Det Kongelige Danske Videnskabernes Selskab Biologiske Skrifter, bind 7, nr. 4

Dan. Biol. Skr. 7, no. 4 (1952)

# LICHEN-HEATHS AND PLANT SUCCESSIONS AT ØSTERBY ON THE ISLE OF LÆSØ IN THE KATTEGAT

BY

TYGE W. BÖCHER



København i kommission hos Ejnar Munksgaard 1952 DET KONGELIGE DANSKE VIDENSKABERNES SELSKAB udgiver følgende publikationsrækker:

L'Académie Royale des Sciences et des Lettres de Danemark publie les séries suivantes:

Oversigt	over selskabets	virksomhed (8°)	
	(Annuaire)		

Historisk-filologiske Meddelelser (8°) Historisk-filologiske Skrifter (4°) (Histoire et Philologie)

Arkæologisk-kunsthistoriske Meddelelser (8°) Arkæologisk-kunsthistoriske Skrifter (4°) (Archéologie et Histoire de l'Art)

Filosofiske Meddelelser (8°) (Philosophie)

Matematisk-fysiske Meddelelser (8°) (Mathématiques et Physique)

Biologiske Meddelelser (8°) Biologiske Skrifter (4°) (Biologie) Dan. Vid. Selsk. Overs. Dan. Hist. Filol. Medd.

Dan. Hist. Filol. Skr.

Dan. Arkæol. Kunsthist. Medd. Dan. Arkæol. Kunsthist. Skr.

Bibliografisk forkortelse Abréviation bibliographique

Dan. Filos. Medd.

Dan. Mat. Fys. Medd.

Dan. Biol. Medd. Dan. Biol. Skr.

Selskabets sekretariat og postadresse: Ny vestergade 23, København V. Selskabets kommissionær: EJNAR MUNKSGAARD's forlag, Nørregade 6, København K.

L'adresse postale du secrétariat de l'Académie est: Ny vestergade 23, Copenhague V, Danemark.

Les publications sont en vente chez le commissionnaire: EJNAR MUNKSGAARD, éditeur, Nørregade 6, Copenhague K, Danemark. Det Kongelige Danske Videnskabernes Selskab Biologiske Skrifter, bind **7**, nr. 4

Dan. Biol. Skr. 7, no. 4 (1952)

# LICHEN-HEATHS AND PLANT SUCCESSIONS AT ØSTERBY ON THE ISLE OF LÆSØ IN THE KATTEGAT

BY

TYGE W. BÖCHER



København i kommission hos Ejnar Munksgaard 1952

#### PRINTED IN DENMARK BIANCO LUNOS BOGTRYKKERI

#### 1. Introduction.

The isle of Læsø lies in the northern part of the Kattegat between Jutland and Sweden. Apart from some higher dune areas in the northern and eastern part the level surface rarely exceeds 30 feet above the sea. The island is entirely built up of alluvial deposits, and most soils consist of sand or sand covered by a mor layer. More than half is not cultivated, being chiefly occupied by various dwarf shrub heaths, *Molinieta*, a number of different dune vegetations and salt marshes. The eastern part in the vicinity of the village Østerby is a narrow peninsula about five miles in the direction west-east and two miles from north to south (fig. 1). In this part less than a quarter is now cultivated and the influence of man in the uncultivated areas is very limited. Along the shore the vegetation may be almost entirely natural and thus very well suited for ecological research.

The Østerby region was visited by me in 1939 and 1948. In both years most importance was attached to observations of the vegetation rich in lichens which is developed on drift sand or sandy gravel behind the beach. Some of the results from 1939 were published in a previous paper (1941 b), which further contains some analyses of lichen heaths from the northernmost part of Jutland (the Skaw). The lichen-dune vegetation of the latter area was first studied by RAUNKLER (1913; see RAUNKLER 1934 pp. 332—338). Other analyses of lichen heaths on dune soils in different parts of Denmark are found in BÖCHER 1941 a, 1945, and 1947.

From the previous paper on the dune vegetation of Læsø (1941 b) we may summarize the following facts:

(1) Profile transects on various points on the north side of the peninsula from the beach to the closed dwarf shrub vegetation (the dune heath) reveal rather few zones owing to the low content of carbonates and the low pH values of the sand on the foreshore and the youngest dunes. The green fixed dune communities which in other parts of Denmark are frequently inserted between the white and the typical grey dunes with acid soils are absent or fragmentarily developed owing to insufficient supply of basic particles blown in from the sea shore. On the other hand the grey dune vegetation with abundant lichens and *Corynephorus canescens* covers large areas and varies very much. It is found on the old inner coastal dunes as well as on the inland dunes and in the blow-outs formed on the dune heaths.

(2) The lichen heath vegetation of the grey dunes comprises the following sociations:
(a) Corynephorus-Cornicularia aculeata-soc. frequently rich in Polytrichum piliferum.
On acidic sand and gravel; frequent in blow-outs of the inland dunes, here succeeding a pioneer stage dominated by Polytrichum.

Fig. 1. Map showing the eastern part of the isle of Læsø (the Østerby peninsula). Most of the analyses of vegetation contained in the present paper were undertaken on the north side of the peninsula between Bansten Bakke and Syrodde.

4



Nr.4

(b) Corynephorus-Cladonia destricta-soc. On acid sand, as a rule exposed to wind, sometimes even in places where a slight removal of sand takes place. Occurs together with the preceding sociation or mixed with it. Many observations make a succession from a Corynephorus-Cornicularia-soc. to a Corynephorus-Cl. destricta-soc. very probable.

(c) Corynephorus-Cladonia rangiformis- and furcata-sociations. These sociations are mainly found on the coastal dunes, in places with moderately acid soil. In similar places a Corynephorus-Cladonia alcicornis-soc. occurs. The latter is furthermore found as very small patches in inland dunes.

(d) Corynephorus-Cladonia mitis-soc., the most important type of lichen heath dominated by Cladinae, in particular C. mitis, but also containing C. sylvatica, tenuis, impexa, and rangiferina. Carex arenaria and Ammophila sometimes abundant. The type occurs as the typical grey dune vegetation on old coastal dunes and inland dunes. The lichen carpet is very dense. The soil is acid with a somewhat higher content of organic matter than in the preceding sociations. Where the organic content increases further, as in the oldest parts of the peninsula, Corynephorus is subordinate, while Festuca ovina is most dominant, forming a dense Festuca ovina-Cladina-soc.

(e) Corynephorus-Cetraria nivalis-soc. occurs together with the Cladina-type, but prefers less protected places where the competition with the species of Cladina is less intense. Lichen heaths with Cetraria islandica as a dominant, on the other hand, are mainly found on somewhat sheltered spots.

The floristic composition of these types of lichen heath appears from Tables 2, 8, and 9 in Böcher (1941 b).

(3) Blow-outs are formed in the white and grey dunes as well as on the dune heath (*Calluna-Empetrum*-heath) farther inland. Where the blow-outs are surrounded by lichen heath or *Calluna-Empetrum*-heath a number of successions from open sand to lichen heath and further to dwarf shrub heath may take place. In many blow-outs the bottom is soon colonized by *Empetrum*, *Salix arenaria*, and *Calluna*. From these central heath patches where the soil may be less dry, the heath vegetation expands and invades open sand as well as lichen heath on the slopes of the hollows, but it is hardly able to settle on the driest spots and those parts of the slopes where the wind erosion is particularly strong.

(4) On the border between the *Calluna-Empetrum*-heath and the lichen heath of the grey dunes a similar succession may take place resulting in a formation of a dwarf-shrub subclimax vegetation. In many cases, however, a degeneration of the dwarf shrubs occurs. In particular *Calluna* is inclined to die, thus forming spaces (destruction hollows or areas) which are colonized by lichens or *Empetrum*. In certain cases blow-outs may be formed where the dwarf shrubs have disappeared.

During the author's stay on Læsø in 1939 some permanent quadrates were selected for a close study of the successions. In some cases the degree of cover per square metre was estimated for all species by means of the HULT-SERNANDER scale and the distribution of the dwarf shrubs and the lichen heath mapped. The selected areas were marked out by means of four concrete poles in the corners (fig. 4). In 1948 the permanent quadrates were reinvestigated. The results of these reinvestigations as well as a number of supplementary studies of the lichen heath and of the succession of the vegetation leading from embryonal dune to lichen heath are contained in the present paper.

The Østerby peninsula ends in a spit of land called Bløden Hale (fig. 1). In the southern part of this spit as well as on the small islet of Knotten south of the point of Bløden Hale the dunes are very young and low.



Fig. 2. Large newly formed area on the southernmost part of Bløden Hale. Low dunes covered by Agropyrum repens and Salsola kali. Ammophila is invading some of the dunes. T.W.B. phot. 1948.

They are formed on a very broad sandy beach which constantly increases owing to the supply of fresh sand being washed ashore by the south-going current. The first stages are characterized by the occurrence of plants which are halophilous and demand an admixture of manure, in particular from dead seaweeds.

(1) Suaeda maritima stage on saline and more or less manured and moist sand.

(2) Salsola kali-Cakile maritima stage on somewhat saline and manured sand, which is drier. Subordinate species are Atriplex hastata, A. sabulosa, Suaeda maritima, Agropyrum repens, A. junceum, Agrostis stolonifera, Plantago maritima, and Glaux maritima.

(3) Agropyrum-Elymus stage on very low, embryonal dunes, repeatedly subject to changes during springtides. Soil almost as at the preceding stage, but less manured, whenever Agropyrum junceum dominates. A. junceum- and Elymus-sociations are only developed on the islet of Knotten, not on the southernmost part of the spit, which may be due to the cattle grazing there. On the other hand, the southern point of the spit has large areas covered with Agropyrum repens-soc. (fig. 2) containing Cakile and Salsola, the latter sometimes in great abundance.

(4) Ammophila stage. Ammophila invades low, young dunes which may be comparatively stabilized and consist of neutral sand with a very low content of salt or manure. pH in the soil was measured at 6.6–6.8 and the electrical conductivity varied between 56 and 58.<sup>1</sup> Frequent: Honckenya peploides. Scattered: Elymus, Agropyrum junceum, A. repens, Festuca rubra, Eryngium maritimum, Circium vulgare, C. arvense, Taraxacum sp., and Carex arenaria. (See also fig. 2).

Stages 1—4 are the only ones occurring on the islet of Knotten and the southernmost part of Bløden Hale. In order to follow the succession a number of squares forming a belt transect from the eastern to the western beach of the islet were analyzed. The line was marked in 1939 by a concrete pole and a large wooden pole. Unfortunately both poles had disappeared in 1948. The concrete pole had probably been covered by drift sand and the wooden pole set adrift by the sea. Although the exact position of the transect could not be localized again it was clear that the area occupied by Ammophila had been enlarged considerably, thus giving evidence of the succession Agropyrum-Elymus stage  $\rightarrow$  Ammophila stage.

Evidence of successions from stages like (1)—(2) to Agropyrum-Elymus stages and further on to an Ammophila stage was obtained by observations in another part of Denmark (Korshage, cf. Böcher 1952).

From the southern point of Bløden Hale and northwards the land becomes older and older and at the same time the dunes grow higher. One mile from the point they reach a height of 7 feet and at the lighthouse near the northeast corner of Læsø (Syrodde) 23 feet. The highest dunes (38 feet) are found west of Syrodde and on Jegens Odde. With increasing age the soil changes from circumneutral to acid reaction and a leaching of the sand becomes more pronounced. In the vegetation these changes lead to a succession from white to grey dune vegetation. The belts found from south to north on the Bløden Hale evidently correspond to successional stages:

(5) Carex arenaria—Festuca rubra—Ceratodon stage. The invasion of Carex arenaria or Festuca rubra frequently results in the formation of a  $\pm$  closed vegetation which, however, in the first stages frequently lacks cryptogams. Several sociations belong to this stage, thus (a) Ammophila-soc. with Festuca rubra, Jasione montana, Hypochoeris radicata, and Viola tricolor; (b) Carex arenaria-Honckenya-Galium verum-soc.; (c) Carex arenaria-soc. sometimes with abundant Eryngium maritimum and patches of Galium verum; (d) Festuca rubra-Galium verum-soc. with Bromus mollis,

<sup>1</sup> The figures given are the rest-conductivity,  $K_{zo^{\circ}} - (K_H^{+})_{zo^{\circ}} \cdot 10^6$ , (specific conductivity at 20° C from which the conductivity of the hydrogen ions is subtracted, cf. H. SJÖRS 1946).

Cerastium semidecandrum, Sedum acre, Poa pratensis, Agrostis tenuis, and Potentilla anserina. (e) almost as the preceding but with Ceratodon, Tortula ruralis, and Brachythecium albicans; (a) occurs mainly on dune slopes while (b)—(e) cover the more or less level areas between the dunes. The variation in the vegetation undoubtedly is a result of rather important soil differences. Carex arenaria seems to indicate a soil which is poor in easily soluble salts while Festuca-Galium-Sedum acre, etc., may be connected with richer soils. In a place with abundant Carex arenaria pH was 6.2 and the conductivity value 18. Another spot dominated by Festuca-Galium showed a pH-value of 6.1 and a conductivity value of 58, thus a value of the same magnitude as that found at Stage 4.

(6) Hypnum cupressiforme-Cladonia stage. This stage may follow stages with Ceratodon or Tortula-Brachythecium albicans. Hypnum cupressiforme is dominant together with Festuca rubra, but it is still possible to find weak specimens of Brachythecium albicans. Characteristic is the frequent occurrence of a number of lichens as well as Dicranum scoparium, Rhacomitrium canescens, Corynephorus canescens, Hypochoeris radicata, Hieracium pilosella, Teesdalea nudicaulis, Trifolium arvense and Rumex acetosella. Among the lichens the following are most important: Cladonia alcicornis (sometimes dominant), C. furcata (sometimes dominant), C. rangiformis, C. fimbriata, C. chlorophaea, Cornicularia aculeata and Peltigera canina. Cladonia mitis is very rare. There are also at this stage several sociations. The Festuca-Galium verum-Hypnum cupressiforme-soc. occurs on somewhat less dry ground than the F. rubra-Cladonia alcicornis-furcata-soc. pH in these sociations was measured to be 5.5 and 5.3 and the rest conductivity to be 38 and 32.

(7) Cladina-stage. The first patches dominated by species of the Cladina group occur a little more than a mile north of the southern point of Bløden Hale. The most important lichens are Cladonia mitis and Cornicularia aculeata. Of secondary importance are Cladonia sylvatica, rangiferina, impexa, uncialis, gracilis, pityrea, chlorophaea, furcata, alcicornis, Cetraria islandica, nivalis (very rare), Peltigera canina, P. rufescens and malacea. Corynephorus and locally Empetrum nigrum may dominate. Characteristic are further Calluna, Juniperus, Viola canina, Hieracium umbellatum, Armeria vulgaris, and Aira praecox. At this stage species like Galium verum, Trifolium arvense, Agrostis tenuis and Brachythecium albicans may still occur indicating a moderate poorness of the soil. pH and conductivity were measured in an Ammophila-Corynephorus-Cladonia mitis-Cornicularia-soc. and in an Empetrum-Cladonia mitisimpexa-soc. The pH values were 5.1 and 5.7 and the rest conductivity values 40 and 36, thus figures about the same level as at the preceding stage.

(8) Calluna-Empetrum-Cladina stage. At this final stage the heath invades the Cladina-vegetation. A stable subclimax heath may result, in particular on somewhat protected or less dry spots. In exposed or very dry places a degeneration of the dwarf shrubs may take place and frequently heath and lichen-vegetation are almost at equilibrium (see below). Particularly characteristic of this stage is a number of lichens occurring on old dead or dying twigs of the dwarf shrubs (Parmelia physodes, Cetraria glauca, C. chlorophylla, Usnea hirta) or on the ground where Calluna (or Empetrum)

have disappeared: *Cladonia glauca* and *C. floerkeana*. From this stage which is reached at Syrodde (the northeast corner, cf. fig. 1) there are three soil analyses giving the pH-values 4.3, 4.6, and 5.2 and the rest conductivity values 15, 30, and 14. These values are in good agreement with those found in still older vegetations on the Østerby peninsula and therefore this stage seems to constitute a termination of more or less complete stoppage also with regard to the soil development. There is further good agreement with the pH and conductivity values from *Corynephorion* and related communities in South Sweden (ANDERSSON & WALDHEIM 1946).

The succession of mosses and lichens described above reminds highly of that mentioned by RICHARDS (1929) from Blakeney Point in Norfolk. According to RI-CHARDS the first invaders are *Brachythecium albicans*, *Ceratodon* and *Tortula*. Later settlers are *Cornicularia aculeata* and *Cladonia furcata* and finally *Cladonia sylvatica*.

#### 3. The succession from lichen heath to dwarf-shrub heath.

This succession was studied in particular on Jegens Odde, the northernmost part of the Østerby peninsula (cf. fig. 1), on two permanent quadrates (I—II). On both quadrates the vegetation was mapped. In the large Quadrate II a system of connected squares each of 1 square metre were laid down and within these the degree of cover was estimated for all species. The analyses were made in 1939 and 1948.

Quadrate I (fig. 3). This quadrate was placed on a spot where Calluna had formed a heath patch surrounded by lichen heath (*Cladina* heath). The spot is seen on fig. 8 in Böcher 1941 b. In 1939 the southeast corner of the Calluna patch was bordered by an *Empetrum* patch, which seemed to enlarge its area fairly rapidly. The Calluna patch itself seemed also to be enlarging, but at the same time the Calluna had died away from three central areas and formed three enlarging rings. In the three destruction areas a colonization of lichens and *Empetrum* took place. The spot seemed particularly interesting as enlarging and dying-away of Calluna and competition between *Calluna* and *Empetrum* could be observed simultaneously there. In 1948 a considerable extension of the Calluna rings as well as of the Empetrum patches could be recorded (see fig. 3). The system of Calluna measured  $4 \times 2.3$  m in 1939 and  $5 \times 2.8$  m in 1948. The *Empetrum* patches inside the *Calluna*-area were considerably enlarged and had been able to gain a foothold in areas occupied by living *Calluna*. Empetrum shoots began bridging two of the destruction areas (B-C in fig. 3). Other Empetrum shoots from the large patch in the southeast corner of the quadrate tried to bridge the *Calluna* ring. The flora in the destruction areas was not considerably changed. This appears from analyses of Areas B and C:

1939: On the ground: Cornicularia aculeata, Cladonia floerkeana, coccifera (?), glauca, furcata, destricta, alcicornis (the latter only in Area C) and more scattered C. mitis, impexa, Hypnum cupressiforme, Corynephorus canescens, and (only Area C) Galium verum. On old or dying twigs of Calluna: Parmelia physodes, Cetraria glauca, and C. chlorophylla.

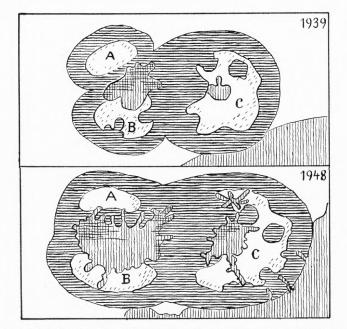


Fig. 3. Permanent Quadrate I ( $6 \times 3$  m) showing the development of a system of *Calluna* rings and *Empetrum* patches. Vertical hatching: *Empetrum*. Horizontal hatching: *Calluna*. Interrupted oblique hatching: *Parmelia physodes* on old twigs of *Calluna*. No hatching: *Cladina* mat. A.B.C. three destruction areas, cf. text.

1948: Additional plants in Area B not observed in 1939: Cladonia uncialis, Usnea hirta, Dicranum scoparium, Hieracium umbellatum, and Lotus corniculatus. Additional plants in Area C.: Cladonia tenuis, uncialis, and Hieracium umbellatum. Not refound: Hypnum cupressiforme, Cl. coccifera (?).

The centrifugal growth of *Calluna* reminds of the fairy-ring formation of different macromycetes. It seems probable that *Calluna* in the course of years makes the soil unfavourable for itself and, therefore, it can only thrive and flower in the periphery of the rings. In inland heath districts of Jutland *Calluna* generally dies away after a period of 30 years. This disappearance of *Calluna* may also be a result of changes in the soil produced by the plant itself. At all events it takes very long time before new *Calluna* plants appear on the spots or within such enlarging destruction areas as those in Quadrate I, where seedlings of *Calluna* were absent in both years of observation. On the other hand young *Calluna* plants occurred in several places outside the rings in the *Cladina* carpet. *Empetrum* may be less particular with regard to the soil and this seems to explain its ability to invade the destruction areas of *Calluna*. In addition to the two plants observed in 1939 a third plant occurred in 1948 in the northern corner of destruction area C. (Cf. fig. 3).

Quadrate II (figs. 4—6). This large quadrate was subjected to a more detailed analysis. From the mapping of the vegetation the following facts appear. In 1939 the eastern part of the quadrate (4—8, c—g) was occupied by a wide *Calluna*-ring with a large central *Empetrum* patch. The resemblance to Quadrate I was great, but the stage seemed much more advanced. The ring was closed no longer; in the northeast corner (8 c—d) and at another point (7 f) *Empetrum* had broken through it or had filled out a gap in it. In 1948 the *Calluna*-ring was breaking up into small isolated parts. In some of these the *Calluna* shoots were almost hidden in the vigorous

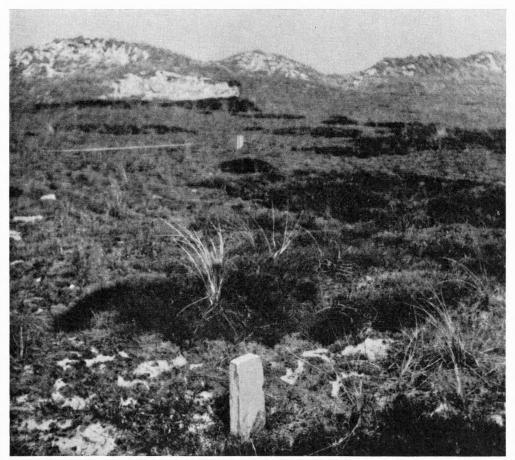


Fig. 4. Permanent Quadrate II in the grey dune areas at the point Jegens Odde. A vertical line through the middle of the picture cuts two of the corner pegs (1 g to the southwest in the foreground, 8 a behind, cf. figs. 5—6). Quadrate III is to the right of the blow-out in the background in the higher coastal dunes. T.W.B. phot. 1948.

*Cladina*-mat (e. g. 6 c), in others the *Calluna* shoots seemed able to compete with the lichens. The situation in 1948 may probably show the final stage of the development of the *Calluna*-ring. Future investigations will probably demonstrate the complete disappearance of it.

In the squares 6—7, b—c, a strong *Calluna* plant occurred in 1939. This plant had been able to enlarge its area in spite of the vigorous lichen mat surrounding it. Another young, very small plant in 3 a perished. If such plants succeed in competing

with the lichens they will undoubtedly be starting points of larger *Calluna* patches which later enlarge and finally die away in the central parts.

A very intricate system of expanding *Calluna*-patches occurred 1939 in Squares 1–4, e–g. The individual patches merged to some extent and some of them

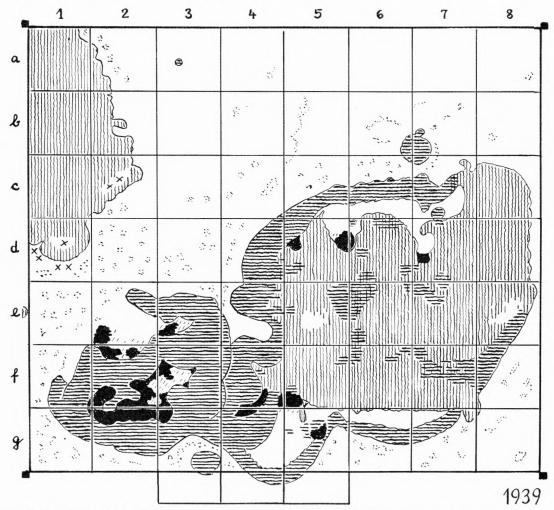


Fig. 5. Permanent Quadrate II in 1939, showing the grid and the distribution of the same species or communities as in fig. 3. Black: dead *Calluna*, ×: dead *Empetrum*. Small dots: open sand spaces in the *Cladina* mat. Other signatures cf. fig. 3.

had central destruction areas which also merged. From the observations made in 1948 it became evident that one of these vigorous *Calluna* patches (in 2-3 f) had been able to invade an old destruction area of another *Calluna*-patch, thus showing that the rule mentioned above is not without exceptions or that it must be confined only to apply to seedlings of *Calluna*, which also were missing in all destruction areas in Quadrate II.

Two large *Empetrum* patches could be studied in the quadrate. One of them was surrounded on all sides with *Cladina* heath, but only the eastern part of it got inside (Squares 1-2, a-d). The other, as already mentioned, had developed in an old destruction area of a *Calluna* patch. The growth of the first *Empetrum* patch

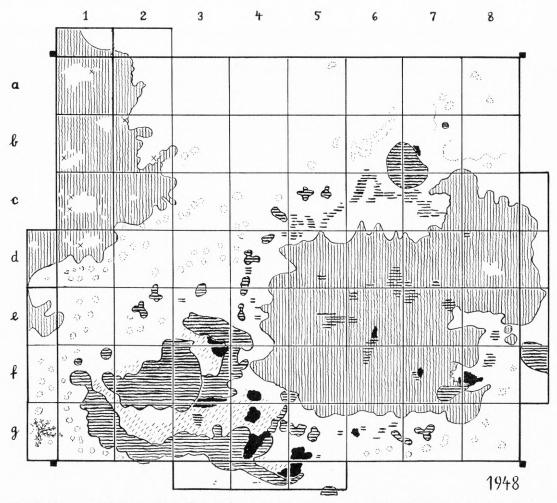


Fig. 6. Permanent Quadrate II in 1948. In 1 g a specimen of *Salix arenaria* has just got a shoot inside. More vigorous *Calluna* areas have contours whereas *Calluna* almost hidden in the *Cladina* mat is without a contour. Otherwise as in fig. 5.

during nine years was not very impressive, and it was evident that the shoots in 1948 were more scattered and that some small openings had appeared in the patch which to a great extent had been occupied by *Cladina*. The patch which first was surrounded by a *Calluna* ring showed an interesting divergent behaviour. Those parts which developed behind the extending *Calluna*-ring were clearly checked while those parts which in 1939 had broken through the ring generally showed more progress (see 8 c—d, 7-8 f—g) although a slight retrogression could be recorded in parts of 8 c.

Table 1 contains a summary of all occurrences and covering values in the two years of observation. The first three columns concern the whole permanent quadrate, the last two give the constancy percentage and average covering for ten selected Cladina heath squares (3 abc, 4 ab, 5 ab, 6 a, 7 a and 8 a) and ten dwarf-shrub heath squares (2 f, 3 f, 4 f, 5 ef, 6 def, 7 ef). Owing to the subjective moment in the determination of the degree of covering only large differences in covering values can be regarded as significant. On the other hand rather small differences between the two years with regard to occurrences or constancy must be considered significant. A considerable decline for Ammophila, Corynephorus, Festuca rubra, Hypochoeris radicata, Jasione, Cladonia impexa, C. rangiferina, and Cornicularia aculeata can be established and simultaneously an increase for *Hieracium umbellatum*, *Empetrum*, Cladonia mitis, C. gracilis, Cetraria islandica, C. chlorophylla, Parmelia physodes and the bryophytes. A moderate decrease in covering is found for *Calluna vulgaris* in the dwarf-shrub squares, a fact which corresponds very well to the more luxuriant growth of the epiphytes on old Calluna twigs, especially Parmelia physodes. The total number of occurrences in 1939 (662) is only slightly higher than that in 1948 (635) a fact which in particular may be connected with the decrease in occurrence of Ammophila, Corynephorus, and others. The decrease for Ammophila and Galium verum and the increase of the bryophytes may be results of a change in the soil complex (increase in acidity) while the decrease for Corynephorus, Hypochoeris, Jasione, and perhaps *Carex arenaria* may be connected with climatic conditions (cold winters) during the passed nine years (see below p. 16).

From the year 1939 we have a pH measurement from the soil underneath the *Cladina* mat in Quadrate II. The value (5.1) is higher than that from the same vegetation in 1948 (4.6). A soil sample from a place with degenerating *Calluna* collected in 1948 proved to be very different from that of the *Cladina* carpet the same year. Apart from its higher content of organic matter it was more acid (pH 3.9), but otherwise its conductivity value even after subtraction of the conductivity of the hydrogen ions was comparatively high (68 as against 30 in the soil under the lichen carpet).

The most important fact which appears from the investigation of Quadrate II is the very limited progress of the dwarf-shrub heath taken as a whole. The total covering for the two dwarf shrubs is 184 (1939) and 202 (1948) thus giving a difference of 18, which is hardly sufficient for a demonstration of an advance of the *Calluna-Empetrum* heath. As moreover a number of lichens have increased in frequency it seems in this case more adequate to speak about an equilibrium between lichen heath and *Calluna-Empetrum* heath. This is very interesting and gives an explanation of the apparent stable arrangement of the vegetational zones along the sea. The typical "grey dune"-vegetation (lichen heath) almost always occupies a zone between the white dunes or green fixed dune-communities and the dwarf-shrub heath. In certain cases the dwarf shrubs may invade lichen heath and fairly rapidly change it into a dwarf-shrub heath; with decreasing distance from the beach this advances more and more sluggishly and finally the succession may stop or go the other way when sometimes the lichen mat recovers lost ground. In this connection it may be mentioned

			19	939					1948		
Permanent Quadrate II	Nos. of occurrences (max: 56)	Sum of covering values <sup>1</sup>	Highest covering value <sup>2</sup>	Constancy per cent and average covering; lichen heath	Constancy per cent and average covering; dwarf-shrub heath	Nos. of occurrences (max: 56)	Sum of covering values <sup>1</sup>	Highest covering value <sup>2</sup>	Constancy per cent and average covering; lichen heath	Constancy per cent and average covering; dwarf-shrub heath	
Ammophila arenaria Corynephorus canescens. Festuca rubra Carex arenaria Hieracium umbellatum Hypochoeris radicata Jasione montana Galium verum Plantago maritima Calluna vulgaris Empetrum nigrum Viola canina Salix arenaria	$\begin{array}{c} 48\\ 37\\ 10\\ 56\\ 38\\ 29\\ 19\\ 13\\ 0\\ 32\\ 30\\ 5\\ 0\\ 317 \end{array}$	79 49 10 87 38 29 19 13 0 91 93 5 0 0	$ \begin{array}{c} 3 \\ 3 \\ 1 \\ 3 \\ 1 \\ 1 \\ 1 \\ 1 \\ 5 \\ + \\ - \\ - \\ - \\ - \\ - \\ - \\ - \\ - \\ - \\ -$	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{cccccc} 70 & 1 \\ 0 \\ 0 \\ 100 & 1.4 \\ 50 & 1 \\ 0 \\ 50 & 1 \\ 0 \\ 100 & 3.2 \\ \cdot 80 & 4.1 \\ 0 \\ 0 \end{array}$	$27 \\ 14 \\ 6 \\ 55 \\ 41 \\ 7 \\ 12 \\ 9 \\ 1 \\ 33 \\ 37 \\ 5 \\ 1 \\ 248$	$\begin{array}{c c} 31 \\ 14 \\ 6 \\ 59 \\ 52 \\ 7 \\ 12 \\ 9 \\ 1 \\ 81 \\ 121 \\ 5 \\ 1 \\ 399 \\ \end{array}$	$2 \\ 1 \\ + \\ 2 \\ 1 \\ 1 \\ 1 \\ + \\ 5 \\ 5 \\ 1 \\ + $	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$\underbrace{(\mathbf{x}_{1})}_{\mathbf{x}_{1}} \times \underbrace{(\mathbf{x}_{1})}_{\mathbf{x}_{2}} \times \underbrace{(\mathbf{x}_{2})}_{\mathbf{x}_{2}} \times \underbrace{(\mathbf{x}_{2})}_{\mathbf{x}$
Cladonia mitis — sylvatica } 3	56	207	5	100 4.2	100 2.6	56	218	5	100 4.7	<b>100</b> 2.5	(<)
<ul> <li>tenuis</li> <li>impexa</li> <li>rangiferina</li> <li>furcata</li> <li>gracilis</li> <li>gracilis</li> <li>uncialis</li> <li>destricta</li> <li>cornuta</li> <li>cornuta</li> <li>floerkeana</li> <li>floerkeana</li> <li>floerkeana</li> <li>chlorophaea</li> <li>pityrea</li> <li>glauca</li> <li>verticillata</li> <li>alcicornis</li> <li>islandica</li> <li>glauca</li> <li>glauca</li> <li>cornicularia aculeata</li> <li>cornicularia aculeata</li> <li>subaurifera</li> <li>subaurifera</li> <li>Sum</li> <li>Sum</li> </ul>	$\begin{array}{c} 35\\ 35\\ 52\\ 1\\ 29\\ 24\\ 4\\ 0\\ 2\\ 7\\ 3\\ 18\\ 0\\ 15\\ 0\\ 12\\ 9\\ 3\\ 11\\ 1\\ 1\\ 1\\ 18\\ 0\\ 0\\ 2\\ 0\\ 343 \end{array}$	$ \begin{array}{c} 38\\ 103\\ 1\\ 29\\ 24\\ 4\\ 0\\ 2\\ 7\\ 7\\ 3\\ 18\\ 0\\ 15\\ 0\\ 12\\ 12\\ 3\\ 111\\ 1\\ 55\\ 18\\ 0\\ 0\\ 2\\ 0\\ 0\\ 0\\ 2\\ 0\\ 0\\ 565\\ \end{array} $	$\begin{array}{c} 2\\ 5\\ +1\\ 1\\ 1\\ +1\\ +1\\ +1\\ 1\\ 1\\ 1\\ 2\\ 1\\ 1\\ +2\\ 1\\ -+\\ +\end{array}$	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{c} \textbf{80} \ 1.2 \\ 70 \ 1 \\ 0 \\ 20 \ 1 \\ 20 \ 1 \\ 0 \\ 0 \\ 20 \ 1 \\ 10 \ 1 \\ 40 \ 1 \\ 0 \\ 20 \ 1 \\ 0 \\ 0 \\ 0 \\ 30 \ 1 \\ 0 \\ 30 \ 1 \\ 50 \ 1 \\ 0 \\ 0 \\ 10 \ 1 \\ 0 \end{array}$	$\begin{array}{c} 27\\ 44\\ 2\\ 36\\ 20\\ 4\\ 2\\ 8\\ 12\\ 5\\ 16\\ 1\\ 17\\ 2\\ 11\\ 17\\ 2\\ 11\\ 8\\ 8\\ 11\\ 7\\ 34\\ 29\\ 2\\ 1\\ 2\\ 1\\ 366 \end{array}$	$\begin{array}{c} 27\\ 80\\ 2\\ 36\\ 20\\ 4\\ 2\\ 8\\ 12\\ 5\\ 16\\ 1\\ 17\\ 2\\ 1\\ 10\\ 9\\ 11\\ 7\\ 37\\ 35\\ 2\\ 1\\ 2\\ 1\\ 2\\ 1\\ 575\\ \end{array}$	$1 \\ 5 \\ + 1 \\ 1 \\ 1 \\ + \\ + 1 \\ + \\ + \\ 1 \\ + \\ 2 \\ 2 \\ 1 \\ + \\ 2 \\ 3 \\ + \\ + \\ + \\ + \\ + \\ + \\ + \\ + \\ +$	$\begin{array}{c} 20 \ 1 \\ 100 \ 3 \\ 0 \\ 50 \ 1 \\ 10 \ 1 \\ 10 \ 1 \\ 0 \\ 0 \\ 0 \\ 10 \ 1 \\ 20 \ 1 \\ 0 \\ 30 \ 1 \\ 0 \\ 30 \ 1 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\$	$\begin{array}{c} 70 & 1 \\ 20 & 1 \\ 0 \\ 40 & 1 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\$	(1)
Dicranum scoparium Hylocomium schreberi Hypnum cupressiforme Sum	$\begin{array}{c} 2\\ 0\\ 0\\ \end{array}$		1	0 0 0	0 0 0	$ \begin{array}{r} 13\\1\\7\\21\end{array} $	$\begin{array}{r}13\\1\\7\\21\end{array}$	1 + +	$\begin{array}{ccc} 10 & 1 \\ 0 \\ 0 \end{array}$	$30 \ 1 \\ 10 \ 1 \\ 40 \ 1$	< (<) <

TABLE 1.

<sup>1</sup> In the calculation the covering values + (the species only just present) and 1 (covering below  $\frac{1}{16}$  of the square) have both been reckoned as 1. <sup>2</sup> Covering scale according to Hult-Sernander: 5 (covers more than  $\frac{1}{2}$  of the square, 4 (covering between  $\frac{1}{2}$  and  $\frac{1}{4}$  of the square), 3 (between  $\frac{1}{4}$  and  $\frac{1}{18}$ , 2 (between  $\frac{1}{8}$  and  $\frac{1}{16}$ , 1 (below  $\frac{1}{16}$ , + only just present in a single specimen and with an extremely low covering. <sup>3</sup> Mainly typical *C. milis, C. sylvatica* occurring much scattered and *C. tenuis* only intermixed with the other *Cladina* species in a few squares.

that *Cladina*-species can invade the destruction areas which are first colonized, in particular by *Cladonia floerkeana* and *glauca*. This happened in the northern corner of Area C in Quadrate I, where in 1948 a vigorous *Cladina*-mat was developing.

# 4. Lichen-heath vegetations in relation to sand supply and sand removal by the wind.

Heavy sand accretion as well as strong erosion will destroy any type of lichen heath, whereas more moderate covering or wind influence will lead to ecologically different types of lichen heath. In the dunes or gravelly flats along the north coast of the Østerby peninsula both extremes occur.

On the point Jegens Odde a special study was made of the influence of sand covering. In 1939 a permanent quadrate (No. III) was established immediately behind the higher "white" sea-coast dunes (see fig. 4 in the background). West of the quadrate there were a large and a small blow-out from which sand was carried away and deposited more easterly. The quadrate, which was 25 square metres included two vegetational units. The ten northernmost and the five westernmost square metres were occupied by an Ammophiletum with scattered lichens (in particular Cladonia mitis, sylvatica, and Cornicularia aculeata), whereas the southeast corner had more the character of a lichen heath (Table 2). Although the lichens obtained rather high covering values it was always possible to see the sand between the individuals. In 1948 the small blow-out west of the quadrate had expanded in an easterly direction and consequently the sand covering had gradually become severer. Table 2 gives a number of values showing a number of minor changes which undoubtedly mainly are the results of the increased sand supply. The lichens seem to have difficulties in keeping up with the covering; only vigorous podetia of *Cladonia mitis-sylvatica* or vigorous specimens of *Cornicularia* hold their own. On the other hand the increasing sand supply had been of advantage to Festuca rubra, Carex arenaria, Hieracium umbellatum, and perhaps Viola canina. The decrease for Corynephorus may be due to frost during the very cold winters 1940–42. In Rørvig in North Zealand this effect was followed more closely in the same couple of years and it was quite evident there that this species in 1948 had not recovered its old frequency from before the severe winters. This weakening influence of heavy frost agrees with the suboceanic distribution of Corynephorus, and the decrease for other suboceanic species (Hypochoeris radicata, Jasione) in Quadrates II-III may further accentuate this connection. It is not probable that the sand itself should weaken Corynephorus. This species will endure a much stronger sand covering by sending new shoots up through the sand (WARMING 1909 fig. 66). It is surely a somewhat acidophilous plant, but the fresh sand from the blow-outs is moderately acid (pH 5.0-6.4, mostly about 6.0) and may thus be very suitable for it.

In 1939 pH in sand from the quadrate was found to be 5.9 and in 1948 the same figure was recorded in the northern part (with few lichens), while a pH of

TABLE 2.

$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$				19	39					1948		
$\begin{array}{c} \mbox{Corynephorus canescens} & 25 & 54 & 3 & 100 & 1.6 & 100 & 2.7 & 22 & 24 & 2 & 80 & 1 & 90 & 1.1 & 57 & 18 & 18 & 11 & 50 & 1 & 90 & 1.4 & 57 & 125 & 26 & 2 & 100 & 1 & 100 & 1.1 & 25 & 30 & 2 & 100 & 1.3 & 100 & 1.2 & 67 & 100 & 1.3 & 100 & 1.2 & 67 & 100 & 1.3 & 100 & 1.2 & 67 & 100 & 1.3 & 100 & 1.2 & 67 & 100 & 1.3 & 100 & 1.2 & 67 & 100 & 1.3 & 100 & 1.2 & 67 & 100 & 1.3 & 100 & 1.2 & 67 & 100 & 1.3 & 100 & 1.2 & 67 & 100 & 1.3 & 100 & 1.2 & 67 & 100 & 1.3 & 100 & 1.2 & 67 & 100 & 1.3 & 100 & 1.2 & 67 & 100 & 1.3 & 100 & 1.2 & 67 & 100 & 1.3 & 100 & 1.2 & 67 & 100 & 1.3 & 100 & 1.2 & 67 & 100 & 1.3 & 100 & 1.2 & 67 & 100 & 1.3 & 100 & 1.2 & 67 & 100 & 1.3 & 100 & 1.2 & 67 & 100 & 1.2 & 100 & 40 & 1 & 1 & 1 & 1 & 1 & 10 & 10$	Quadrate	of (Ma	Sum of covering values	Highest covering value	nstancy I average Northern	Constancy per cent and average covering. Southern area		of val	Highest covering value	istancy I average Vorthern		
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $	Corynephorus canescens. Festuca rubra Carex arenaria Hieracium umbellatum Hypochoeris radicata Jasione montana Viola canina	$25 \\ 0 \\ 25 \\ 25 \\ 4 \\ 2 \\ 5$	$54 \\ 0 \\ 26 \\ 26 \\ 4 \\ 2 \\ 5$	$\begin{array}{c c}3\\-\\2\\2\\1\\+\end{array}$	<b>100</b> 1.6 0 <b>100</b> 1 <b>100</b> 1 0 0	<b>100</b> 2.7 0 <b>100</b> 1.1 <b>100</b> 1.1 40 1 20 1	$22 \\ 18 \\ 25 \\ 25 \\ 1 \\ 1 \\ 9$	$ \begin{array}{c} 24 \\ 18 \\ 30 \\ 42 \\ 1 \\ 9 \end{array} $	$2 \\ 1 \\ 2 \\ 2 \\ + \\ +$	80 1 50 1 100 1.3 100 1.7 10 1 10 1	<b>90</b> 1.1 <b>90</b> 1 <b>100</b> 1.2 <b>100</b> 1.6 0 0	$(\mathbf{x}) = (\mathbf{x}) + ($
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	Cladonia mitis — sylvatica } — tenuis — impexa — scabriuscula — rangiformis — furcata — gracilis — uncialis — coccifera	$ \begin{array}{c} 1 \\ 1 \\ 0 \\ 0 \\ 12 \\ 2 \\ 1 \\ 0 \end{array} $	$ \begin{array}{c} 1 \\ 1 \\ 0 \\ 0 \\ 12 \\ 2 \\ 1 \\ 0 \end{array} $	1 1 	$\begin{array}{c} 0 \\ 0 \\ 0 \\ 30 \\ 1 \\ 0 \\ 0 \\ 0 \\ 0 \\ \end{array}$	$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	$5 \\ 1 \\ 1 \\ 2 \\ 9 \\ 0 \\ 1 \\ 1$	$5 \\ 1 \\ 1 \\ 2 \\ 9 \\ 0 \\ 1 \\ 1$	$     \begin{array}{c}       1 \\       1 \\       + \\       + \\       1 \\       + \\     $	$\begin{array}{c} 0 \\ 0 \\ 10 \\ 1 \\ 20 \\ 1 \\ 20 \\ 1 \\ 0 \\ 0 \\ 10 \\ 1$	$50 \ 1 \\ 10 \ 1 \\ 0 \\ 50 \ 1 \\ 0 \\ 10 \ 1 \\ 0$	

5.4 was found in the southeast corner where the sand supply was less. Here the rest conductivity value was very low, being 15 against 47 in the northern part of the quadrate. The further succession in Quadrate III will probably be in the direction of an *Ammophiletum* rich in *Festuca*, *Carex*, and *Hieracium*, but almost without lichens.

The succession on Bløden Hale and northwards from embryonal dunes on the beach to lichen-grown grey dunes has already been mentioned. This transition depends on increasing age and acidity but is rather independent of sand supply or removal of sand. Locally increasing supply or removal can stop, check, or modify the succession, but these factors will always be of local importance in newly formed dune areas until the chemical soil development approaches or has reached a final stage. The age and the soil development being the most important factors in the dune areas between Syrodde (the northeast corner) and Bløden Hale, the removal of sand and direct influence of wind upon the vegetation increases in importance from the point Syrodde and westwards. This appears from the fact that the higher coastal dunes disappear in that direction, and erosion by the sea becomes more and

Dan. Biol. Skr. 7, no.4.

3

more violent. In the vicinity of Østerby a low erosion slope is formed and from time to time areas covered with lichen heath or *Empetrum-Calluna*-heath fall down and are removed by the sea (cf. fig. 7 in BÖCHER 1941 b). The strongest wind erosion results in the formation of blow-outs and it is a very common feature that destruction areas or hollows in the dry *Calluna-Empetrum* heath form starting points for blowouts. With regard to the blow-outs and especially the importance of different lichen vegetations for the recolonization of them reference may be made to the author's previous paper. In what follows the subject is the dependence of certain vegetations on such wind influences as do not result in or have not yet resulted in blow-out formation.

Weak influences of this kind produce only minor differences in the composition of the lichen heath, while influences which reach the level of erosion transform the vegetation entirely. Large lichen podetia and loose sand, especially the smallest sand particles, are removed by the wind and a more or less gravelly or stony flat forms with a very special lichen flora. A number of lichens seems to prefer this kind of vegetation, thus in particular *Alectoria vexillifera*, *chalybeiformis*, *Stereocaulon* sp., *Cladonia destricta*, and *C. cervicornis*.

There are also, however, lichens which profit by a weaker wind action presumably owing to a decrease in vitality of the typical *Cladonia mitis* as well as of *C. sylvatica* and *impexa*. In particular *Cetraria nivalis* and *Cladonia alpestris* may belong to this category.

Cetraria nivalis (L.) Ach. The first scattered specimens occur in the dune slopes at Syrodde (constancy percentage in 2 quadrates of 10 m<sup>2</sup> 10-20, covering: +). At Jegens Odde (Ouadrate II Table 1) it occurs also very scattered but obtained in a single square (8 g) the covering value of 2. Between this point and the harbour of Østerby it reaches dominance on west-facing, very gently sloping ground. Here it occurs in vegetation which is also dominated by *Cladonia destricta* and contains much Corynephorus and Cladonia mitis var. prostrata. Similar vegetations are described in the previous paper from dune areas farther inland. All these vegetations are rich in Corynephorus and frequently contain open spaces where sand and gravel are laid bare. A dense lichen mat mainly dominated by Cetraria nivalis occurs frequently in Scandinavian mountains as well as at the heads of the Southwest Greenland fjords, but is very rare in Denmark. In 1948, however, such a vegetation was found on the Østerby peninsula in the oldest parts of the area in some low inland dunes a little north of the main road and south of the lost village of Hals which was destroyed by sand-drift long ago. Five analyses (squares) of this Cetraria nivalis heath are surveyed in Table 3. The vegetation differs from the more open vegetations of the dunes or gravelly flats along the north coast by the occurrence of species like Festuca ovina, Agrostis tenuis, Luzula multiflora, and Achillea millefolium. It covers rather a large area so that the yellow colour of the dominant can easily be seen at quite a long distance. The vegetation alternates with patches dominated by Calluna or Empetrum together with Cetraria and on less exposed parts of the area with patches of Cladina-heath with the same dwarf shrubs and Salix arenaria. It very much resembles

lichen heaths with *Cetraria nivalis* described from Northwest Zealand and Central Jutland (BÖCHER 1947 and 1941 a).

*Cladonia alpestris* (L.) Rabh. This lichen is not so frequent as *Cetraria nivalis*. It is absent from Syrodde—Jegens Odde, but occurs between the latter point and the harbour of Østerby scattered in the *Cladina* heath. Only in one place it obtains a



Fig. 7. Cladonia alpestris forming patches in the grey dune areas between Jegens Odde and the harbour of Østerby, T.W.B. phot. 1948.

high covering value (Table 3 No. 6, fig. 7). This place was on a low flat hill and was more protected than the *Cetraria nivalis-Cladonia destricta*-vegetation and less so than the pure *Cladina* heath. In other parts of the Østerby peninsula the species occur on *Empetrum* heaths on exposed ridges and sometimes in destruction hollows in the heath (BÖCHER 1941 b Table 10 Nos. 11—16 and fig. 10).

Cladonia destricta Nyl. occurs much scattered at Jegens Odde but farther west soon gets a prominent place in the vegetation. It is clearly the most important Cladonia in the most exposed situations on acid and poor soils. Only C. mitis var. prostrata may sometimes on less exposed ground be of the same importance. In five

3\*

AB	I IC	~	
AD			

No	1	2	3	4	5	Constancy	6
${}^{\rm pH}_{{}^{\rm K_{20}^{\circ}}}$ — $({}^{\rm K}_{{ m H}^+})_{{}^{20}^{\circ}} \cdot 10^6$	4.7 51	_	$\begin{array}{c c} 4.5\\ 29 \end{array}$		$\begin{array}{c} 4.5\\22\end{array}$	per cent Nos. 1—5	4.3 15
Corynephorus canescens	3	_	_		+	40	+
Festuca ovina	+	_		2	1	60	
— rubra	+		-	_		20	1
Agrostis tenuis	1	1	2	2		80	
Ammophila arenaria	+		1	1	1	80	1
Carex arenaria	+	+	+	+	-	80	+
Luzula multiflora	-		+			20	
Hieracium umbellatum	1	+	1	1	1	100	
— pilosella	-		-		-	$\begin{array}{c} 0\\ 20\end{array}$	+
Typochoeris radicata         Achillea millefolium	_	+		+		$\frac{20}{20}$	
Jasione montana.	1	1	1	1	1	100	_
Galium verum	-	_	+	-	+	40	
Calluna vulgaris	1		2	2	+	80	
Empetrum nigrum				_	-	0	2
Viola canina						0	1
Rumex acetosella	-		+		+	40	-
Cladonia alpestris	_					0	5
— mitis	2	2	1	2	1	100	4
— sylvatica	4	4	+	+	+	60	-
— tenuis			+	+	+	60	
— rangiferina			1	+	+	60	+
— impexa			1	1	1	60	
— scabriuscula	_		+		+	20	
— uncialis	-		+	+	-	40	
— gracilis	+		+	+		60	+
— glauca	-	-	+	+		40	
— fimbriata	-		-	+	+	40	
— chlorophaea	+	+	-	+	+	80	-
— coccifera	5	+ 5	5	5	5	$\begin{array}{c} 20\\ 100 \end{array}$	+
Cetraria nivalis	5	5	5	<b>5</b> +	5	20	1
— crispa Cornicularia aculeata	+	1	1	1	1	100	1
Polytrichum piliferum	+	-	-	-	+	40	
Dicranum scoparium	+	+	_	+	+	80	
Hypnum cupressiforme           Vehene mutang	-		+	-	+	40	
Webera nutans Cephaloziella sp	-	+++++++++++++++++++++++++++++++++++++++	+++++++++++++++++++++++++++++++++++++++	+		$40 \\ 60$	

of the square analyses in Table 4 (Nos. 6—10) which were made in the inner zone of the gravelly flat west of the Østerby harbour the species was constant and obtained high covering values. As distinct from the two above-mentioned species it will stand a moderate removal of sand. It has a very vigorous system of rhizines which adhere to the grains of sand and small stones and will therefore withstand very violent winds. It is certainly a very characteristic element in the vegetation of the exposed gravelly flats, but it is not exclusive to this habitat. It occurs in pure acid sand at exposed stations and also on bare wet raw humus in heather moors (see BÖCHER 1941 a, 1941 b).

Alectoria vexillifera (Nyl.) Stzbrgr (= A. cincinnata (Fr.) Lynge). This arctic lichen seems completely bound to the windy gravelly flats. As the vegetation in which it occurs is of special interest a number of square analyses were undertaken partly at the station where I detected it in 1939 west of the harbour of Østerby (Table 4

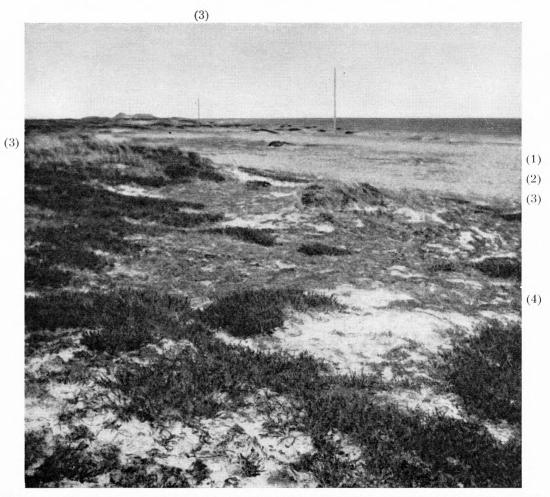


Fig. 8. Gravelly flat on the north coast of Læsø at "Bansten Bakke". (1) maritime belt with scattered herbs and squamulate *Cladoniae*. (2) transitional belt with thin lichen vegetation composed mainly by *Cornicularia*—*Cladonia destricta*. (3) *Cornicularia*—*C. destricta* soc. with *Alectoria vexillifera*. (4) Dense *Cornicularia*—*Cladonia destricta*—*C. mitis prostrata*-heath with *Empetrum*-patches. T.W.B. phot. 1948.

Nos. 1—10), partly at a new station "Bansten Bakke" farther west (Table 4 Nos. 11—15). A profile transect from the first locality is mentioned in Table 3 and p. 10 in Böcher 1941 b). The area at "Bansten Bakke" resembles that at the harbour very much. Just above a low erosion slope at the beach there is a gravelly plain with much scattered plants. *Plantago maritima* and *Armeria vulgaris* are here

TABLE 4.

No         pH $K_{20}^{\circ} - (K_{H^+})_{20}^{\circ} \cdot 10^6$	$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	Con- stan- cy per cent. Nos. 1—5	6     7     8     9     10       5.4     5.0       23     21	Con- stan- cy per cent. Nos. 6—10	$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	Con- stan- cy per cent. Nos. 11-1
(1) Corynephorus canescens Festuca rubra Hieracium umbellatum. Jasione montana Plantago maritima Armeria vulgaris Empetrum nigrum Viola canina Lotus corniculatus	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$     \begin{array}{r}       100 \\       60 \\       0 \\       80 \\       0 \\       40 \\       20 \\       0 \\       0 \\       0     \end{array} $	$\begin{array}{c} + 1 & 1 & + + \\ 1 & + 1 & 1 & + \\ - & + & + & + 1 \\ 1 & 1 & + & - & 1 \\ - & - & - & - & - \\ - & - & - & - & 1 \\ - & + & 1 & + + \\ - & - & - & - & - & 1 \end{array}$	$     \begin{array}{r}       100 \\       100 \\       80 \\       80 \\       0 \\       20 \\       80 \\       0 \\       0     \end{array} $	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{c} 80\\ 20\\ 60\\ 40\\ 60\\ 0\\ 80\\ 40\\ 20\\ \end{array}$
(2) Alectoria vexillifera — chalybeiform Cladonia destricta — cervicornis — cf. pyxidata — strepsilis Stereocaulon sp	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$     \begin{array}{r}       100 \\       60 \\       80 \\       80 \\       40 \\       20 \\       100     \end{array} $	$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	$     \begin{array}{r}       100 \\       0 \\       100 \\       60 \\       20 \\       0 \\       80     \end{array} $	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$100 \\ 0 \\ 60 \\ 20 \\ 0 \\ 40$
(3) Cladonia mitis var. pro- strata — furcata — gracilis — coccifera — floerkeana — chlorophaea — glauca — alcicornis Cornicularia aculeata Lecidea granulosa	$\begin{array}{c} - & + & - & - \\ - & - & - & - & - \\ - & - & -$	$20 \\ 0 \\ 20 \\ 0 \\ 0 \\ 60 \\ 100 \\ 100 \\ 20$	$\begin{array}{c} + & - & - & - & - \\ - & - & - & + & - \\ + & - & - & + & - \\ + & - & - & + & - \\ + & - & - & - & - \\ + & - & - & - & - \\ 2 & + & + & 1 \\ 4 & 4 & 4 & 2 & 3 \\ - & - & - & - & - \\ \end{array}$	$20 \\ 0 \\ 20 \\ 60 \\ 20 \\ 0 \\ 20 \\ 100 \\ 100 \\ 0$	$\begin{array}{c} + & + & + & 1 & - \\ - & + & + & + & - & - \\ + & - & + & + & + \\ - & - & - & + & - \\ - & - & - & + & - \\ - & - & - & + & - \\ 2 & + & - & 1 & + \\ 5 & 4 & 5 & 5 & 4 \\ - & - & - & - & - \end{array}$	$     \begin{array}{r}       80 \\       40 \\       0 \\       80 \\       20 \\       20 \\       20 \\       80 \\       100 \\       0     \end{array} $
(4) Parmelia saxatilis — mougeottii Rhizocarpon obscuratum — reductum Sarcogyne simplex Acarospora smaragdula Lecidea erratica — sorediza — pycnocarpa Lecanora polytropa — badia	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	$\begin{array}{c} 0\\ 20\\ 100\\ 40\\ 20\\ 40\\ 40\\ 0\\ 0\\ 20\\ 0\\ 0\\ 0\\ 0\\ 0\\ 0\\ 0\\ 0\\ 0\\ 0\\ 0\\ 0\\ 0$	$\begin{array}{c} + & + & - & - & - \\ + & - & - & - \\ 2 & + & + & + \\ - & - & - & - \\ - & - & - & - \\ - & - &$	$\begin{array}{c} 40\\ 20\\ 100\\ 0\\ 0\\ 0\\ 0\\ 0\\ 0\\ 0\\ 0\\ 0\\ 0\\ 0\\ 0\\ $	$\begin{array}{c} - 1 & \\ + 1 & - 2 & + \\ - + - & - & - \\ - & - & - & - \\ - & - & - &$	$20 \\ 40 \\ 80 \\ 0 \\ 20 \\ 0 \\ 0 \\ 60 \\ 20 \\ 20 \\ 20 \\$
(5) Polytrichum piliferum	- + +	40	$1 \ 1 \ + \ 1 \ +$	100	+ 1 2 + 2	100

Flowering plants, (2) lichens which are characteristic of the community, (3) lichens occurring on sand, (4) lichens on the small stones (kindly determined by M. SKYTTE CHRISTIANSEN, M.Sc), (5) bryophytes.

rather important, less so are *Corynephorus*, *Jasione*, *Hieracium umbellatum*, *Cladonia alcicornis*, and *cervicornis*. This extreme belt may be influenced by salt spray; on fig. 8 it is called (1). The next belt (Fig. 8 (2)) contains the first specimen of *Alectoria* 

vexillifera and there the lichens are more abundant, especially Cornicularia and Cladonia destricta. Of some importance is likewise Polytrichum piliferum. Among the higher plants Festuca rubra, Viola canina, Lotus corniculatus, and Empetrum have entered the vegetation. The analyses in Table 4 (Nos. 11—15) are all from the third belt (3). In the background on the left this belt is rather broad (in fig. 8 indicated by arrows). Here Alectoria vexillifera is constant and rather abundant. In this belt the lichen flora of the small stones further is best developed, it consists mainly of Rhizocarpon obscuratum. In the fourth belt (4) the lichens cover the ground. A Cornicularia-Cladonia destricta-mitis var. prostrata-heath occurs which, however, frequently is interrupted by Empetrum patches or small sandy or gravelly areas with the same vegetation as in belt (3). In the closed lichen mat small stones may protrude and not rarely they are overgrown by Parmelia saxatilis.

In Southwest Greenland Alectoria vexillifera grows in places which from an ecological point of view resembles the Læsö type of habitat very much. I saw it in 1946 on gravelly ridges or stony fell fields (barrens) in places highly marked by wind influence. At Ivigtut it occurred in the very characteristic Salix uva ursi barren land community. The analyses of this community will appear in a later paper on the Greenland vegetation.

Alectoria chalybeiformis (L.) Röhl. is another characteristic species of the gravelly plains. It was seen in some of the squares at Østerby. I have further noticed it at Rørvig on exposed lichen heaths at the sea (cf. Böcher 1945 p. 152). DAHL (1950) found it in Greenland on rocks and on the top of windy hills together with Alectoria vexillifera and ochroleuca.

In 1939 two rather small permanent quadrates were made in vegetations rich in *Cladonia destricta* on the gravelly plains. Both had a bad fate. One was placed in belt No. 5 in the profile transect at Lergravsbakke mentioned on p. 8 in BÖCHER 1941 b. But there the more extreme belts 2—3 in 1948 were removed by the sea and the next two belts covered with fresh sand. The only plants left in the quadrate were a specimen of *Empetrum*, which had been able to form a low dune, and further *Festuca rubra*, *Hieracium umbellatum*, and *Plantago maritima*. All lichens and several others had disappeared.

The other quadrate was made on the *Alectoria vexillifera* locality west of the harbour of Østerby. In 1948 the corner pegs were taken away by someone and it was therefore impossible to find the place exactly. The quadrate, however, was cut by a line indicated by two sea-marks and its approximate situation could be established through counting of steps along this line. It was therefore possible to ascertain that no larger changes had occurred in that area during the nine years. It thus appears that such gravel-plain communities as are the result of strong wind influences can be very stable unless new blow-outs are formed or removal of sand takes place and disturbs the balance.

#### References.

ANDERSSON, O., & WALDHEIM, S. 1946. Bidrag til Skånes Flora. 35. Tortella inclinata som komponent i skånsk sandstäpp-vegetation.—Bot. Notiser 1946, pp. 103—120.

Böcher, T. W. 1941 a. Vegetationen på Randbøl Hede.-Dan. Biol. Skr. 1, no. 3.

- 1941 b. Beiträge zur Pflanzengeographie und Ökologie dänischer Vegetation. I. Über die Flechtenheiden der Insel Läsö.—Dan. Biol. Skr. 2, no. 1.
- 1945. Beiträge zur Pflanzengeographie und Ökologie dänischer Vegetation. II.—Dan. Biol. Skr. 4, no. 1.
- 1947. Festuca polesica Zapal., its Chromosome Number and Occurrence in Denmark.— Bot. Notiser 1947, pp. 353—360.
- 1952. Vegetationsudvikling i forhold til marin akkumulation. I. Korshage ved indløbet til Isefjord.—Bot. Tidsskr. **49**, pp. 1—32.
- DAHL, E. 1950. Studies in the Macrolichen Flora of South West Greenland.—Meddelelser om Grønland 150, Nr. 2.

RAUNKLÆR, C. 1913. Formationsstatistiske Undersøgelser paa Skagens Odde. —Bot. Tidsskr. 33, pp. 197—243.

— 1934. The Life Forms of Plants and Statistical Plant Geography (Oxford). VIII. Statistical Investigations of the Plant Formations of Skagens Odde (the Skaw), pp. 303—342.

RICHARDS, P. W. 1929. Notes on the Ecology of the Bryophytes and Lichens at Blakeney Point, Norfolk.—The Journ. of Ecology 17, p. 127.

SJörs, H. 1946. Myrvegetationen i Övre Långanområdet i Jämtland.—Arkiv f. Botanik **33** A No. 6.

TANSLEY, A. G. 1939. The British Islands and their Vegetation. Cambridge.

WARMING, E. 1909. Dansk Plantevækst. 2. Klitterne. København & Kristiania.

Indleveret til selskabet den 16. maj 1951. Færdig fra trykkeriet den 14. juni 1952.

# Det Kongelige Danske Videnskabernes Selskab

# **Biologiske Skrifter**

### Dan. Biol. Skr.

1.

2.

3. 4.

Bind 3 (kr. 60.50)	kr. ø.
OLSEN, SIGURD: Danish Charophyta. Chorological, Ecological and Biological Investigations. 1944	22.00
JESSEN, KNUD, and HELBÆK, HANS: Cereals in Great Britain and Ireland in Prehistoric and Early Historic Times. 1944	8.50
GRAM, K., JØRGENSEN, C. A., OG KØIE, M.: De jydske Egekrat og deres Flora. 1944	26.00
ORLA-JENSEN, S., OLSEN, ERIK, and GEILL, TORBEN: Senility and Intestinal Flora. A Reexamination of Metchnikoff's Hypothesis. 1945	4.00

# Bind 4 (kr. 72.00)

1.	BÖCHER, TYGE W.: Beiträge zur Pflanzengeographie und Ökologie dänischer Vegetation. II. Über die Waldsaum- und Graskrautgesellschaften trockener und halbtrockener Böden der Insel Seeland mit besonderer Berücksichtigung der Strandabhänge und Strandebenen. 1945	20.00
2.	SøRENSEN, THORVALD, and GUÐJÓNSSON, GUÐNI: Spontaneous Chromosome-Aber- rants in Apomictic Taraxaca. Morphological and Cyto-Genetical Investigations. 1946	10.00
3.	Böcher, Tyge W., Christensen, Tyge, and Christiansen, M. Skytte: Slope and Dune Vegetation of North Jutland. I. Himmerland. 1946	
	BÖCHER, TYGE W.: Dichothrix gelatinosa sp. n. Its Structure and Resting Organs. 1946	2.00
5.	ROSENVINGE, L. KOLDERUP, and LUND, SØREN: The Marine Algæ of Denmark. Contributions to their Natural History. Vol. II. Phæophyceæ. III. Encoeliaceæ, Myriotrichiaceæ, Giraudiaceæ, Striariaceæ, Dictyosiphonaceæ, Chordaceæ, and	
	Laminariaceæ. 1947	14.00
6.	RAVN, J. P. J.: Om Nyker-Omraadets Kridtaflejringer. 1946	4.00
7.	KNISELY, MELVIN H., BLOCH, EDWARD H., and WARNER, LOUISE: Selective Phago- cytosis. I. Microscopic Observations concerning the Regulation of the Blood Flow through the Liver and other Organs and the Mechanism and Rate of	
	Phagocytic Removal of Particles from the Blood. 1948	10.00

### Bind 5 (kr. 82.50)

1.	NIELSEN, ANKER: Postembryonic Development and Biology of the Hydroptilidæ. A Contribution to the Phylogeny of the Caddis Flies and to the Question of the Origin of the Case-Building Instinct. 1948	30.00
2.	Jørgensen, Erik G.: Diatom Communities in Some Danish Lakes and Ponds. 1948.	18.00
3.	LEMCHE, HENNING: Northern and Arctic Tectibranch Gastropods. I. The Larval Shells. II. A Revision of the Cephalaspid Species. 1948	18.00
4.	SØRENSEN, THORVALD: A Method of Establishing Groups of Equal Amplitude in Plant Sociology Based on Similarity of Species Content and its Application to Analyses of the Vegetation on Danish Commons. 1948	7.50

E	Nerson Tran, On the Application of the Section Dest Classel Zone Sector to	
э.	NILSSON, TAGE: On the Application of the Scanian Post-Glacial Zone System to	
	Danish Pollen-Diagrams, 1948	9.00

### Bind 6

# (uafsluttet / en cours de publication)

ORLA-JENSEN, S., ORLA-JENSEN, ANNA D., and SNOG-KJÆR, AGNETE: Biological Researches on the Silage Process. 1948	2.00
LUND, SØREN: The Marine Algæ of Denmark. Contributions to their Natural History. Vol. II. Phæophyceæ. IV. Sphacelariaceæ, Cutleriaceæ, and Dictyotaceæ. 1950.	10.00
TUXEN, S. L.: Über den Lebenszyklus und die postembryonale Entwicklung zweier dänischer Proturengattungen. 1949	10.00
PAULSEN, OVE: Observations on Dinoflagellates. Edited by Jul. Grøntved. 1949.	9.00
THOMSEN, MATHIAS: Weismann's Ring and Related Organs in Larvae of Diptera. 1951.	15.00
NIELSEN, ANKER: Contributions to the Metamorphosis and Biology of the Genus Atrichopogon Kieffer (Diptera, Ceratopogonidæ). With Remarks on the Evolu- tion and Taxonomy of the Genus. 1951	16.00
BÖCHER, TYGE W.: Cytological and Embryological Studies in the Amphi-Apomictic	9.00
DEGERBØL, MAGNUS: Recent Discoveries of Remains of Mammals from Glacial Deposits in Denmark. Dicerorhinus kirchbergensis (Jäger), New to the Fauna of Denmark; Megaloceros giganteus (Blumenbach) and Bison priscus (H. v. Meyer). 1952	5.00
	<ul> <li>Researches on the Silage Process. 1948.</li> <li>LUND, SØREN: The Marine Algæ of Denmark. Contributions to their Natural History. Vol. II. Phæophyceæ. IV. Sphacelariaceæ, Cutleriaceæ, and Dictyotaceæ. 1950.</li> <li>TUXEN, S. L.: Über den Lebenszyklus und die postembryonale Entwicklung zweier dänischer Proturengattungen. 1949.</li> <li>PAULSEN, OVE: Observations on Dinoflagellates. Edited by Jul. Grøntved. 1949.</li> <li>THOMSEN, MATHIAS: Weismann's Ring and Related Organs in Larvae of Diptera. 1951.</li> <li>NIELSEN, ANKER: Contributions to the Metamorphosis and Biology of the Genus Atrichopogon Kieffer (Diptera, Ceratopogonidæ). With Remarks on the Evolu- tion and Taxonomy of the Genus. 1951.</li> <li>BÖCHER, TYGE W.: Cytological and Embryological Studies in the Amphi-Apomictic Arabis Holboellii Complex. 1951.</li> <li>DEGERBØL, MAGNUS: Recent Discoveries of Remains of Mammals from Glacial Deposits in Denmark. Dicerorhinus kirchbergensis (Jäger), New to the Fauna of Denmark;</li> </ul>

### Bind 7

### (uafsluttet / en cours de publication)

1.	NYGAARD, GUNNAR: Hydrobiological Studies on some Danish Ponds and Lakes. Part II: The Quotient Hypothesis and some new or little known Phytoplankton	
	Organisms. 1949	40.00
2.	CHRISTENSEN, PAUL J. HOLST: Studien über die postembryonale Entwicklung bei Cochlidion limacodes Hufn. (Fam. Cochlididae, Lepidoptera). 1950	10.00
4.	BÖCHER, TYGE W.: Lichen-Heaths and Plant Successions at Østerby on the Isle of Læsø in the Kattegat. 1952	5.00