerly, 2) more southerly, 3) more continental regions?

1—2). Along the Atlantic coast of Europe, a distinction may be made between at least 5 different heath types (not taking the moist heath series into account). Each of these consists of a number of sociations which we cannot here deal with in detail. The northernmost type is a *Rhacomitrium hypnoides* heath, in which dwarf shrubs frequently may be present in rather large quantities; the transition e. g. to *Empetrum Rhacomitrium* heath is quite gradual. Already at Lofoten, in sheltered places, *Empetrum*, *Calluna*- or *Vaccinium myrtillus-Hylocomium* sociations occur (Du Rietz 1925, pp. 47—50). Farther south (in Møre) there is a transition from heaths rich in *Rhacomitrium* to heaths rich in *Hylocomium*, and at the same time *Calluna* and *Erica cinerea* play the principal part in drier soil, while *Vaccinium myrtillus* rather keeps to moist northern slopes. The development of the heath farther south (British Isles, France, Spain, Portugal) has been mentioned earlier in this work. In England and northern France one passes from *Calluna-Erica cinerea* heath to *Calluna-Erica cinerea-Ulex* heath, which again in southern France are replaced by the heaths of Les Landes (e. g. *Erica scoparia-Molinia*-Soc.) which forms a transition type to Macki. South of France the heath becomes montane (the Pyrenees, northern Portugal, the Azores); on the Continent *Erica vagans, cinerea, scoparia* and *umbellata* are the dominants in heaths; in the Azores there is on the other hand a characteristic *Calluna-Thymus-Dabeocia* heath (Guppy 1917).

The vertical zonation corresponds very well with the horizontal one. In his description of the mountains of Cumberland Leach (l. c. p. 89) says that the heath (*Calluna*, frequently with *Erica cinerea*) is the dominating type of vegetation between a height of 400 and 650 m. At 650 m. above the sea *Calluna* reaches a vertical frequency limit, seeing that it is only found in sheltered localities higher up in the mountains. The heath here consists of *Empetrum* and *Vaccinium myrtillus* and *vitis idæa*, but is otherwise restrained by Alpine grass-land (*Festuca vivipara-Alchemilla alpina*). On the tops fell-field and *Rhacomitrium hypnoides* heaths are found. In the mountains of Wales similar conditions prevail according to Price Evans (1932). *Calluna* here reaches its optimum between 335 and 488 m. above the sea. The *Ulex*-species are associated with the lowland. Above 488 m. *Empetrum*, *Vaccinium myrtillus* and *Festuca vivipara* become more frequent. Nearest the top (762—884 m.) there are lichen or *Rhacomitrium* heaths, frequently with *Empetrum* and *Vaccinium*. There is no doubt that the English *Calluna* zone corresponds with the Faroes Atlantic-cold-temperate zone (0—300 m. above the sea) which higher up is replaced by a transition zone, dominated by grass-vegetation (*Nardus*, *Festuca vivipara*), and then again at a height of 500 m. above the sea merges into the Alpine zone with fell-field, *Rhacomitrium* heaths and snow patches (Böcher 1937 b, p. 196).

3) The heath in the Faroes and W.-Norway (partly) is situated within the "maritime Kahlregion" (Du Rietz); in an easterly, more continental direction the heaths are frequently alpine or conditioned by culture, which makes comparisons difficult. If, however, we keep to the coast zone, allied heaths will be found in more continental regions in about the same latitude as the Faroes. The more

continental type corresponding with the *Calluna-Erica cinerea* heath with a southern exposition seems to be a *Calluna* or a *Calluna-Arctostaphylos uva ursi* heath. At Mandal and in several other places in southern Norway there were such dry heaths on southern slopes, while the northern slopes had a *Calluna* vegetation with much *Vaccinium myrtillus* (at Mandal f. inst. *Empetrum, Vaccinium vitis idæa, Cornus suecica, Arnica, Deschampsia flexuosa, Potentilla erecta* and *Hylocomium* species). Such heaths are, however, practically not to be distinguished from most of the Danish ones, and therefore it is surely justifiable to regard our *Calluna-Arctostaphylos* and perhaps also *Calluna-Empetrum* or the *Calluna-Empetrum-Vaccinium vitis idæa* heath with *Hylocomium* and *Cladina* (cf. Mølholm Hansen, 1932) as sub-oceanic types corresponding with the euoceanic heaths of the Faroes and western Norway.

Tüxen & Diemont (1936) describe the transition in the heath-vegetation from west to east in the lowland of north-western Europe. The western *Erica-cinerea-Ulex europæus*-Assoziation (with *Calluna*) is, in Germany, replaced by the sub-oceanic *Calluneto-Genistetum*, which in its turn further east gives way to a still more continental *Calluna-Antennaria*-Assoziation. In Jutland there is an interesting transition between the Scano-Danish heath (*Calluna, Empetrum, Vaccinium vitis idæa, Arctostaphylos uva ursi* and northerly exposed *Vaccinium myrtillus*, now and then *Cornus suecica*) and the more southerly *Calluna-Genista* heath.

It is evident that both in the direction east to west and north to south it will be possible to distinguish these heath types objectively by means of the computation of the B.D. percentages, and at the same time it will be possible in that way to obtain an ecological-geographical characterization of the heaths in question. It is the idea to attempt something in this line in a future work on Scano-Danish heaths.

8. Problems regarding the History of the Heath Flora of the Faroes.

Ostenfeld (1901 b) and Warming (1903) were of opinion that the Faroes during the glacial epoch had been entirely devoid of plants and that the flora had immigrated postglacially by a landbridge (Ostenfeld), or across the sea (Warming) from the British Isles. The investigations of later years have to some extent changed the idea of conditions during the glacial age. A number of botanical and zoological arguments have been advanced in support of the idea that, during the last glacial epoch, a rather large fauna and flora must have been able to live in several localities of the North. As to the Faroes the zoological material (Wolff 1928, Spärck 1929, West 1929, Lindroth 1931) point very much in the direction that the Faroes cannot have been entirely glaciated during the last ice age; a number of animals must be supposed to have lived in the islands since the last interglacial epoch. In the freshwater fungus *Heteromeyenia ryderi* Spärck has further found an American element in the fauna of the Faroes[1]. This species is at present widely distributed in Atlantic America (from Nova Scotia to Florida), but in Europe it is only found in the Faroes, on the island Mull off western Scotland and in western Ireland. There is here a parallel of the American element in the flora of Ireland, and this element is regarded as a relic of the last interglacial period (Fernald, Nordhagen, Praeger), where there is supposed to

[1] In *Habenaria albida* var. *straminea* Morris we have an example of an American element in the flora of the Faroes (see Fernald 1929).

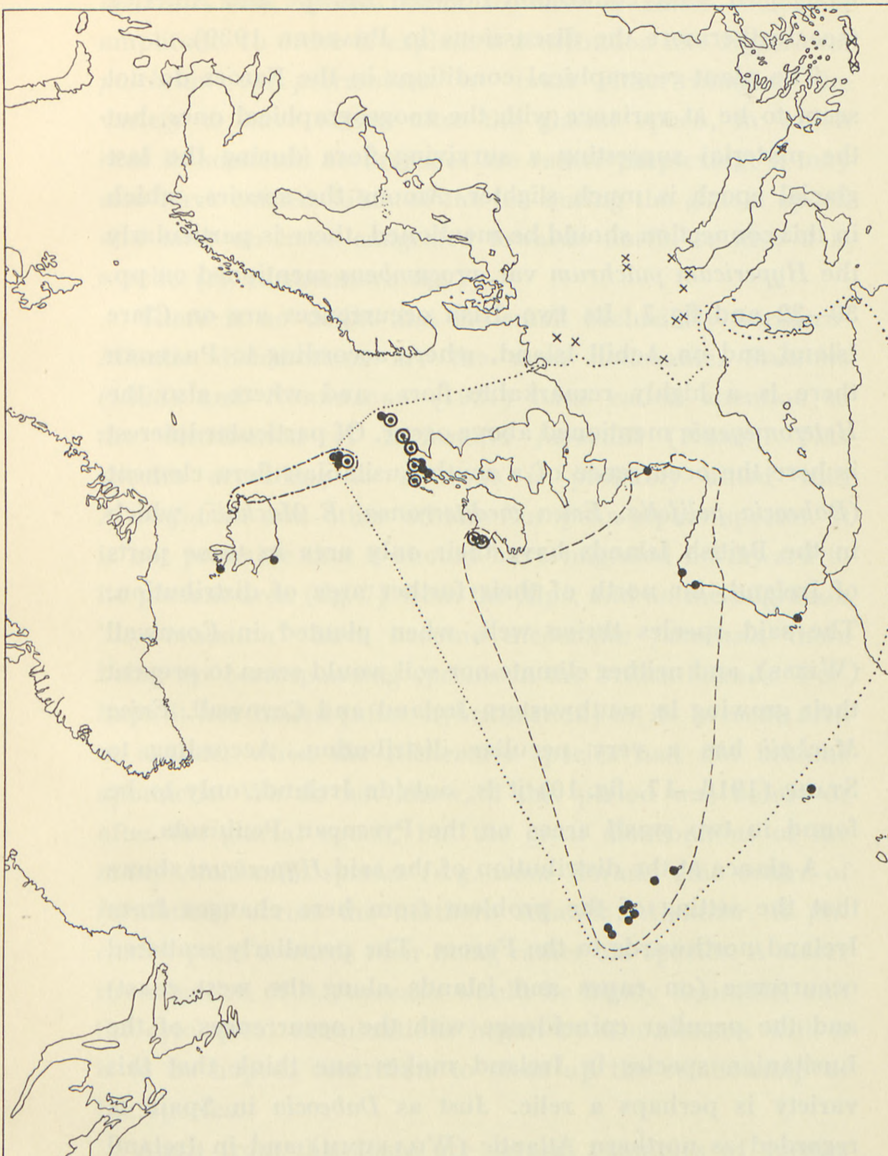


Fig. 7. Distribution of *Anagallis tenella* (·····, ×: scattered occurrences) according to Lüdi (in Hegi's Flora), *Dabeocia polifolia* (— — —) according to Stapf, *Alchemilla færöensis* (—·—·—), *Hypericum pulchrum* var. *procumbens* ⊙ and *Plantago lanceolata* var. *dubia* subvar. *eriophora*: ● (see for this type the text pp. 33—36).

have been some connection between Europe and America (see furthermore the discussions in Praeger 1939).

The plant-geographical conditions in the Faroes do not seem to be at variance with the zoogeographical ones, but the material suggesting a surviving flora during the last glacial epoch is much slighter. Among the species, which in this connection should be mentioned, there is particularly the *Hypericum pulchrum* var. *procumbens* mentioned on pp. 30—32 and fig. 7. Its two Irish occurrences are on Clare Island and on Achill Island, where according to Praeger there is a highly remarkable flora, and where also the *Heteromeyenia* mentioned above occur. Of particular interest is here the occurrence of a south-Lusitanian flora element (*Dabeocia polifolia, Erica mediterranea, E. Mackaii*) which in the British Islands have their only area in these parts of Ireland, far north of their further area of distribution. The said species thrive well, when planted in Cornwall (Weiss), and neither climate nor soil would seem to prevent their growing in southwestern Ireland and Cornwall. *Erica Mackaii* has a very peculiar distribution. According to Stapf (1916—17, fig. 10) it is, outside Ireland, only to be found in two small areas on the Pyrenean Peninsula.

A glance at the distribution of the said *Hypericum* shows that the setting of the problem from here changes from Ireland northwards to the Faroes. The peculiarly scattered occurrence (on capes and islands along the west coast) and the peculiar coincidence with the occurrences of the Lusitanian species in Ireland makes one think that this variety is perhaps a relic. Just as *Dabeocia* in Spain is regarded as northern Atlantic (Willkomm) and in Ireland as southern, in the same manner the *Hypericum* variety is regarded as southern on the Faroes, but as northern in

Ireland. Both species seem to have a small ecological amplitude. In order to explain a distribution like *Hypericum pulchrum* var. *procumbens* we must either imagine the variety to have arisen after the glacial epoch, in which case its scattered occurrences are rather perplexing; it may also have existed south of the ice during the glacial epoch and later on have emigrated towards north, or also it is a relic (cf. furthermore fig. 7).

There is no doubt that the small exclusively northern-Atlantic distributions are the most noticeable. Simmons (1898) and Nordhagen (1931) have called attention to the distribution of *Alchemilla færøensis* (Buser). This species according to Simmons is probably allied with *A. conjuncta* and other middle-European-alpine species. It is not probable that it should have migrated northward to its present area (fig. 7) from the Alps, and on the migration "by mutation" have become *Alchemilla færøensis,* there being no corresponding species in the British Islands. Perhaps it has arisen (after hybridization) in its present area at a time, when the *Alchemilla* species had not become apomictic. We do not know, if this period was before or after the glacial epoch, but the great distributions of the many *Alchemilla* species (e.g. from Eurasia (the centre of formation) across the northern Atlantic: *A. minor, A. filicaulis*) point towards their being rather old species. A closer investigation of *A. færøensis* would be highly desirable, and the cytological examinations begun by Gudjónsson will, it is to be hoped, contribute to clear up the relationship of the species.

Apart from this there are several examples of species the distribution of which falls within the northern-Atlantic area. Degelius (1935, p. 192) mentions a good deal of

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liver mosses and some lichens, *Juncus Kochii* and *Hymenophyllum peltatum*. These species must have arisen after the glacial epoch, or else they must have made the journey out and back to the south during the glacial epoch, without leaving traces of this journey in the form of scattered finds towards south or occurrences in more southerly mountain regions, or also they are relics. Degelius rather leans to this opinion: "Mehrere Umstände sprechen dafür, dass das ozeanische Florenelement, das im grossen und ganzen als ein Reliktelement des Tertiärs in Europa aufzufassen sein dürfte, an eisfreien Küstenstrichen der vereisten Partien von Nordwesteuropa (wenigstens im Süden) weiterleben konnte."

Besides the "good" species, there are also some varieties which are associated with the northern-Atlantic area. In reality some of these varieties (races) are well-defined, and the transition from species to variety often depends upon an estimate, so that the use of them as plant-geographical arguments only meets one difficulty, *viz.* that our knowledge of them is frequently defective. Besides the above-mentioned *Hypericum* variety I will call attention to the following varieties:

Veronica officinalis var. *glabrata* Fristedt; "an excellent form" (clear variety) according to Rostrup 1870. Material from the Faroes (transplant series and progeny individuals) maintain their appearance in culture. Individuals from alpine localities are difficult to cultivate in Copenhagen. The variety is distributed over Scandinavia (Ångermanland (Fristedt), the Stockholm region, southern Norway near Oslo and several other localities, farther north in Ranen), but it is hardly alpine in any of these places; besides it is to be found in the Faroes and Iceland and probably also in Scotland ("a nearly glabrous form" on Glas Thulachan, Perthshire (Druce) according to Williams, Loch Maree side, West Ross according to DRUCE 1929 "var. *glabrata* Bab"[1]). A closer examination should be made of the fact, whether the type which in HEGI's Flora is mentioned as "*f. glabrescens* Bolle" (Rüdersdorf at Berlin) and is designated "fast kahl" has anything to do with var. *glabrata* Fristedt.

Polygala vulgaris var. *Ballii* (Nym.) Ostf. A very much disputed variety (or rather group of races). All agree in the desire to distinguish a variety, but the material from the various regions does not prove to be alike; the Irish plant is different from that of the Faroes, and there also prove to be difficulties in referring all British var. *Ballii* to the same taxonomical unity (see PRAEGER, WILLIAMS). Plants which have been referred to this variety or allied varieties, are found from the Faroes (rather common), Scotland (DRUCE l. c. "a lowland limestone plant with profuse blue flowers") and Ireland (see PRAEGER, 93, 422), here they have from of old been identified on Ben Bulben, where at present we have the only habitat of *Arenaria ciliata* ssp. *hibernica* Ostf. & Dahl. The localities are all calcareous; (both on Ben Bulben and Glenade it grows together with *Dryas*). In the Faroes, on Kodlur at Ejde, I also saw it together with *Dryas*. In Norway the variety was first found by Ostenfeld on Mögsterøen (HOLMBOE Bergens Mus. Årbok. Naturvidsk. rekke. No 10, 1917—18); according to information given by Dr. KNUT FÆGRI it is furthermore to be found in four localities, all in Sunnhordland near Bergen and all calcareous. It really seems, as if we have a northern-Atlantic calciphilous group of races, the individual elements of which, owing to isolation (caused by the last glaciation?) are rather different. It should further be mentioned that more remotely allied types seem to occur in southern Europe (the eastern Pyrenees, BENNET 1878), San Sebastian (Herb. Cop.); see also WILLIAM's remark on *P. vulgaris* var. *Pindicola* (p. 522).

Finally may be mentioned the *Geranium Robertianum* ssp. *celticum* which was set up by OSTENFELD (1919), and which has a particulary narrow area in western Ireland; also *Plantago lanceolata* var. *depressa* Rostr. which is to be found in the Faroes and the Shetlands (BEEBY 1907), and the var. *dubia* subvar. *eriophora* of *Plantago lanceolata* mentioned on p. 34. The latter should be sub-

[1] In the earlier editions of BABINGTON's Manual there was a var. *glabra* (st. l. & calyx smooth; on mountains) but subsequently this variety was abandoned (PUGSLEY in a letter).

jected to a closer examination as, with the exception of the Shetlands, it seems rare in the British Isles. Williams only mentions pronouncedly hairy plants from the Shetlands, but it is probable that Druce's plants from West Ross belong to this subvar. The hairiness can, to some extent, be modified by outward conditions glass house plants being less hairy than open air plants. This makes it difficult in herbaries to distinguish the otherwise sharply defined type (see figs. 5—6) cf. discussions on hairiness etc. of *Pl. lanceolata* plants from England in Rep. Bot. Exchange Club 1911, p. 115. Perhaps there is here a northern Atlantic stock of relics (Vestmannaeyr, the Faroes, the Shetlands, Scotland) of an otherwise Mediterranean-Azorian plant.

All in all, the total zoological-botanical material from Scandinavia, Ireland, the Faroes and Iceland as well as from Greenland, is large enough to set up a rather plausible supposition, *viz.* that a great part of the present flora in the said countries may have existed there since the last interglacial period. The quartary-geological material, however, puts certain obstacles in the way of this hypothesis. Scattered investigations of English bogs pointed rather in the direction of there having been an arctic flora in ice-free places during the last glacial epoch (see the Discussion in Weiss 1934); pollenstatistic investigations in Ireland (Jessen & Farrington 1938) show somewhat similar features. The species found are, however, all lowarctic-subarctic.

As neither the biogeographical nor the quartary-geological material can be overlooked, it follows that a synthesis of the material of the two groups must be attempted. But here we necessarily enter the fields of aut-ecological and race biological investigations, the latter to examine whether the presumed stocks of relics are genetically different from one another and from the species in its entirety (cf. my theory on biotype-elimination by migration across the Atlantic (*Eriocaulon septangulare, Anthoxanthum* et. al.)).

We must try to find out whether the stock of biotypes of *Eriocaulon*, which is to be found in Ireland, is at all able to live elsewhere in Europe in otherwise similar localities. If it thrives excellently and spreads locally when being transplanted to English bogs, this is an indication that the Irish occurrence is a result of the survival of the species from the glacial epoch in Ireland and the later local spreading there. If it cannot thrive outside Ireland, this may be due to the fact that during its migration there it has become hyper-oceanic; the distribution in Ireland then becomes climatically determined, but in this (and in several other cases) it is difficult to imagine a post-glacial immigration from America, and so the biotype elimination would take place in the interglacial period and later continued during the last glaciation. The species in that case, however, becomes a kind of relic[1].

Through the aut-ecological investigations we must try to understand how the Lusitanian and Atlantic species[2] could exist simultaneously with a glacial epoch. The studies of the Faroes heath which are mentioned on pp. 3—14 show that in any case the *Calluna-Erica cinerea* heath contains relatively southern species. It will then be of value to investigate what is the state of the latter when exposed to greater cold.

In studying the flora of the heath when approaching its vertical line of growth, it appears that a great number of the species here enters into other vegetational types than heath. In further illustration of this a few examples will be given:—

[1] Cf. furthermore the discussion in PRAEGER 1939.

[2] As to the Ecology of *Arbutus unedo* at Killarney in Ireland see TURNER & WATT (1939).

The Faroes. *Nardetum* at a height of 460 m., rich in species and probably covered by snow in the winter: *Blechnum*! *Potentilla erecta, Orchis maculatas, Galium saxatile, Calluna* (cf. Böcher 1937 b, p. 175).

South-facing herb-field, rich in species and 500 m. above the sea, probably covered by snow during the winter: *Galium saxatile, Anthoxanthum, Polygala serpyllacea, Brunella vulgaris, Hypericum pulchrum* v. *procumbens, Carex pilulifera, Veronica officinalis* v. *glabrata* (Böcher l. c., p. 179).

South-facing snow-patch, 670 m. above the sea: *Nardus, Veronica officinalis* v. *glabrata, Anthoxanthum, Galium saxatile, Blechnum, Potentilla erecta* (Böcher l. c., p. 182).

Grimmia heath, 360 m. above the sea: *Nardus, Anthoxanthum, Galium saxatile, Deschampsia flexuosa, Carex pilulifera, Luzula silvatica* (sterile). (Ostenfeld 1901 a, p. 32).

Grimmia heath 570 m. above the sea: *Deschampsia flexuosa, Galium saxatile, Veronica officinalis, Pinguicula, Anthoxanthum, Carex "flava"* (Ostenfeld l. c., p. 48).

Grimmia heath with *Nardus* and *Lycopodium alpinum* 360 m. above the sea: *Potentilla erecta, Galium saxatile, Anthoxanthum, Luzula silvatica* (sterile). (Ostenfeld l. c., p. 53).

Moist slope at a height of 400 m., the soil covered by *Anthelia julacea: Nardus* and *Juncus squarrosus* as dominants, besides i. a. *Narthecium* (sterile), *Potentilla erecta, Scirpus cæspitosus* (Ostenfeld l. c., p. 56),

The above-mentioned *Grimmia* heaths and more particularly the "moist slope" are surely in a large degree covered by snow during the winter.

In Norway I had in several localities an opportunity to observe how *Calluna*, the higher one gets, became more and more a snow-patch plant. As an example I may mention that it was observed on the top of Vaarstøl at Bykle in a south-facing *Vaccinium myrtillus* heath close to a typical snow-patch together with *Phyllodoce cœrulea* and *Salix herbacea*, but was absent in the more snow-bare *Loiseleuria-Empetrum* heath rich in lichens.

There thus seems to be a connection between snow-patch (and herb-slope) and oceanic species (cf. Böcher 1938, pp. 286—287), which is easily understood, as the cover of snow causes the microclimate of the habitat to become relatively oceanic (small temperature amplitude, moist soil etc.).

In this connection must also be mentioned a species like *Dabeocia polifolia*. According to Praeger this species reaches up to 600 m. above the sea at its northern limit in Ireland; in the Pyrenees *Dabeocia* is subalpine and covered by snow for five months. In the Azores it is according to Guppy (l. c. p. 433) most common between a height of 1700 and 2500 m., but comes in scattered individuals down to about 800 m. above the sea. During the winter it is here exposed to frost, snow and wind, in the summer to drought and sun.

This discussion may be summarized as follows: The occurrence of low-subarctic species during the last glaciation and at the beginning of the post-glacial epoch need not exclude the occurrence of southern species. There may have been a low-arctic vegetation near the ice, whereas local, microclimatic oases existed on the south-facing slopes on the outermost capes or the freely situated islands, washed by the Golf Current, where the southern species could exist sheltered by snow against the winter cold. Along the Blosseville Coast the southern element is associated with the southern snow-covered herb slopes on capes and nunataks here, however, only slightly influenced by the Golf Current (the Irminger Current). Even though we imagine the temperature to fall several degrees, it is probable that snow-patches may have been able to form on the southern slopes of the lowland with a great deal of rather southern species, particularly those mentioned in the examples given above. Many of these have, however, now their optimum in heaths and related communities, i. e. pronouncedly temperate lowland communities. In the examples *Erica cinerea* and *Carex binervis* are lacking, the most southerly of the heath species which on an average require 2° in January. It is therefore much more difficult to imagine a glacial survival of these species; however, it must be borne in mind how rough our thermic limitation of the plant areas is, and how little we know of the climate conditions resulting in a glacial epoch. As far as the Faroes are concerned *Erica cinerea* and similar species may perhaps at a rather early period have been able to immigrate postglacially from the south, but as to western Norway this is much more difficult, cf. Holmboe (1927), Degelius (l. c.).

The flora and vegetation of the Faroes must be examined once more from other points of view. Ecological and race-biological investigations are required on a large scale. As an example may be mentioned an interesting problem connected with *Pirola minor*. This temperate species is in the Faroes only found as alpine and most frequently sterile. What then is the relation of the Faroes biotypes to this species in its entirety? For all the problems which have been dealt with here, also other glaciological investigations will naturally be highly needed.

Dr. Knut Fægri has helped me with the planning of my voyage in Norway and later on with information as to the occurrence of the said varieties in that country. Dr. H. W. Pugsley, England, and Dr. Lloyd Praeger, Eire, have supplied me with information as to the occurrence of the species in Great Britain and Ireland, while Mr. Aug. Hesselbo has kindly determined a great part of the mosses mentioned in the treatise (more particularly liver mosses). To all of these I express my sincere thanks and I also beg to thank the Rask Ørsted Fond for defraying the expences of the translation of the treatise.

Copenhagen, October 1939.

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T. B. phot.

Fig. 1. Southwest-facing *Calluna-Erica cinerea* heath at Torvadalsá at Klaksvig (Bordö Vig), cf. Table 2, Nos. 4 and 6. My wife at the edge of a dense patch of heath on the border line of the grass-moss-community.

T. B. phot.

Fig. 2. South-facing slope with *Calluna-Erica cinerea* heath at Bordö Vig; in the foreground a transition vegetation very rich in grasses. The photograph taken on an unusually beautiful summer day, so hot that the evaporation of the earth caused the formation of misty clouds.

T. B. phot.

Fig. 1. *Calluna-Erica cinerea* heath at Haugesund in Norway (the shooting ranges at Kvala), cf. Table II, No. 8. Besides *Erica* and *Calluna, Juniperus communis* is seen.