

Borrelyngen on Bornholm, Denmark

A heath on rocky ground. Exploitation and vegetation
from antiquity to the present day

By VALD. M. MIKKELSEN



Biologiske Skrifter **38**

Det Kongelige Danske Videnskabernes Selskab
The Royal Danish Academy of Sciences and Letters

Kommissionær: Munksgaard · Copenhagen 1991

The Royal Danish Academy of Sciences and Letters

publishes four monograph series, an Annual Report and, occasionally, special publications. The format is governed by the requirements of the illustrations, which should comply with the following measures.

	<i>Authorized Abbreviations</i>
<i>Historisk-filosofiske Meddelelser</i> , 8°	Hist.Fil.Medd.Dan.Vid.Selsk. (printed area 175 × 104 mm, 2700 units)
<i>Historisk-filosofiske Skrifter</i> , 4° (History, Philosophy, Philology, Archaeology, Art History)	Hist.Filos.Skr.Dan.Vid.Selsk. (printed area 2 columns, each 199 × 77 mm, 2100 units)
<i>Matematisk-fysiske Meddelelser</i> , 8° (Mathematics, Physics, Chemistry, Astronomy, Geology)	Mat.Fys.Medd.Dan.Vid.Selsk. (printed area 180 × 126 mm, 3360 units)
<i>Biologiske Skrifter</i> , 4° (Botany, Zoology, Palaeontology, General Biology)	Biol.Skr.Dan.Vid.Selsk. (printed area 2 columns, each 199 × 77 mm, 2100 units)
<i>Oversigt, Annual Report</i> , 8°	Overs.Dan.Vid.Selsk.

The Academy invites original papers that contribute significantly to research carried on in Denmark. Foreign contributions are accepted from temporary residents in Denmark, participants in a joint project involving Danish researchers, or partakers in discussion with Danish contributors.

Instructions to Authors

Manuscripts from contributors who are not members of the Academy will be refereed by two members of the Academy. Authors of accepted papers receive galley proof and page proof which should be returned promptly to the editor. Minidisks etc. may be accepted; contact the editor in advance, giving technical specifications.

Alterations causing more than 15% proof charges will be charged to the author(s). 50 free copies are supplied. Order form, quoting a special price for additional copies, accompanies the page proof. Authors are urged to provide addresses for up to 20 journals which may receive review copies.

Manuscripts not returned during the production of the book are not returned after printing. Original photos and art work are returned when requested.

Manuscript

General. – Manuscripts and illustrations must comply with the details given above. The original ms. and illustrations plus one clear copy of both should be sent to the undersigned editor.

NB: A ms. should not contain less than 32 *printed* pages. This applies also to the Mat. Fys.Medd., where contributions to the history of science are welcome.

Language. – English is the preferred language. Danish, German and French mss. are accepted and in special cases other languages. Where necessary, language revision must be carried out before final acceptance.

Borrelyngen on Bornholm, Denmark

A heath on rocky ground. Exploitation and vegetation
from antiquity to the present day

By VALD. M. MIKKELSEN



Biologiske Skrifter **38**

Det Kongelige Danske Videnskabernes Selskab
The Royal Danish Academy of Sciences and Letters

Kommissionær: Munksgaard · Copenhagen 1991

Abstract

An outline is given based on historical references, old maps and some palynological investigations, of the exploitation of and the vegetation on Borrellyngen through time.

Borrellyngen (the heath of Borre) is situated on the northern part of Bornholm, a Danish island in the Baltic.

Since 1978 Borrellyngen has been the subject of botanical ecological investigations.

The subsoil is ice eroded granite covered by a thin layer of soil (usually 0-40 cm). Only some large depressions and narrow valleys traversing the area contain somewhat thicker layers of soil.

The area was cleared mechanically in 1979 and afterwards grazed by sheep.

Today most of the area is covered by a *Calluna* heath which is very poor in species and contains several naked protruding rocks. In places, where there are thicker layers of soil, some wetness preferring species such as *Molinia coerulea*, *Eriophorum angustifolium*, *Trichophorum caespitosum* and *Juncus spp.* can be found.

In 1979/81 the vegetation was analysed in several transects. All sample plots (about 500) were levelled and the thickness of the soil was measured. These investigations were repeated in 1984/86.

Chemical analyses of both mor and sand were made in both periods.

The variation of soil humidity was followed from 1980 to 1986 and compared with the climate. The soil humidity data from 1980 and 1981 are expressed as water in % of field capacity, whereas the level of the free water table in a depression covered by a *Calluna-Molinia* community was used from 1981 to 1986.

The summers of 1982 and 1983 were extremely warm and dry and had great influence on the vegetation, especially by killing much *Calluna* on sloping, well drained terrain with a thin layer of soil. The resulting bare soil was eroded away, leaving bare rocks. Measurements of pH showed that these changes can not have been due to acid precipitation.

The water supply of the plants, especially in dry periods, is dependent on the field capacity in the mor layer, which varies proportionally to the thickness of the soil. Therefore many of the species have a distribution in the area, which is dependent on soil thickness.

Since 1979 the area has been managed as a nature reserve (clearing and some sheep grazing) but the changes of the vegetation, such as the increase of *Deschampsia flexuosa*, seems to indicate that the sheep grazing has not been quite sufficient to preserve the *Calluna* dominated heath.

VALD. M. MIKKELSEN

Department of Botany

Royal Veterinary and Agricultural University

Rolighedsvej 23

DK-1958 Copenhagen V

Denmark

KEY WORDS:

Agrostis stricta, *Calluna vulgaris*, *Deschampsia flexuosa*, *Molinia coerulea*, *Trichophorum caespitosum*, heath, commons, field capacity in mor, summer-drought, sheep grazing, nature conservation management, history of vegetation, Bornholm.

Contents

I	Introduction	5
II	History	5
	The great common of Højlyngen	5
	Borrelyngen	11
	Before 1800	11
	1800-1945	11
	After 1945	13
	Nature conservation management after 1977	14
III	Ecological-botanical investigations 1979-86	18
	Methods	18
	Vegetation and terrain	18
	Soil chemistry	19
	The humidity of the soil	20
	Climate	21
IV	The terrain and its influence on the vegetation	21
V	The soil and its influence on the vegetation	22
	Chemical conditions	22
	The thickness of the soil	23
	Field capacity and the thickness of the soil	25
	Humidity of the soil	26
	The climate and the variation of soil humidity from 1980 to 1986	29
	The dry summers of 1982 and 1983 and their effect on the vegetation	31
VI	Distribution of plant species compared to thickness of the soil	35
VII	The vegetation in 1979/81 and in 1984/86	37
	1. Survey of the plant communities	37
	2. <i>Calluna</i> heath	37
	Trees and shrubs	39
	Dwarf shrubs	39
	Herbs	39
	Bryophytes	40
	Lichens	40
	Areas without vegetation	40
	3. Clearing in former wooded area	40

4. <i>Calluna-Molinia</i> communities	41
The depression at the central 0-parcel	42
The <i>Calluna-Molinia</i> community in the northern W-E transect	44
The <i>Calluna-Molinia-Juncus</i> community in the N-S transect	45
5. <i>Vaccinium-Molinia-Deschampsia</i> community	46
VIII General conclusions	47
1. The influence of climate and man on the vegetation	47
2. The <i>Calluna</i> heath in 1979/81 and in 1984	47
3. Nature conservancy	48
IX Acknowledgements	50
X References	51

I Introduction

The investigations referred to in this paper are made in that part of the old common of Borrelyngen which belongs to the State Forest District of Bornholm, cf. fig. 1. Most of the investigations were made in part 690 (Habbedam).

Borrelyngen (the heath of Borre) is situated 3 km SW of Allinge on the northern part of Bornholm, a Danish island in the Baltic, cf. fig. 2. The eastern limit of the investigated area is a NNW-SSE running glen called Ravnedalen which continues in the

glen Paradisdalen. The western limit is another N-S running glen called Borredalen on old maps which hits Paradisdalen 1 km SSE of Hammershus.

The northern part of Borrelyngen (parts 686-689, cf. fig. 1) was acquired by the State in 1973 and has since been managed as a nature reserve. Part 690 was acquired in 1977 and has been managed as nature reserve since 1979. It has been cleared and grazed by sheep. The development of the vegetation has been followed since the autumn of 1978.

II History

The great common of Højlyngen

The Danish name Højlyngen may be translated as "The Highland heath". However, the "highland" of Bornholm is only relatively high; between 100 and 160 m above sea level.

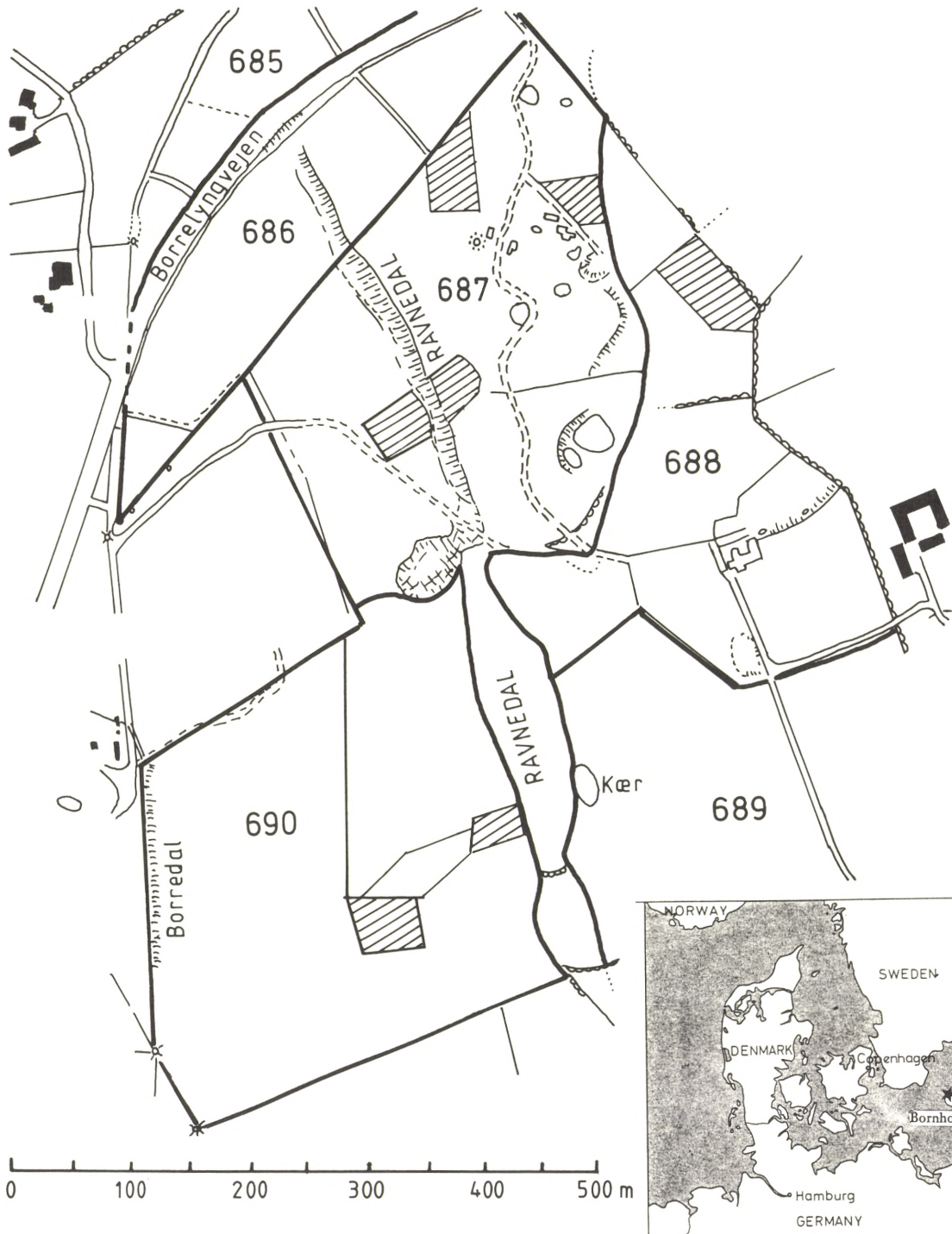
From the 13th century and well into the 19th century the central part of Bornholm was covered by wide areas of commons and heaths belonging to the King and used by the farmers of the island. It was called Højlyngen and extended about 12.000 ha; about 20 % of the island.

The pollen diagram, fig. 3 (from Mikkelsen 1966) shows the development of the vegetation on Bornholm from about 4000 BC to somewhat after AD 1200. In the period before about AD 1200, forest of oak and beech dominated, but after AD 1200 heaths, commons, and fields increased considerably. The site of the pollen diagram was in the Baltic Sea about 5 km east of Nexø (on the east coast of the island, cf. fig. 2), therefore it depicts more or less the development of the vegetation on Bornholm as a whole. However, supplementary

pollen diagrams from bogs in the area of the former great common (Mikkelsen 1953, 1963 and 1966) show that the central part of Bornholm was covered by oak forest from antiquity to the Early Middle Ages, while heather and grasses were unimportant during this period.

The increase in heaths and commons shown in the pollen diagram took place about the same time as cornflower (*Centaurea cyanus*) became common (about AD 1200, cf. Mikkelsen 1986), and when the surface of the water rose in Lake Ankermyr (about 1 km N of the investigated area) probably because of the increase in humidity about AD 1250 (RS I) (Mikkelsen 1953).

In the period between AD 1200 and AD 1800 most of the forests on Bornholm were cut down, and about AD 1800 heather, grasses and some shrubs covered both the central part of the island and some areas near the coast. By the end of the 18th century the last remains of the forest in the central parts of the island – Almindingen – was reduced to an area of 165 ha old miserable forest (Zartmann 1935).

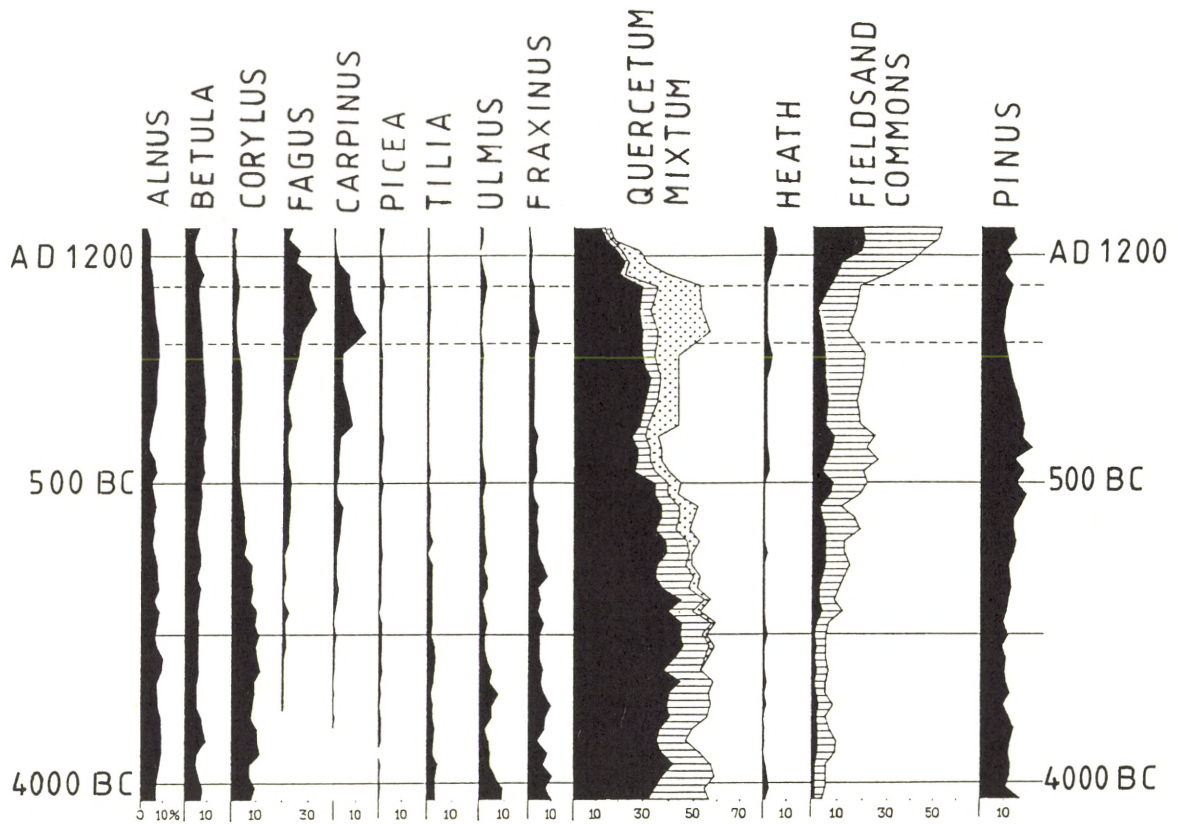




○ Borreløng X Site of the pollen diagram

Fig. 1. Map showing the parts of Borreløng belonging to the State Forest Department of Bornholm. 0-parcels hatched. In part 690 is shown the N-S transect and the two E-W transects. Several granite quarries can be seen in part 687. Borreløngvej: the modern road. Kær: pond. Location map inserted. Drawn after the official map of the State Forest Department.

Fig. 2. The map of Thura from 1756 showing the extension of the great common Højlyng marked with signature for heath. The northern heath areas: Borreløng, Slotslyng and Hammeren are without signature for heath. The localities for Borreløng and the site of the pollen diagram fig. 3 entered.



The heaths, pastures and shrubs were used as commons and were of the greatest importance for the living conditions on Bornholm.

Information on the great common of Højlyngen can be found in the papers of Thura 1756, Skovgaard 1804, Jørgensen 1901 and Zartmann 1935.

Thura records that Stor-Lyngen (= Højlyngen) stretched from Hammershus in the NW to Nexø in the E and it was used by the inhabitants for cutting heather and peat. Furthermore it was used as pasture for their livestock even though there was not much grass but more heather.

Thura also recorded that most of the forest on Bornholm had been cut down, but that good forests of birch could still be found in the parishes of Olsker and Rø. The former one must be the forest called Hestehaven, about 1 km S of the area investigated. On the draft map from 1784 of the archives

Fig. 3. Pollen diagram from the Baltic Sea about 5 km E of Nexø (after Mikkelsen 1966). *Quercetum mixtum*: black: *Quercus*, hatched: *Ulmus* + *Tilia* + *Fraxinus*, dotted: *Fagus* and *Carpinus*. Fields: *Artemisia*, *Centaurea cyanus*, *Cerealia*, *Chenopodium*, *Polygonum*, and *Rumex*. Commons: *Graminea* (wild), *Plantago*, and *Pteridium*. *Picea* and *Pinus* undoubtedly far-off transported. Dating based on comparisons with other pollendiagrams. The site of the pollen diagram inserted in fig. 2.

of the Cadastral Register, it is called Birkeløkken (= the enclosure with birch).

Zartmann 1935 reported some detailed information about the use of Højlyngen. In 1782 the total number of grazing animals was: 5485 horses, 6879 heads of cattle, 22808 sheep, and 4512 pigs. The number of geese was not counted. About 1806 the farmers collected 13.400 cart-loads of heather and 18.000 cart-loads of peat from Højlyngen every year. Furthermore Zartmann records that the meat



of lamb from Bornholm was considered especially delicious because of the many aromatic herbs on Højlyngen.

Skovgaard 1804 recorded that each of the ap-

Fig. 4. Part of draft map (originally 1:4000) from 1784 of the archives of the Cadastral Register showing Vestermarken in Olsker and Ringemarken in Rutsker. The modern road and the boundaries of the forest parts in Borrellyngen are entered.

prox. 900 farms on Bornholm kept on average 20 sheep, but there were several deviations from this average. Many of the farms on North-Bornholm had hundreds of sheep. As an example of such a farm he mentioned Brogaard, which lies close to the area examined. These sheep were kept out during winter and had to feed themselves like today's sheep on the Faroe Islands. In part 686 in Borrellyngen, W of Ravnedalen, can still be seen a ruin similar to the sheep shelters found in the Faroe Islands.

Furthermore Skovgaard mentions that wild horses lived in Højlyngen as late as the middle of the 18th century. Zartmann recorded that many of the farm horses spent most of their time on Højlyngen. The horses were small and six of them were necessary to draw a wheelplough. Since the Middle Ages the wild horses had belonged to the church and were caught only once a year for mating. The last wild horses belonging to the church of Rø became extinct about 1780.

Red deer were common on Højlyngen until the beginning of the 18th century. Zartmann reported that in 1683 in the parish of Klemmsker more than a third of the farms were waste because the harvest was eaten by wild animals, i.e. red deer.

The presence of red deer in Borrellyngen is indicated by the name Hjortesletten (= the plains of the red deer) on the draft map from 1784 (fig. 4). According to Zartmann the number of red deer decreased during the 18th century. In 1745 only 100 head were mentioned, and in 1776 the last red deer on Bornholm was shot. Today Bornholm is without red deer, but roe-deer were introduced shortly before 1900. Højlyngen was grazed by livestock and red deer and the farmers harvested heather, cut peat and collected trees and shrubs for fuel and housebuilding. This usage kept the woodland away from the central part of Bornholm, and heather and grasses became more and more widespread in the common of Højlyngen.

Since the Middle Ages the farm taxes were calculated on the basis of their access to Højlyngen for grazing. At the beginning of the 18th century the population of the island increased considerably

which enhanced the interest in cultivating parts of Højlyngen. Furthermore the ownership of the area became a problem. Was it owned by the King or the farmers who used it?

In 1709 the "Exchequer" established that Højlyngen and the other commons should continue to be grazing areas for the farmers of the parishes. In addition a ban on cultivation was issued. In 1726 the "Exchequer" established that all of the commons belonged to the King. The ban on cultivation was repeated several times during the following decades. Like many other bans, these bans on cultivation did not have any effect on Bornholm. Between 1729 and 1760, 587 ha of Højlyngen were cultivated, and from 1769 the "Exchequer" rented out lots of the commons (Zartmann 1935).

In 1848 Højlyngen was allotted. The State became the owner of rather more than 6000 ha, of which 3850 ha was for hiring out to copyholders and 2200 ha for forest planting. The farmers of the parishes got ownership of about 5700 ha. The final arrangement of the part of the farmers had to wait to 1866, when most of it was allocated to plantations, while the rest was reserved copyholders.

A few areas of heathland which could not be cultivated were allotted to neighbouring farms. Borrellyngen was one of these areas.

We have no statistical information on the number of livestock on Bornholm before AD 1800. Table 1 after Zartmann 1935 and Hansen 1988 shows the state of affairs after 1800.

The considerable increase in the human population during the last part of the 19th century was to some degree related to the cultivation of Højlyngen. On the other hand, this meant a considerable decrease in the number of sheep grazing the commons and heaths which resulted in overgrowing with shrubs and trees. Today, most of the former area of Højlyngen is covered by cultivated fields and forests. Only small areas are still dominated by heather. Many of the remaining heath areas are turning into scrubland and forest, but some areas, among them the investigated area, are managed with a view to restoring the open heath.

TABLE 1

	Inhabitants	Cattle	Horses	Sheep
1800	19.000	8.800	8.400	23.000
1838	25.000	13.400	7.800	23.600
1871	32.000	20.300	7.300	28.400
1903	41.000	32.200	8.500	9.200
1920	43.000	45.600	9.900	5.200
1940		41.300	4.800	ca. 300
1972	ca. 47.000	23.800	900	500
1980		22.800	1.300	1.100
1987		16.400	1.800	3.000

Table 1. Number of inhabitants and livestock on Bornholm from 1800 to 1987. After Zartmann 1935 and Hansen 1988.

Borrelyngen

Before 1800

No botanical investigations were made in the area before AD 1800, but some information on the distribution of forest and heathland can be found on old maps.

Bugge Wandel's map from 1676 (in Resen: Atlas Danicus, Bornholm) unfortunately contains no information about the vegetation of Borrelyngen. Neither does the map made by A. P. Kofod in 1763 (in Pontoppidan: Danske Atlas).

The map by Thura from 1756 (fig. 2) gives a good impression of the size of Højlyngen. However, Borrelyngen, the area surrounding Borre Høj (= the hill of Borre), is without signature as well as the neighbouring localities Slotslyngen and Hammeren, which both must have been commons dominated by heather. In his text, Thura included these areas in Højlyngen (cf. above).

Much better information is given on the map by Hammer (on a scale of 1:17000) from 1746-56 (a copy of the original map and a copy made in 1796 can be found in Bornholms Museum, Rønne). Fig. 5a shows a part of the copy drawn in 1796. Other maps containing valuable information are the draft map from 1784 from the archives of the Cadastral Register (1:4000), fig. 4, and the "koncept"-map from 1799-1801 (1:20000) for the map of "Born-

holms Øster og Nørre Herred" made by The Royal Danish Academy of Sciences and Letters, fig. 5b.

Borrelyngen was affected only to a small degree by cultivation in earlier times. The old maps, fig. 4, 5a and 5b, show the following smallholdings: Buggeløkke, Tømmesløkke (in fig. 5a called Paa Slotsgrund), I Dammen (in fig. 4 called Falkestellet), Damvang and Damly (the last two without old names). All these still existing smallholdings are situated outside the part of Borrelyngen which now belongs to the Forest District of Bornholm (parts 687-690).

Part 690 must have been completely unfit for cultivation and no traces of such can be seen. On the other hand, part 687, in the northern part of the area, contains not only a menhir, several burial mounds, and rock engravings from the period between Younger Bronze Age and Pre-Roman Iron Age but also small areas which were cultivated at that time and some of them even in modern times.

On the "koncept" map (fig. 5b) part 690 can be located between Borredal and Ravnedal and south of Finnedal. The map indicates that Ravnedalen contained shrubs, while part 690 was covered by heather. The draft map (fig. 4) shows the same features and Hammer's map (fig. 5a) characterizes the area as a common.

According to these maps and to the descriptions from the close of the 18th century, most of the area was covered by heath which dominated on the thinner soils between bare rocks. On the other hand scrubs of oak, birch and most likely also alder characterized Ravnedalen and the deeper valleys with thicker soil. Without doubt, oak, birch, juniper and black alder also grew in the narrow, low valleys which traverse the area, just as they do today.

1800-1945

The map by Mansa from 1851 (in Bornholms Museum, Rønne) gives no information about the area, but from 1887 we have a detailed map, the 5 cm ordnance map, Hammershus, published by the Topographic department of the General Staff (fig. 5c). According to this map, Ravnedalen and the



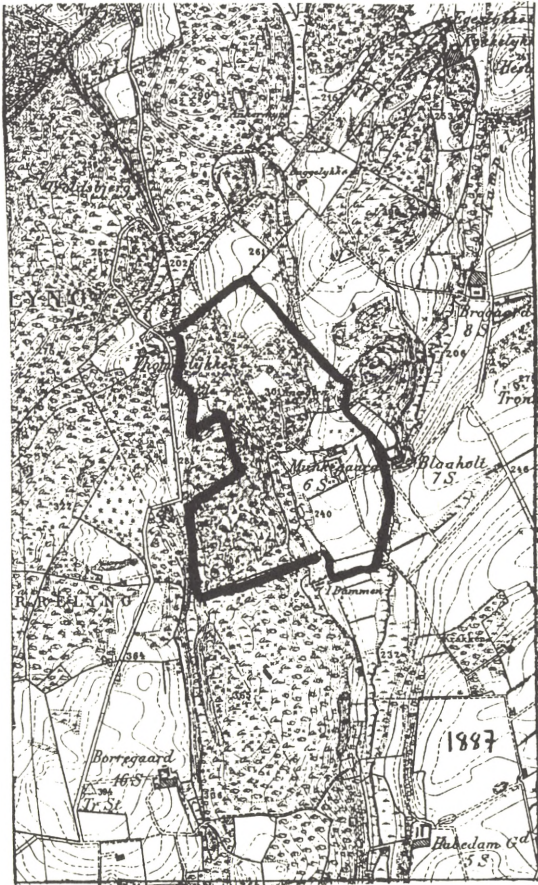
northern part of Borredalen were covered by shrubs and forest, while the area between was covered by heath and bare rock as well as some shrubs. Undoubtedly the area had been grazed so hard that large areas of granite had been laid bare, and heather and shrubs survived mostly in the shallow depressions between the exposed rock. Furthermore the map shows that an area west of part 690 was covered by coniferous forest, most likely pine (*Pinus sylvestris*).

In 1914, the ordnance map of 1887 was corrected (fig. 6a). The signatures indicate that the area was still covered by heath, but with more shrubs and the almost unbroken signature of bare rock in the

Fig. 5. Sections of maps of the area with the State Forest part Borrellyngen entered. a: the map of Hammer measured 1746-58 (1:17000 copy from Bornholms Museum), b: the "Koncept" map from 1799-1801 (1:20000) made by The Royal Danish Academy of Science and Letters, c: the 5 cm ordnance map, Hammershus, of the Topographic department of General Staff, measured 1887.

1887-map is replaced by scattered signatures of bare rock. Undoubtedly this indicate an increase of the overgrowing of the area. The pine forest west of Borredalen was enlarged to the eastern limit of part 690.

In the western part of the old Borrellyng (west of



the modern road) a new type of human encroachment is shown on the map from 1914, a granite quarry. Quarries were not yet marked in the area of the Forest District.

In 1945, new corrections of the ordnance map were made (fig. 6b). As regards the vegetation, no essential changes can be seen. However, the quarry west of the area had been enlarged considerably, and in part 690 a small quarry is marked close to its northern boundary. Furthermore the quarries in part 687 (cf. fig. 1) are shown for the first time. The southern of these was, however, much smaller than today.

The maps give only a rather general impression of the overgrowing of the heath between about 1890 and 1945, which is undoubtedly due to the decrease

in the grazing. On Hammeren, about 4 km north of the area, sheep grazing did not stop until about 1918, but similar information is not available for Borrellyngen.

After 1945

In 1978-79 pine (*Pinus sylvestris*) was widespread among the trees in part 690 together with oak (*Quercus robur*), birch (*Betula pendula*) and juniper (*Juniperus communis*). Most of the pines were cut down during the spring of 1979. The deciduous trees were felled the following autumn. Unfortunately the age of the trees was not measured when they were felled, but in the early spring of 1988 it was still possible to count the growth rings of the stumps of the thicker pines felled in 1979. Of the 33 stumps that were measured 4 were from trees that had germinated between 1911 and 1928, while 25 had germinated between 1929 and 1945 and among these 13 between 1939 and 1945. Only 4 of the trees had germinated after 1945, undoubtedly because only thicker stumps could be examined.

It can not be determined for certain if the oldest of the pines was planted, but undoubtedly they are self-sown dispersed from the plantation west of the area shown on the ordnance map from 1887 (fig. 5a).

The relatively large number of seedlings from the period between 1939 and 1945 may have been caused by increased cutting and clearing in the area during the second world war. During war time a great quantity of heather was cut in Borrellyngen and used for fuel in the dairy at Allinge. The open area produced in this way enhanced the growing conditions for seedlings, just like today when seedlings are common in the open heath areas.

The information extracted from the pine stumps was used when interpreting aerial photos of the area (scale 1:4000) taken by the Geodetic Institute in 1961, 1967, 1974, 1980 and 1986. All photos were from early spring before leafing. This made recognition of single deciduous trees very difficult, but coniferous trees stood out clearly. It was however impossible to distinguish between the different

species of conifers. After 1979, pine and juniper were almost the only coniferous species in the area.

These uncertainties imply that the maps (fig. 7) drawn from the aerial photos may contain some errors. A comparison of the map drawn from the aerial photo from the spring of 1974 with an aerial photo in colour from the autumn of 1973 shows, however, that such errors are negligible. The same conclusion was obtained from a comparison between the aerial photo from the spring of 1986 with an airphoto in colour from the autumn of 1986 and the airphoto from the same time shown in fig. 8.

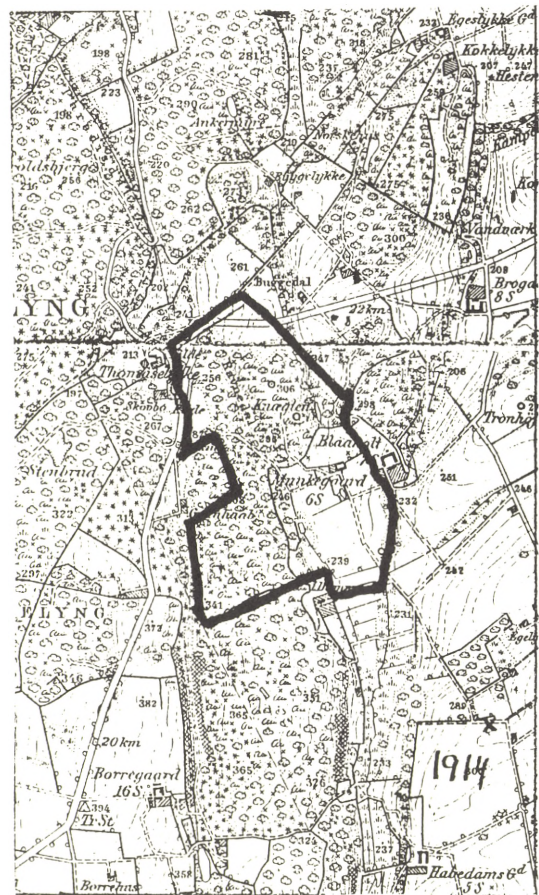
The distribution of coniferous trees shown in the maps (fig. 7) therefore most likely gives a true picture of the overgrowings and clearings in the area between 1961 and 1986.

In 1961 most of the area was open heath. The shrubs and trees were concentrated in the deeper depressions, especially in the valleys. Furthermore many coniferous trees (pines) were found in the northern part of the area and in the SW-corner, both localities close to pine forest in neighbouring areas. The maps from 1967 and 1974 show an increased overgrowing after 1961. The map from 1980 depicts the opening of the landscape caused by the nature conservation management after 1979.

Nature conservation management after 1977

In 1978, part 690 was fenced as a preparation for sheep-grazing, and two 0-parcels (control areas without grazing) were established. One 0-parcel was placed in the centre of part 690, the other near its eastern border to cover both heath and oak forest on the western bank of Ravnedalen (cf. fig. 1).

During spring 1979, many pines and some other trees were cut down in the area, but in the summer of 1979 quite a lot of trees and shrubs remained in the area. Especially the depressions and small valleys were covered by stands of pine (*Pinus sylvestris*), birch (*Betula pendula*), oak (*Quercus robur*), juniper (*Juniperus communis*), aspen (*Populus tremula*), black alder (*Frangula alnus*) and a few spruce (*Picea abies*). The flat areas between the valleys were dominated partly by bare rock and partly by heather (cf. fig. 9).

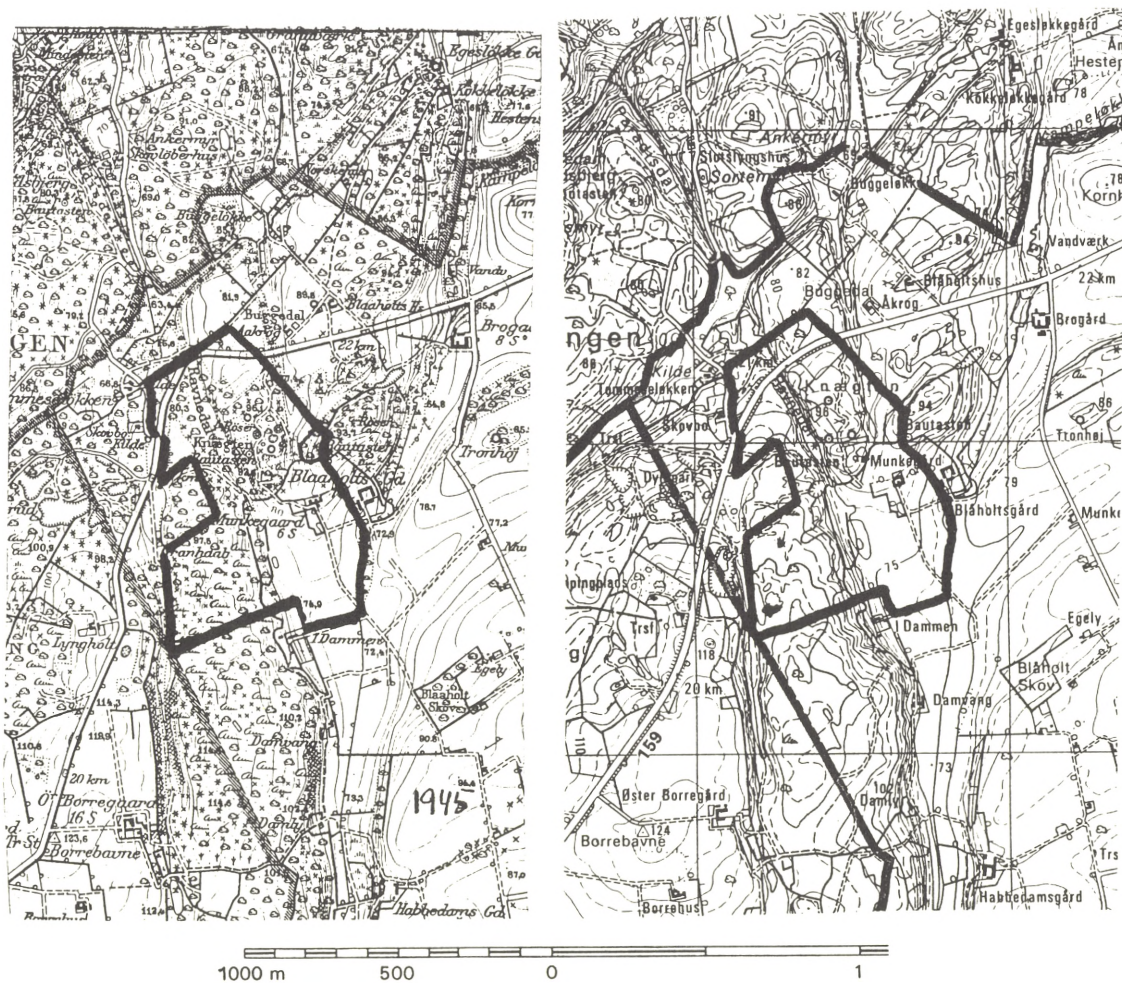


In September 1979 a small number of sheep grazed in the area. The low shrubs of *Populus tremula* and *Frangula alnus* especially were heavily browsed in comparison to the other deciduous trees, while conifers were avoided by the sheep.

In October and November 1979 most of the remaining trees were cut down (cf. fig. 10) in the grazed areas as well as in the ungrazed 0-parcels. Juniper was preserved in the whole area.

Weather condition during the winter of 1979-80 prevented the removal of the cut down stuff, but some of it was burnt in the spring of 1980. The remains were turned into wood chips in the spring of 1981 and removed.

In 1980 and during the two following years a small number of sheep grazed in the area, but after



that time there has only been sheep in the area for short periods. This caused a prolific regrowth from the stumps of birch and oak. The regrowth in the area outside the 0-parcels was cleared mechanically, first in the winter of 1984-85 and again in the autumn of 1987. Thus the area still has the character of open heath with bare rocks and some scattered trees and junipers (cf. fig. 11).

Fig. 6. Sections of ordnance maps with Borrelyngen entered. a: from 1914 (5 cm), b: 1945 (5 cm), c: 1987 (4 cm).

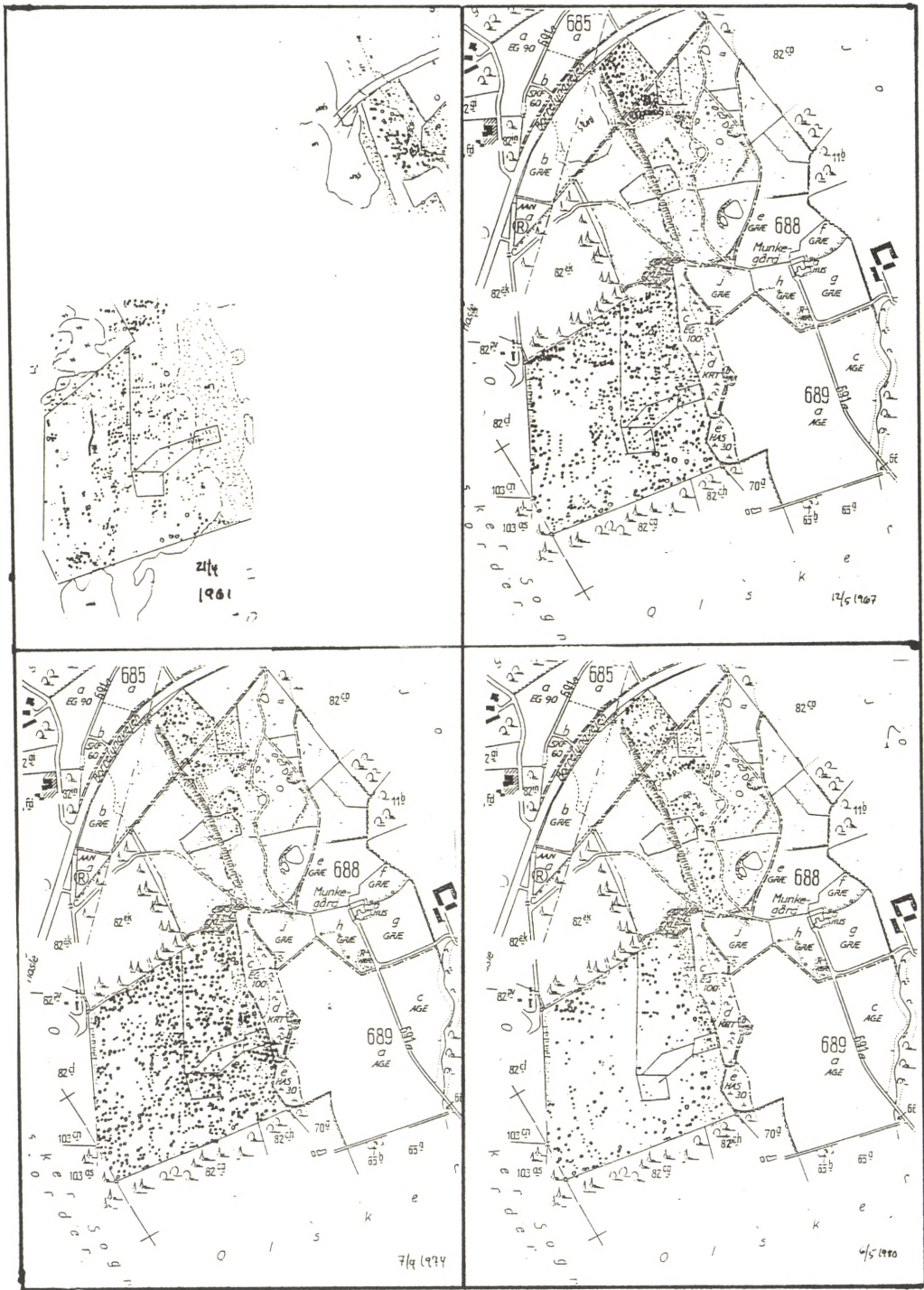




Fig. 7. Distribution in part 690 of conifers (dark dots) in 1961, 1967, 1974 and 1980 after aerial photos taken before leafing. Deciduous forest shown by fine dots. Drawn by V. M.

Fig. 8. Airphoto of the area from Sept. 1986. 0-parcels and transects entered in part 690. Jan Kofoed Winter phot.

III Ecological-botanical investigations 1979-86

Methods

Vegetation and terrain

In the summer of 1979 two transects were established from the central 0-parcel eastwards to the 0-parcel on the eastern border of part 690 (cf. figs. 13 and 14). Furthermore 5 transects each of 20 m were established near the northern border of the central 0-parcel, 10 m inside and 10 m outside the 0-parcel (fig. 21). In 1981 these transects were supplemented with a 200 m long N-S transect from the northwestern corner of the 0-parcel to the northern border of part 690 (fig. 12). The locations of the longer transects are shown in fig. 1.

For each m in the transect a Raunkiær-analysis (circle 0.1 m²) was made, the thickness of the soil (= distance to rock surface) was measured at the centre of the circle which was also levelled (uncertainty about ± 0.1 m). The approximate level above the sea was found by comparison to the contours on the 5 cm ordnance map.

Some plant species of special interest were found only with a low frequency in the transects. As a

Fig. 9. Borrellyngen August 1979 before clearing. The tape measurer indicates the location of a part of the northern E-W transect. In the foreground the depression with *Calluna* and *Molinia* close to the central 0-parcel, in the background the forest in Ravnedalen. V. M. phot.





Fig. 10. Borrellyngen October 1979 after the trees were cut down. The picture was taken from the central part of the area towards east. V. M. phot.

supplement to the information from the transects in 1981 the thickness of the soil was measured at stands close to the N-S transect, where following species were found: *Agrostis stricta* (54 stands), *Carex pilulifera* (66 stands), and *Sieglingia procumbens* (9 stands).

During the very dry summer 1983, several areas of heather (*Calluna vulgaris*) were either dead or severely damaged by drought. In order to investigate this, the thickness of the soil was measured at 105 locations with dead heather and 85 with heavily damaged heather.

The analyses of the vegetation and the measurement of soil thickness were repeated in 1984 in the 3

long transects and in 1986, 3 of the 20 m transects were analysed.

The plant species and the presence of bare soil or rock in each Raunkiær circle were recorded together with the degree of cover for each of them.

The degree of cover was rated on a scale of 6, where 6: $\geq 75\%$, 5: 50-74%, 4: 25-49%, 3: 13-24%, 2: 7-12% and 1: $\leq 6\%$ of the total area of the circle. For calculation of the average degree of cover the following values were used: 6 = 87%, 5 = 63%, 4 = 38%, 3 = 19%, 2 = 9% and 1 = 3%.

Soil chemistry

In 1979 soil samples of the mor layer and the underlying sand were collected from 18 stations on the transects.

In 1984 samples from the same stations were collected, together with samples from the N-S transect.



In 1986 these samples were supplemented with samples from the 20 m transects at the central 0-parcel. A total of 25 samples were collected in 1984 as well as in 1986. The samples were analysed at the Department of Botany. The methods used were the same as those of Hansen 1976, pag. 12-13.

The humidity of the soil

From 1/1 1980 to 2/1 1982 samples of mor and sand were collected from 10 stations in the area about every month (a total of 25 dates). The samples were placed in plastic bags and were weighed 1 or 2 hours after collection and sent to the laboratory for determination of the water content in % of dry weight. From February 1981 the field capacity (the amount of water contained in the sample when all capillaries are saturated with water) was also measured. In the laboratory the fresh samples were saturated with water. After dripping off for 24 hours

Fig. 11. Borrellyngen primo August 1984. The photo is taken from NW corner of the central 0-parcel towards north. In the foreground a small part of the depression with *Molinia coerulea* and *Trichophorum caespitosum*. In the middle *Calluna*-heath with scattered growth of shrubs and trees together with naked ice eroded rocks. The newly bared surfaces are light while the older are grey covered by crustaceous lichens. In the background the pine forest in the neighbouring area. V. M. phot.

they were again weighed. After drying the dry weight of the sample was measured.

After February 1981 the water content was expressed as a percentage of field capacity. The results from samples from 1980 are expressed as percentages of the field capacity determined from the average of 10 samples from the same stations taken in 1981.

Water content as a percentage of field capacity is preferred as an indication of the amount of water available for the plants rather than as a % of dry

weight. However, it must be said that the maxima and minima of water content are contemporaneous in both types of calculations.

Seven of the 10 stations sampled in 1980-81 were situated in areas with a relatively thick soil (≥ 20 cm) where the terrain was rather flat, while three stations were placed on sloping terrain with a somewhat thinner soil layer.

The variation in soil humidity was correlated with the precipitation at the nearest meteorological station, Hammerodde Fyr, which is situated 4.5 km N of the locality. The meteorological station lies at a lower level and close to the sea. Especially there may be some differences in precipitation due to thunderstorms in summertime, but undoubtedly in general the precipitation and temperature of Borrellyngen followed the same pattern as was recorded at Hammerodde Fyr.

In the period from autumn 1980 to summer 1986, the level of the soil water table was measured in two perforated plastic tubes placed in the depression with *Calluna vulgaris* and *Molinia coerulea* on both

sides of the northern border of the central 0-parcel.

During 1981 there was a close parallelism between soil humidity, precipitation and the level of the water table in the tubes (cf. fig. 15), so from 1982 to 1986 only the water table in the tubes was measured. In the very dry periods of Juli-August 1984 the water content in % of field capacity in samples of mor and sand from several stations was measured as a supplement to the records of the water table.

Climate

The following data from the meteorological station at Hammerodde Fyr have been used: precipitation every half month (1980-81), yearly and monthly precipitation (1980-86), precipitation March-April (1980-86), precipitation June-September (1980-86), precipitation June-July (1980-86), days with maximum temperature $\geq 20^\circ$ (1980-85), average temperature June-August (1980-85). Temperature from 1986 were not available.

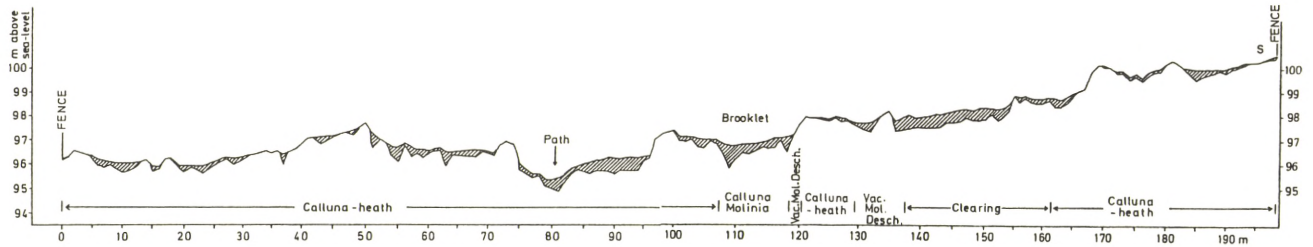
IV The terrain and its influence on vegetation

The southwestern part of the investigated area lies about 105 m and the northern part rather more than 95 m above sea level. In the east it slopes gently towards the steep edge of Ravnedalen, the bottom of which lies 75-80 m above sea level. Borredalen, which forms the western border of the area, has its bottom about 90 m above sea level.

The base rock is granite whose surface was ground smooth during the last Ice Age and which forms typical "roche moutonné" at many places. These protruding rocks are either bare or covered by only a thin layer of soil. In most depressions the thickness of the soil is usually less than 30-40 cm. Such localities with a rather thin layer of soil are mostly characterized by *Calluna-heath*.

Somewhat thicker layers of soil can be found in the broader or narrower shallow valleys which form a network throughout the area. In both the western and eastern part of the area N-S running, 6-8 m broad valleys are found (cf. the transects fig. 13 at 74 m, and fig. 14 at 35 m). A broader N-S running valley runs through the middle of the area (part of it can be seen in fig. 22). This valley meets an E-W running valley containing a brooklet running towards Ravnedalen (cf. the transect fig. 12, between 100 and 120 m). Another bigger E-W running valley is found in the southeastern corner of the area (cf. fig. 4).

In the depression where the soil is more than 30-40 cm thick the vegetation is usually characterized



by *Molinia coerulea*, *Trichophorum caespitosum* and several species of *Juncus* together with *Calluna vulgaris*. Heather also dominated depressions with a thinner layer of soil, and can have a degree of cover $\geq 75\%$ even where there is only a soil layer of a couple of cm. In some cases the cause of heather thriving so well on a very thin layer of soil can be that the roots have found their way through one of the many fine fissures in the rock, but mostly the roots of heather form a dense network on the surface of the rock.

The depressions play an important role in the overgrowing of the area with trees and shrubs. However, *Pinus sylvestris* and *Betula pendula* may also

Fig. 12. N-S transect from the northern border of part 690 to the NV corner of the central 0-parcel (cf. fig. 1). Desch: *Deschampsia flexuosa*, Mol: *Molinia coerulea*, Vac: *Vaccinium myrtillus*. The soil layer is hatched.

germinate in narrow fissures on otherwise bare rock, but those trees usually become small and most of them do not survive an extremely dry summer. In the depressions the development of the trees is much better and the overgrowing usually starts such places. The shrubs in the valleys then form a shelter belt which make the overgrowing possible in the areas between the valleys (cf. the maps from 1961 and 1967 in fig. 7).

V The soil and its influence on the vegetation

Like the other heaths investigated on Bornholm the heath in Borrelyngen is without a hardpan. Therefore the section through the soil shows only a layer of mor of some few centimeters above a usually thin layer of sand, sometimes with some gravel, above the rock surface.

Chemical conditions

Table 2 shows the results of the chemical analyses of the soil samples from 1979 and from 1984-86. Corresponding values from heaths by Hansen 1976 are given for comparison.

As a whole the two studies agree even though they cover different localities on Bornholm. The

most noticeable differences are the values of pH which in 1979 were somewhat lower in Borrelyngen than those found by Hansen in 1976, and the values of conductivity which were higher in Borrelyngen in 1979. Station 55 of Hansen 1979 was placed in part 687 of Borrelyngen (cf. fig. 1). Here he found a conductivity of 200 and 343 μmho (personal communication from K. Hansen). This indicates a smaller real difference between the two studies than is shown by the mean values in table 2.

The values from 1979 in table 2 give no significant differences between the different communities. In the *Calluna*-heath, however, there seems to be a difference between the thicker and thinner soil layers. The values for the nutrients Ca and Mg are

TABLE 2

	n	pH	I_t	Ca	Mg	Mn	Na	K	P	Cu	Zn	Fe
MOR												
1979												
Calluna heath, 0-3 cm	2	3.5	234	1.9	0.8	0.03	0.3	0.7	53	4	45	1270
Calluna heath, 4-9 cm	1	3.8	238	2.0	0.9	0.06	0.4	1.2	56	6	43	2440
Calluna heath, \geq 20 cm	9	3.7	246	3.8	1.6	0.30	0.8	1.9	77	5	52	1500
Calluna-Molinia com.	3	3.6	383	1.4	0.9	0.02	0.9	1.2	50	4	58	2470
Calluna-Molinia com.	3	3.6	333	2.4	1.6	0.06	1.2	2.0	54	4	37	1210
1984												
Calluna heath, 0-3 cm	2	4.3	400	2.5	1.2	0.6	0.5	0.8	13			
Calluna heath, \geq 20 cm	16	3.9	471	3.1	1.5	0.2	0.6	0.6	11			
Calluna-Molinia com.*	2	3.5	577	1.4	1.0	0.5	0.5	0.8	5			
Calluna-Molinia com.	3	4.0	501	2.3	1.4	0.7	0.7	0.5	10			
Calluna-Molinia-Juncus com.	1	4.0	433	7.2	3.0	1.9	0.6	0.4	10			
Vac.-Mol.-Desch. com.	1	4.0	497	3.2	1.7	0.6	0.6	0.5	4			
SAND												
1979												
Calluna heath, 4-9 cm	1	3.9	166	0.2	0.2	0.1	0.1	0.4	30	2	12	2140
Calluna heath, 10-19 cm	1	3.9	133	0.2	0.2	0.1	0.1	0.3	26	0.4	8	920
Calluna heath, \geq 20 cm	9	4.0	94	0.1	0.2	0.1	0.1	0.2	24	0.1	3	930
Calluna-Molinia com.	3	4.0	80	0.1	0.2	0.1	0.1	0.1	12	0.1	5	250
Calluna-Molinia com.	3	3.8	60	0.1	0.2	0.1	0.1	0.1	17	0	4	120
1984												
Calluna heath, \geq 20 cm	16	4.5	128	0.4	0.2	0.4	0.4	0.1	7			
Calluna-Molinia com.*	2	3.9	52	0.4	0.6	0.4	0.4	0.1	5			
Calluna-Molinia com.	3	4.3	115	0.4	0.2	0.4	0.4	0.1	6			
Calluna-Molinia-Juncus com.	1	4.6	106	0.8	0.3	0.4	0.4	0.01	7			
Vac.-Mol.-Desch. com.	1	4.7	108	0.3	0.2	0.00	0.5	0.03	6			
KH, 1976: Cal heath, Mor	24	4.0	176	2.7	1.1	0.09	0.14	0.7	44	2.7	20	998
KH, 1976: Cal heath, Sand	24	4.5	50	0.3	0.1		0.05	0.1	9			

*1986

Table 2. Chemical analyses of soil samples from Borrellyngen 1974 and 1984-86. Ca, Mg, K, Na, and Mn in meq/100 g soil. P, Cu, Zn, and Fe in ppm. Conductivity (I_t) in μ mho.

highest where the layer is thick, most likely because the leaching is greater where the layer is thin.

Generally, the values from 1984-86 differed from those from 1979 by: 1. higher pH in both mor and sand, so that the values from 1984-86 are of the same magnitude as found by Hansen 1976, 2. the conductivity in the mor layer increased, and 3. the content of P decreased in both mor and sand.

As fig. 9 shows, in 1979 the area was much overgrown. However, the localities for sampling were without trees and shrubs. In 1984 most of the trees and shrubs in the area were removed, so the light conditions had changed considerably. Furthermore

the supply of leaves and needles was reduced. Such changes may have influenced the chemical conditions in the soil.

The thickness of the soil

The transects (figs. 13-14) shows that the thickness of the soil varies very much in the area, but usually the soil layer is rather thin. Table 3 gives the distribution of the different soil-thickness categories in each of the plant communities in % of the total number of samples.

The most widespread plant community is the

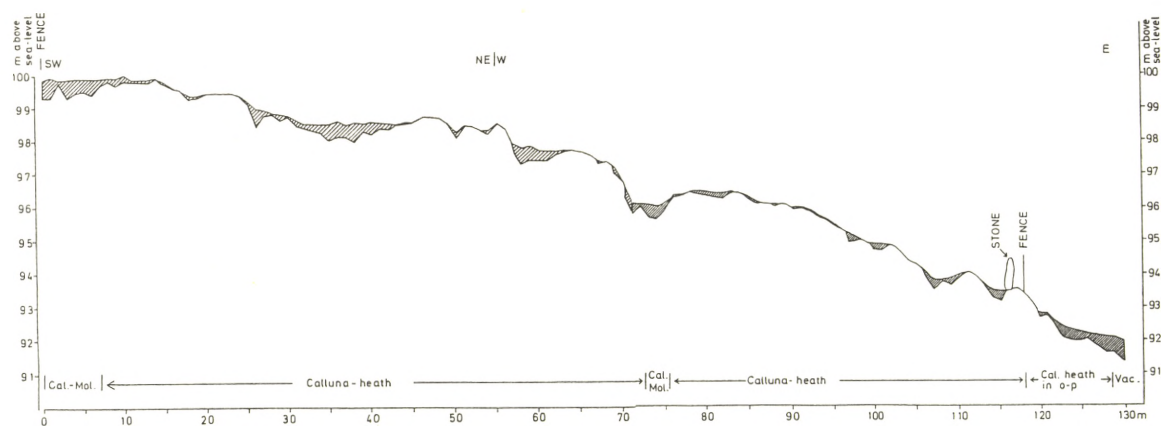


Fig. 13. The northern W-E transect from the central 0-parcel (11 m east of the NW corner) to the 0-parcel at Ravnedalen (10 m south of the NW corner) and 12 m into the 0-parcel (cf. fig. 1).

Calluna-heath, which generally is characterized by a thin layer of soil (mean values 15.8 and 19.8 cm) and 40-50% of the samples has a thickness less than 10 cm. Only 10-12% of the samples have more than 40 cm soil.

The three *Calluna-Molinia* communities has mean

values of 42.0, 42.7 and 43.1 cm, and about 90% of the samples have a soil layer of 20 or more cm.

The regenerating clearing, which before 1979 was covered by a close stand of mostly pine, also had a high mean soil thickness value, 35.2 cm. More than half of the samples had a soil thickness ≥ 40 cm. Undoubtedly the rather thick layer of soil

Fig. 14. The southern W-E transect from the central 0-parcel (3.2 m south of the NE corner) to the SW corner of the 0-parcel at Ravnedalen (cf. fig. 1).

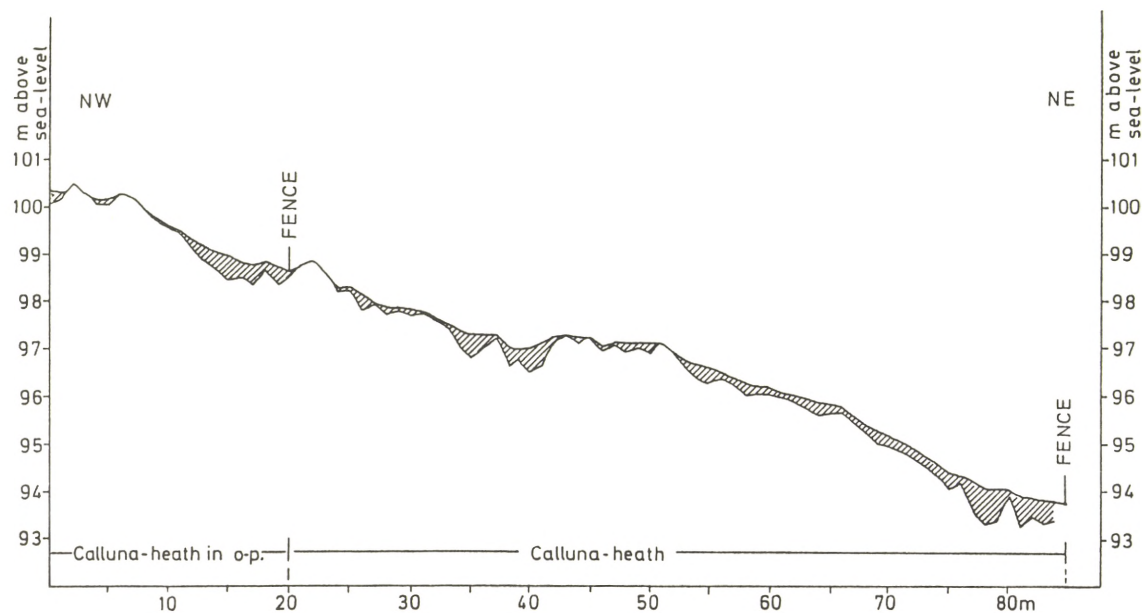


TABLE 3

Thickness in cm	Calluna heath in transects	Calluna heath in 0-parcels	Calluna-Molinia com. in North. W-E transect	Calluna-Molinia-Juncus com. in N-S transect	Calluna-Molinia com. in- and outside central 0-parcel	Clearing in N-S transect	Vaccinium-Molinia-Deschampsia com. in N-S transect
0-3	33.9	32.9	–	–	–	4.3	9.5
4-9	16.6	7.0	10.5	–	1.6	8.7	28.6
10-19	17.5	12.9	–	5.3	4.7	13.0	9.5
20-29	13.2	16.5	10.5	15.8	14.5	13.0	4.8
30-39	7.7	17.6	10.5	31.6	20.2	4.3	4.8
40-49	5.7	4.7	21.1	21.1	19.7	32.6	19.0
50-59	2.7	5.9	36.8	15.8	30.6	19.6	9.5
60-69	2.4	2.4	10.5	5.3	7.3	4.3	14.3
70-79	0.3	–	–	–	1.6	–	–
80-89	–	–	–	–	–	–	–
90-	–	–	–	5.3	–	–	–
\bar{m}	15.8	19.8	43.1	42.0	42.7	35.2	29.1
n	749	85	19	19	193	46	21

Table 3. Distribution of soil thickness in the different plant communities in the transects and in the *Calluna-Molinia* community in and outside the central 0-parcel. The number of samples in each category of thickness in % of the total number of samples in the community (n). \bar{m} : average, n: number of samples.

explains the faster growth of the trees in this locality.

The *Vaccinium* community is heterogenous both with respect to plant species and thickness of the soil. In Borrellyngen, like in other Danish heaths, *Vaccinium* prefers northfacing slopes.

Field capacity and the thickness of the soil

During the period 1981-84, field capacity (in % of dry weight) was determined in 112 samples of mor and 58 samples of sand.

Table 4 shows the variation in field capacity in mor samples from: 1. a depression dominated by *Calluna* and *Molinia* and which had a soil layer of 20 or more cm, 2. *Calluna*-heaths on soil ≥ 20 cm, 19-10 cm, 9-4 cm and 3-0 cm, 3. a single sample from a *Vaccinium* community on a soil ≥ 20 cm.

Of the samples from the *Calluna-Molinia* community, 81 % had a field capacity above 400, and the mean value of the samples was 670.

TABLE 4

Mor	Calluna-Molinia	Calluna heath				Vaccinium
	≥ 20 cm	≥ 20 cm	19-10 cm	9-4 cm	3-0 cm	≥ 20 cm
< 300	2	8	33	100	67	
300-399	17	23	20	–	33	100
400-499	17	28	40	–		
≥ 500	64	42	7	–		
n	47	39	15	7	3	1
\bar{m}	670	450	338	231	220	377

Table 4. Distribution of field capacity in mor layers in 3 communities in 1981 to 1984. The number of samples in each category of thickness in % of the total number of samples in the community (n). \bar{m} : average.

In the *Calluna*-heath the field capacity was highest in samples from the area with a thick soil layer (mean value 450) and decreased with decreasing soil thickness. Heath on soils of 9-4 cm and 3-0 cm

TABLE 5

Field capacity	Sand	Calluna-Molinia	Calluna heath		Vaccinium
		≥20 cm	≥20 cm	19-10 cm	≥20 cm
< 20		43	6		
20-39		43	39	33	
40-59		4	32	33	100
≥ 60		9	23	33	
n		23	31	3	1
m̄		22	44	53	47

Table 5. Distribution of field capacity in sand layers in 3 communities in 1981 to 1984. The number of samples in each category of thickness in % of the total number of samples in the community (n). \bar{m} : average.

had mean values of 231 and 220. Hansen 1979 found a mean value of the field capacity in mor on Bornholm of 226. Field capacity from station 55 in Borrellyngen was 220 and 430 (K. Hansen, personal communication). Both these values are within the variation of field capacity in *Calluna*-heath on soil \geq 20 cm (cf. table 3).

The content of humus was higher where the soil was thicker and the content of mineral substance was highest in the thin soil layers. This undoubtedly explains the parallel variation in field capacity and soil thickness.

The field capacity in the sand samples, table 5, was much lower (mean values from 53 to 22) than for the mor samples. Contrary to the values for mor, the mean values for sand were lowest in the *Calluna-Molinia* community. The sand layer in this community was much thicker than in the other communities, and contained less humus than the thin layer of sand between the rock surface and the mor.

Humidity of the soil

The level of the area is higher than the surroundings and therefore without afflux. So the humidity of the soil is totally dependent on the precipitation, and there is a difference between the water content in soil in badly drained areas, e.g. many depres-

sions, and in well-drained areas, such as on sloping terrain.

The plants are dependent on the available water in the soil and when the content of water is very low compared with the field capacity, there may be difficulties for the plant.

Fig. 15 shows the connection between: 1. the content of water in percent of field capacity, 2. the level of the free water table in relation to the soil surface, and 3. the precipitation in each half month from January 1980 to December 1981. The water % is given for two kinds of terrain, viz. 5 stations in flat terrain in depressions and 3 stations on sloping terrain. The graphs show the average values, but all the graphs for the single stations have the same maxima and minima as the graphs of the average values.

The water content on sloping terrain was generally lower than on flat areas, especially the minima.

In the sand layers the water content was mostly above field capacity, except during a dry period in July 1981 when the water content in sand layers on sloping terrain was lower than the field capacity.

In winter time the water content in the mor layer in the depressions was near field capacity corresponding to the level of the water table being in the neighbourhood of the soil surface. An exception was in January 1980, but at that time the area was covered by a thick layer of snow containing the recent precipitation. The melted snow gave the peak on the curve in April.

On sloping terrain the water content of the mor was usually lower than field capacity in winter time, corresponding to the relatively dry surfaces of the soil noticed when visiting the area.

During spring and summer, the water content in the mor layer was much lower on both types of terrain than during autumn and winter. Figure 15 shows a clear connection between water content and recent precipitation. In both years the precipitation in April and May was low and correspondingly very low values for the content of water were found. Also in 1981 the precipitation was very low between the 16th of June and the 15th of July. This,

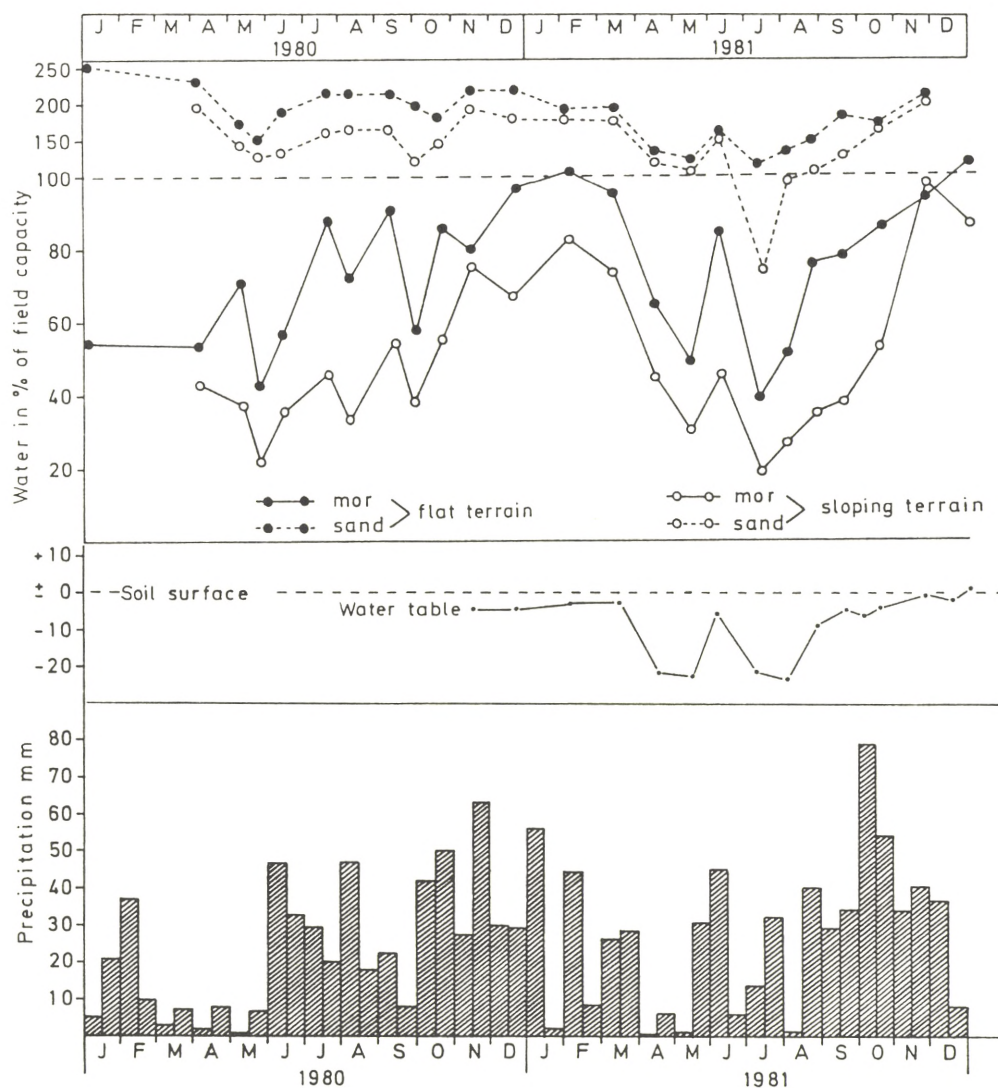


Fig. 15. 1. Content of water in % of field capacity in mor and sand from flat and sloping terrain, 2. The water table in plastic tubes in relation to soil surface in the depression with *Calluna* and *Molinia* near the N border of the central 0-parcel, 3. Precipitation every ½ month from January 1980 to December 1981. The average values of 5 stations on flat terrain and 3 on sloping are used in the curves for water content.

combined with the higher temperature in summer, caused a marked minimum for the percent of water in July. The same period in 1980 had a higher pre-

cipitation and the curves for the water percent showed no minimum.

The curve showing the level of the free water table in relation to the soil surface in 1981 contained the same variations during the year and was therefore used as an indication of the variations in the humidity in the soil during the following years.

Thamdrup 1939 refers to investigations of heaths in Jutland. In the paper is i.a. given a comparison of the variation of the water content in the soil lay-

ers of the heaths and the precipitation at the neighbouring meteorological stations. Thamdrup measured the water content as % of fresh weight. However, his curves for water express maxima and minima at the same time as they would do if based on dry weight or field capacity. The latter was however not measured.

Thamdrup found a pronounced parallelism between precipitation and the water content in the mor layers as well as in the other layers of the soil. Low precipitation in summer was noted to have a greater effect on the content of water than low precipitation in colder periods.

Hansen 1979 investigated the water content in mor and sand in July 1971 both just after rain and after 2 weeks of drought and found a considerable decrease in the water content after drought. He noticed that drought may contribute to the specific plant distribution in a heath area. As will be shown later (page 31) this was confirmed, as the very warm and dry summers in 1982 and 1983 had a great influence on the vegetation in some localities in Borrellyngen.

Contrary to the heath in Borrellyngen several of the heaths investigated by Thamdrup (1939) contained a hardpan, and Thamdrup noticed that besides the mor layer the hardpan has great importance as a water reservoir during dry periods.

In order to make a comparison between the two types of heaths the water content in the soil layers was calculated as a % of dry weight in a locality on sloping terrain in Borrellyngen and in Thamdrup's station 25 (a dry heath on a hill island in W Jutland).

Samples from Borrellyngen were taken from 3 stations at 12 different dates in the period from 10/12 1980 to 28/11 1981. It can be noted that the summer of 1981 was not especially dry and warm, and except for April, the year differed not much from mean values of precipitation.

From Thamdrup st. 25 the period from 12/2 1937 to 15/1 1938 was used. The precipitation was very high in June 1937, and was below mean values in July and August, but there was no particularly dry

TABLE 6

	\bar{m}	max	min	n
Borrellyngen, mor	218	417	81	12
Borrellyngen, sand	39	57	21	12
Thamdrup, st. 25, mor	142	218	68	23
Thamdrup, st. 25, hardpan	43	57	29	21
Thamdrup, st. 25, bleached sand	10	19	2	23

Table 6. Water content in % of dry soil weight. The locality in Borrellyngen was a *Calluna* heath on sloping terrain with about 20 cm soil and no hardpan. Values from 20/12 1980 to 28/11 1981 are used. The locality of Thamdrup was a *Calluna* heath in W. Jutland. Values from 12/12 1937 to 15/1 1938 are used, and calculated from Thamdrup 1939, table 8 and fig. 37, where the water content was determined as % of fresh weight.

period during the summer, and regarding precipitation the year was in no way extreme.

Therefore a comparison of the average water content in the soil layers of the two localities may be justifiable.

Table 6 shows the mean values and maximum and minimum values in the soil layers from the two localities.

The mor layer contained much more water in Borrellyngen than in W Jutland, undoubtedly because the field capacity was greater on Bornholm than in W Jutland (cf. Hansen 1979, table 10). The same was the case regarding the maximum values. The difference was smaller regarding the minimum values, but because none of the two periods contained a real warm and dry summer, the minimum values of table 6 are not the absolute minimum values. The lowest water content in the mor layer in Borrellyngen was measured on the 8th August 1982 and was 29 % of dry weight.

The values for water content of sand in Borrellyngen and hardpan in W Jutland were almost identical, while the values for bleached sand in W Jutland were much lower, especially the minimum value of 2 %. This was much lower than the lowest water content value measured for the sand layer of Borrellyngen, namely 8 % on the 8th of August 1982.

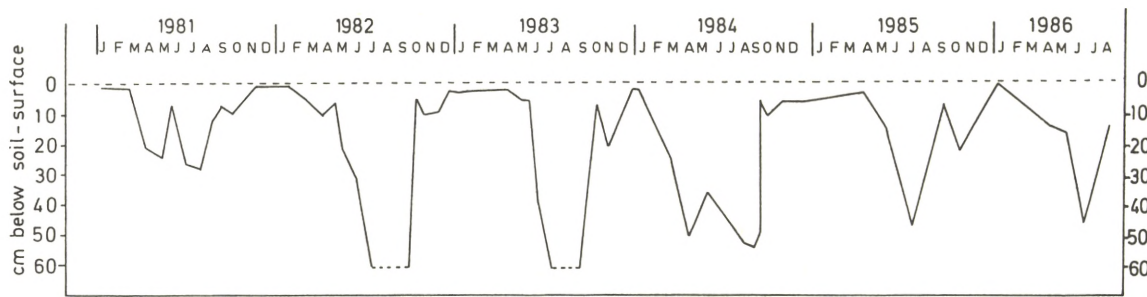


Fig. 16. The level of the water table in the *Calluna-Molinia* community near the central 0-parcel measured in plastic tubes from 1981 to 1986.

Table 6 shows that there is a great difference between the water balance of the sand layer in Borrellyngen and the bleached sand in the heaths of W Jutland.

As the field capacity of the hardpan was not measured it is impossible to tell if the amount of available water varied in the same way for the sand layer in Borrellyngen and for the hardpan in W Jutland. However, the graphs for water content for the hardpan in W Jutland and the sand in Borrellyngen, on which the values of table 6 are based were almost identical, which may indicate an analogy between the two types of soil.

The climate and the variation of soil humidity from 1980 to 1986

Fig. 16 shows the variation of the level of the free water table in the plastic tubes in the depression on both sides of the northern border of the central 0-parcel from 1981 to 1986. As explained above this expressed the general variation in the soil humidity in the depression during the same period.

As shown in fig. 15, the soil humidity was somewhat lower on sloping terrain than in the depressions but the variations in water content in the two types of locality was proportional. Periods with extremely low levels of water in the depressions correspond to periods when the water content in the

mor layers may have been critically low for the vegetation on sloping terrain.

The level of the water table followed a similar pattern during all of the 6 years. During winter (December-February) it was near the soil surface. It sank during the spring, and was 30 to more than 60 cm below the soil surface during summertime. The lowest level was usually found in the warmer period of July and in August. In 1981 and in 1984 the level was also low in spring (March and April). The absolute lowest levels were found in the summers of 1982 and 1983 when the water table was more than 60 cm below the soil surface, and thus below the bottom of the plastic tubes.

During September-October the water level again rose towards the winter level near the soil surface which was usually reached in November. In October 1983 and 1985 precipitation was extremely low and caused small minima in the water level.

The extreme low water tables were found only when extremely low precipitation was combined with the higher summer temperatures. Low precipitation in the colder period gave only less pronounced minima (cf. also Thamdrup 1939, p. 46-47).

A comparison of the curve fig. 16 with the climatic data from Hammerodde Fyr, table 7, shows that just the summers of 1982 and 1983 were extremely dry and warm. Precipitation in the period June to September in those two years were 138 and 144 mm against an average of 194 mm for 1980-86 and 214 mm for 1931-60. Precipitation in the period June to July were even more extreme in 1982 and 1983 compared to the averages of 1980-86 and 1931-60,

TABLE 7

	1980	1981	1982	1983	1984	1985	1986	\bar{m} 1980 1986	\bar{m} 1931- 1960
Precipitation, year	543	657	538	542	556	609	578	574	562
Precipitation, mar.-apr.	20	62	67	119	16	81	74	62	66
Precipitation, jun.-sept.	225	202	138	144	241	208	203	194	214
Precipitation, jun.-jul.	129	97	58	31	145	93	137	99	101
Days with max. temp. $\geq 20^\circ$	13	19	39	43	15	20	–	25*	–
Mean temp., june-august	15.0	15.0	16.4	16.7	15.1	15.4	–	15.6*	16.1

Table 7. Precipitation and temperature at Hammerodde Fyr 1980 to 1986, and the average values for the periods 1980 to 1986 and 1931-1960. *) only for the period 1980 to 1985.

namely 58 and 31 mm against 99 and 101 mm. Furthermore the summer temperature was higher during these two years. In 1982 and 1983 39 and 43 days respectively had a maximum temperature $\geq 20^\circ$ against 13, 19, 15 and 20 in 1980, 1981, 1984 and 1985. The average temperature for June-Au-

gust was 16.4° and 16.7° in 1982 and 1983 against 15.0° to 15.4° the other years.

As a supplement to and control of the study of the water level changes in the plastic tubes, the water content (in % of field capacity) were measured during the dry summer of 1982. Samples were collected

TABLE 8

Mor	Calluna- Molinia	Calluna heath				Vaccinium
	≥ 20 cm	≥ 20 cm	19-10 cm	9-4 cm	3-0 cm	≥ 20 cm
flat terrain	48(40-58)	41(26-56)	37(29-41)	27(21-38)	22(17-27)	
sloping terrain	19(15-22)	15(13-16)	13(10-16)	8(5-14)	12	14
n (flat terrain)	5	5	5	3	2	0
n (sloping terrain)	2	2	2	4	1	1

Table 8. Water content in % of field capacity 23/7 1982 in mor layers from all soil samples collected that day.

TABLE 9

Sand	Calluna- Molinia	Calluna heath		Vaccinium
	≥ 20 cm	≥ 20 cm	19-10 cm	≥ 20 cm
flat terrain	87(80-94)	63(53-83)	70	–
sloping terrain	67	42(29-56)	18(17-18)	31
n (flat terrain)	5	5	1	–
n (sloping terrain)	2	2	2	1

Table 9. Water content in % of field capacity 23/7 1982 in sand layers from all soil samples collected that day.

TABLE 10

Mor	11/7 81	23/7 82	8/8 82	/8 84
Calluna-Molinia ≥20 cm soil n = 5	43 (27-55)	48 (40-58)	30 (24-33)	51 (37-66)
Calluna heath ≥20cm soil flat terrain, n = 2	40 (36-43)	46 (35-36)	12 (11-12)	29 (28-29)
Calluna heath ≥20cm soil sloping terrain, n = 2	16 (13-18)	15 (13-16)	9 (6-11)	17 (14-20)
Calluna heath 19-10 cm soil sloping terrain, n = 1	26	16	6	43

Table 10. Water content in % of field capacity in mor layers in the dry periods of 1981, 1982 and 1984. Only data from stations investigated every time are included.

TABLE 11

Sand	11/7 81	23/7 82	8/8 82	24/8 84
Calluna-Molinia ≥20 cm, n = 4	118 (57-158)	89 (84-94)	61 (47-83)	96 (81-132)
Calluna heath ≥20cm soil flat terrain, n = 2	91 (52-129)	70 (58-83)	21 (17-25)	50 (49-50)
Calluna heath ≥20cm soil sloping terrain, n = 2	69 (37-100)	42 (29-56)	14 (12-17)	23 (18-27)
Calluna heath 19-10 cm soil sloping terrain, n = 1	85	18	10	47

Table 11. Water content in % of field capacity in sand layers in the dry periods of 1981, 1982 and 1984. Only data from stations investigated every time are included.

from the stations used in fig. 15 supplied with stations on similar localities.

The 23rd of July 1982, 20 mor and 11 sand samples were collected on more or less flat terrain and 11 mor and 7 sand samples on sloping terrain.

Table 8 shows averages and variations of water in % of field capacity in mor samples from different communities and different categories of soil thick-

ness both in more or less flat and sloping terrain. Notice the low values, especially on sloping terrain.

The values for the sand samples, table 9, are similarly low. Hence, this investigation confirms the relation between the water table in the plastic tubes and the humidity of the soil.

In 1982 the dry and warm weather continued after July 23rd and the 8th of August 1982 mor samples from 10 stations and sand samples from 9 stations were collected. From these stations data from 11th of July 1981 and 23rd of July 1982 were also available. Furthermore samples from the same stations were collected in August 1984.

Tables 10 and 11 show the water content in % of field capacity in mor and sand samples from different communities, terrain and soil thickness on these 4 dates. The values, especially on sloping terrain, were extremely low in August 1982.

The dry summers of 1982 and 1983 and their effect on the vegetation

In 1982 and even more pronouncedly in the sum-

TABLE 12

Calluna	Soil in cm				n
	≥20	19-10	9-4	3-0	
Dead	-	16	45	39	105
Heavily damaged	1	32	49	18	85
\bar{m}	0.5	24.0	47.0	28.5	

Table 12. Distribution in % of *Calluna vulgaris* damaged by drought in the 4 categories of soil thickness. Analysed 8/8 1983 near the N-S transect.

TABLE 13

	Dead	Heavily damaged	n
19-10 cm	39	61	44
9-4 cm	53	47	89
3-0 cm	73	27	56

Table 13. Distribution in % of dead and heavily damaged *Calluna vulgaris* according to thickness of soil.



mer of 1983, rather big areas of *Calluna* withered and died. The same was the case for several of the young *Betula* trees, cf. figs. 17 and 18.

In order to get an impression of the relation between drought and soil the depth of the soil were measured on the 8th of August 1983 in 105 tufts of dead *Calluna* and in 85 stands of *Calluna* on which most of the shoots had died.

Table 12 shows the distribution of the drought stricken *Calluna* against soil thickness. It is remarkably that among 190 stations with damaged *Calluna* only one had a thickness of soil ≥ 20 cm, and 84 % of the dead and 67 % of the heavily damaged examples were found where the soil layer was thinner than 10 cm.

Table 13 gives the relationship between dead and damaged *Calluna* for three categories of soil thickness. Where the soil was 10-19 cm 39 % of the *Calluna* were dead and 61 % damaged. Almost the

Fig. 17. Borrellyngen August 1982. *Calluna vulgaris* strongly drought-stricken (a light colour on the picture). Also several *Betula* had withered. In the foreground to the right can be seen undamaged *Calluna* and *Quercus*. In the background the forest in Ravnedalen. V. M. phot.

same numbers were found on soil 4-9 cm thick, while on a soil layer of less than 3 cm almost $\frac{3}{4}$ were dead.

This distribution of dead *Calluna* was not quite general. In some depressions heather survived on thin soil layers, but on sloping well drained terrain *Calluna* generally was damaged where the layers of soil were thin.

The investigation showed that in an extremely dry summer *Calluna* may be heavily damaged on thin layers of soil. On sloping rock surfaces the dry soil without living roots will crumble and be easily eroded. This soil erosion is then increased by traffic,



Fig. 18. Borrelyngen July 1983. Phot. from the NV corner of the central 0-parcel towards N. Much of the heather is dead. The light parts of the rocks show where the thin layer of soil was removed by erosion. V. M. phot.

e.g. by sheep and other animals.

Photos from the end of the 19th century depict that this kind of soil erosion was widespread on Bornholm on the heaths and commons grazed by many sheep. The pictures show that bare rocks were common. The same is the case in an area about 2 km W of Borrelyngen which have been grazed by goats and sheep for several years.

The *Calluna* heath in the N-S transect was analysed in 1981 just after the overgrowth were cleared, and later in 1984, after the two dry summers in 1982 and 1983. Table 14 shows some of the changes in the vegetation expressed as degree of cover (in %) for different elements of the heath.

TABLE 14

	Soil in cm							
	≥20		19-10		9-4		3-0	
	1981	1984	1981	1984	1981	1984	1981	1984
Calluna vulgaris	71.3	74.3	61.7	70.9	45.1	38.3	23.4	9.0
Deschampsia flexuosa	2.3	4.2	0.8	0.8	0.6	11.8	0.3	4.4
Lichens	0.1	0.1	–	–	0.8	2.0	0.7	2.1
Bryophytes	1.9	6.7	2.0	4.6	2.5	7.1	1.6	4.6
Vegetation totally	78.8	89.0	65.7	76.3	57.5	61.7	27.1	22.0
Bare soil	–	1.3	10.3	6.0	17.0	11.9	20.1	11.0
Bare rock	0.1	–	0.8	–	0.6	2.6	28.7	47.1
n	48	55	24	20	30	34	54	48

Table 14. Degree of cover (in %) of *Calluna vulgaris*, *Deschampsia flexuosa*, lichens, bryophytes and areas without vegetation in the *Calluna* heath in the N-S transect in 1981 and 1984.



On soil thicker than 10 cm the degree of cover of *Calluna* was unchanged or a bit increased, while it had decreased considerably on soil layers from 0-3 cm thick (from 23 to 9 pct).

The degree of cover of *Dechampsia flexuosa* had increased somewhat on soil > 20 cm and much more on soil 9 cm thick or thinner.

Lichens had a low degree of cover during both years, but had a slight increase in cover on soil ≤ 9 cm thick. In 1984, bryophytes had a somewhat higher degree of cover than in 1981 in all categories of soil thickness.

The total degree of cover for the vegetation decreased with decreasing soil thickness both years. From 1981 to 1984 total cover increased on soil ≥ 4 cm, but decreased slightly on soil ≥ 3 cm.

Areas without vegetation were divided between bare soil and bare rock. Both had the highest degree of cover where the soil layer was thin.

Fig. 19. Borrelyngen October 1983. Earlier the protruding rock has been covered by *Calluna* growing on a thin layer of soil up to the border between the dark surface with lichens and the light surface. When *Calluna* died on the thin soil, this crumbled and was washed down to the depressions between the rocks, where *Calluna* still thrives. V. M. phot.

The cover for bare soil decreased from 1981 to 1984, and in 1984 bare soil was found almost only where the soil was 0-9 cm thick. However, bare rock, which was most prominent in areas with a soil thickness less than 9 cm, and especially on soil of 0-3 cm (cf. fig. 19), increased considerably in the period. In areas where the soil was 0-3 cm thick the cover of bare rock was 47.1% in 1984 against 28.7% in 1981.

These changes in cover from 1981 to 1984 have different causes. No doubt the increased amount of light caused by the clearings in 1979 favoured the

growth of *Calluna* and other plants of the heath. The cover of all kinds of vegetation increased on soils ≥ 10 cm. The total cover also increased on soils of 9-4 cm. However, the composition of the vegetation changed as *Calluna* decreased somewhat, while *Deschampsia* and the other types of vegetation in-

creased somewhat more. The areas of 0-3 cm soil thickness were characterized by a very strong decrease in *Calluna*, undoubtedly caused by the dry summers of 1982 and 1983. This decrease was followed by an increased degree of cover for bare rock.

VI Distribution of plant species compared to thickness of the soil

The mor layer contained most Ca and Mg where the soil layer was thick (cf. table 2), but of greater importance is without doubt the better conditions regarding soil humidity in the mor on such soil which lessen the stress of drought in dry periods. Therefore it was not unexpected that the investigation shows that soil thickness was correlated to the

distribution of plant species in Borrellyngen.

The heath is rather poor in species and *Calluna* dominates most areas, so the analyses of the transects gave sufficient data only for rather few species (cf. table 15). Therefore a few important species were studied in particular by measuring the thickness of the soil in stands of them near the N-S transect (table 16).

Molinia coerulea, *Trichophorum caespitosum*, and *Eriophorum angustifolium* were found almost exclusively on soil ≥ 20 cm. Concerning *Molinia* this is confirmed by the fact that in communities dominated by *Molinia* the average thickness of the soil was

TABLE 15

	Soil in cm				n
	≥ 20	19-10	9-4	3-0	
1. <i>Molinia coerulea</i>	75	10	15	—	41
<i>Trichophorum caespitosum</i>	77	—	23	—	18
<i>Eriophorum angustifolium</i>	82	18	—	—	12
2. <i>Betula pendula</i>	40	26	21	12	39
<i>Quercus robur</i>	60	11	22	7	17
<i>Pinus sylvestris</i>	51	27	17	5	40
3. <i>Hypnum cupressiforme</i>	40	27	24	10	138
<i>Calluna vulgaris</i>	30	29	24	16	486
<i>Sphagnum</i> spp.	47	24	22	7	15
4. <i>Cladonia</i> spp.	7	21	34	38	94
5. <i>Vaccinium myrtillus</i>	20	15	47	18	9
<i>Deschampsia flexuosa</i>	22	27	26	26	40
Number of samples	236	96	98	168	

Table 15. Distribution in % of some of the species found in the analyses in Borrellyngen 1979-81. The analyses from the clearing in the N-S transect are omitted. The values are calculated as the frequency of the species in the particular category of soil thickness in % of the total of the frequencies in all 4 categories of soil thickness.

TABLE 16

	n	Thickness of soil in cm				\bar{m} degree of cover	\bar{m} Thickness of soil in cm
		≥ 20	19-10	9-4	3-0		
<i>Agrostis stricta</i>	54	—	13	52	35	56	6.4
<i>Carex pilulifera</i>	66	15	17	55	14	76	9.8
<i>Sieglingia procumbens</i>	9	—	66	22	11	79	9.4

Table 16. Distribution in % for three species, on 4 categories of thickness of the soil. The analyses were made in the neighbourhood of the N-S transect. The average degree of cover shows that *Carex pilulifera* and *Sieglingia decumbens* form rather dense tufts while the tufts of *Agrostis stricta* are more open.



rather more than 40 cm (cf. table 3). These 3 species were shown by Hansen 1976 to deviate positively from *Calluna* with respect to the thickness and humidity of the mor layer, i.e. they grow on thicker and more humid soil than *Calluna*.

Betula pendula, *Quercus robur*, and *Pinus sylvestris* were also most frequent on the thicker layers of soil. They were, however, also found on very thin soil layers, where they form dwarf trees. A *Pinus sylvestris* was about 10 cm high with very few bundles of needles, but the stem had a diameter of about 2 cm and it was undoubtedly rather old. It was observed during some years but disappeared after the dry summers. In some cases such trees survived on thin soil because some of their roots had found a deeper fissure in the rocks.

Hypnum cupressiforme, *Calluna vulgaris*, and *Sphagnum* spp. also preferred thicker layers of soil and were

Fig. 20. Borrellyngen August 1982. Stand of *Agrostis stricta* in a fissure in an ice-polished protruding rock. In the central part of the foreground can be seen withered heather. V. M. phot.

more sparse on thin soil. The degree of cover for *Calluna* was highest on the thick layers of soil. A degree of cover $\geq 25\%$ for heather showed the following distribution in the analyses made in 1979: 45, 26, 16 and 13 in the four categories of soil thickness.

On the other hand *Agrostis stricta*, fig. 20, *Carex pilulifera*, and *Cladonia* spp. were most frequent on the thinner layers of soil. This is also in accordance with Hansen 1976 who pointed out that these species deviate negatively from *Calluna* regarding thickness of the mor layer.

Vaccinium myrtillus and *Deschampsia flexuosa* were found on very thin as well as on thick layers of soil.

VII The vegetation in 1979/81 and in 1984/86

1. Survey of the plant communities

The analyses of the vegetation in the transects in part 690 of Borrellyngen (cf. figs. 12-14) can be arranged in 4 groups:

1. *Calluna* heath including bare rock, mostly on rather thin layers of soil.
2. *Calluna-Molinia* communities, where the soil layer is thicker.
3. Clearings in areas which before 1979 had a dense stand of trees.
4. Heterogeneous communities characterized by *Vaccinium*, *Molinia* and *Deschampsia*. *Vaccinium* is mostly found on north facing slopes both on thin and thick layers of soil. On thick soil *Molinia* is most common.

Table 17 gives an impression of the relation between the areas of the four categories of communities in the N-S transects. The reason for using only this transect and not all of them is that the others were analysed before clearing and therefore the dense stands of trees were avoided. The N-S transect was made after the clearing and crossed an area that had carried a dense stand of trees. 78 % of the analyses (each covering 1 m of the transect)

belonged to the *Calluna* heath. The clearing comprised 12 % and the two other communities each 5 %.

Undoubtedly the proportions between the areas found in the N-S transect are not quite representative for the whole area. The overgrowth was thinner in the central area of part 690 than along the borders where the stands were denser. On a rough estimate dense overgrowth occupied 20-25 % of the total area just before 1979. The clearing of part 690 (10 ha) in 1979 resulted in 254 m³ firewood and timber corresponding to a yearly production of about 0.7 m³ per ha from 1945 to 1979, i.e. about 23 % of an estimated yearly production of 3 m³ per ha. Undoubtedly the area of communities on thick, humid soil like the *Calluna-Molinia* community is smaller in the N-S transect than in the whole part 690. Table 17 also contains a distribution based on the estimation just mentioned.

2. *Calluna* heath

Calluna heath dominated the areas with the thinner layers of soil. According to table 3, half of the analyses of the *Calluna* heath had less than 10 cm soil, and only in about 1/3 of the analyses the layer of soil was 20 cm or more. The mean values for soil thickness in the *Calluna* heath was 15.8 cm outside the 0-parcels and 19.8 cm inside them.

The growth of the species was expected to be influenced by the soil thickness. Therefore the analyses were grouped in four categories: soil \geq 20 cm, 19-10 cm, 9-4 cm and 3-0 cm. Table 18 contains the results of the analyses of the vegetation outside the 0-parcels, frequency and degree of cover of the species and of bare rock and soil in 1979/81 and in 1984.

The *Calluna* heath in Borrellyngen was very poor in species. 661 stations each of 0.1 m², i.e. 66.1 m², were recorded and only 27 phanerogam species

TABLE 17

	No. analyses	% in N-S transect	The whole area estimated
Calluna heath	156	78	60
Calluna-Molinia com.	10	5	10
Vac.-Mol.-Desch. com.	10	5	5
Clearing	23	12	25

Table 17. Number of analyses from and distribution in % of the four plant communities in the N-S transect in 1979. An estimated distribution in the whole area of part 690 is given in the column to the right. Vac.: *Vaccinium*, Mol.: *Molinia*, Desch.: *Deschampsia*.

TABLE 18

Borrelyngen: Calluna heath	≥20 cm		19-10 cm		9-4 cm		3-0 cm	
	1979/81	1984	1979/81	1984	1979/81	1984	1979/81	1984
<i>Betula pendula</i>	7 1.2	2 0.1	3 0.2	9 0.6	3 1.3	2 0.1	2 0.1	6 0.4
<i>Frangula alnus</i>	3 0.3	3 0.7	– –	– –	2 0.1	– –	– –	2 0.1
<i>Juniperus communis</i>	1 0.1	– –	– –	– –	+ +	– –	+ +	– –
<i>Lonicera periclymenum</i>	– –	– –	– –	– –	+ +	+ +	– –	3 0.1
<i>Pinus sylvestris</i>	– –	– –	2 0.1	– –	+ +	2 1.1	– –	– –
<i>Quercus robur</i>	1 0.4	2 0.2	– –	+ +	+ –	– –	– –	– –
<i>Salix aurita</i>	– –	– –	– –	2 0.2	– –	2 0.3	+ +	– –
<i>Agrostis canina</i>	– –	1 +	– –	– –	– –	– –	– –	– –
<i>Agrostis stricta</i>	– –	– –	– –	2 0.1	– –	2 0.2	2 0.1	4 0.2
<i>Calluna vulgaris</i>	98 75.6	97 71.1	95 59.4	90 59.2	90 48.9	80 37.2	55 21.7	48 9.6
<i>Carex pilulifera</i>	2 0.1	4 0.7	7 0.7	2 0.1	3 1.4	3 0.2	4 0.5	3 0.3
<i>Deschampsia flexuosa</i>	12 1.3	35 3.8	8 0.5	29 5.5	9 0.5	49 9.8	10 0.8	36 3.4
<i>Juncus bulbosus</i>	– –	– –	– –	– –	– –	– –	– –	+ +
<i>Juncus squarrosus</i>	+ +	– –	– –	2 0.1	2 0.1	– –	– –	– –
<i>Luzula multiflora</i>	+ +	– –	– –	– –	– –	– –	– –	– –
<i>Molinia coerulea</i>	– –	– –	– –	– –	2 0.1	– –	– –	– –
<i>Polypodium vulgare</i>	1 0.1	– –	2 0.1	– –	2 0.2	2 0.1	1 +	– –
<i>Rumex acetosella</i>	– –	– –	– –	– –	+ +	2 0.1	– –	1 +
<i>Sieglingia decumbens</i>	+ +	– –	– –	– –	– –	– –	+ +	1 0.2
<i>Trichophorum caespitosum</i>	– –	1 +	– –	– –	– –	– –	– –	– –
<i>Vaccinium myrtillus</i>	– –	– –	2 0.1	– –	– –	– –	– –	– –
<i>Dicranum scoparium</i>	1 +	7 0.4	2 0.3	3 0.1	3 0.4	3 0.1	3 0.1	4 0.3
<i>Hypnum cupressiforme</i>	26 5.5	28 8.4	11 1.6	33 6.3	5 0.9	17 4.6	5 1.0	6 1.7
<i>Leucobryum glaucum</i>	– –	3 0.4	7 2.8	2 0.2	– –	3 0.3	1 0.1	1 0.6
<i>Pleurozium schreberi</i>	5 0.5	3 0.6	2 0.3	5 1.0	3 1.4	2 0.6	– –	– –
<i>Polytrichum formosum</i>	+ +	1 +	– –	7 0.3	– –	2 0.2	– –	2 0.4
<i>Pseudoscleropodium purum</i>	– –	2 0.4	2 0.3	2 0.2	3 0.3	– –	– –	1 0.1
<i>Cetraria islandica</i>	– –	– –	– –	– –	– –	2 0.1	1 0.1	– –
<i>Cladonia cf. rangiferina</i>	2 0.1	2 0.1	18 0.8	14 0.5	28 1.5	19 0.9	24 1.8	18 1.2
<i>Cladonia spp.</i>	1 +	1 0.1	– –	3 0.1	2 0.1	24 1.4	3 0.1	28 0.9
Bare rock	2 0.1	– –	2 0.2	– –	12 1.2	14 2.1	45 31.2	66 43.0
Bare soil	3 0.7	12 3.1	15 10.2	22 10.6	22 15.5	48 18.4	25 17.8	45 13.1
n	94	104	62	58	58	59	116	110
Number of species per 1/10 m ²	1.60	1.92	1.61	2.05	2.05	2.16	1.11	1.64
Column no.	1	2	3	4	5	6	7	8

Table 18. Frequency (Raunkiær analyses) and degree of cover (in %) in the four categories of soil thickness in the *Calluna* heath outside the 0-parcels in 1979/81 and in 1984. In each column the frequency (whole numbers) is placed first, then the degree of cover (with one decimal). + indicates presence with a frequency less than 0.5 or degree of cover less than 0.05. Apart from the species listed, also the following were present with the stated frequency: Column 1: *Melampyrum pratense* 1; Column 2: *Chamaenerion angustifolium* 2, *Holcus lanatus* 1, *Hypochoeris radicata* +, *Rumex acetosa* 1, *Hepaticae* 1; Column 3: *Picea abies* +, Bryophytes 2; Column 5: *Senecio silvaticus* +, *Mnium hornum* +, Bryophytes 9; Column 6: *Parmelia physodes* +, *Hepaticae* 2; and Column 8: Bryophytes 17.

were found in the analyses (8 trees and shrubs, 2 dwarf shrubs and 17 herbs). Only 7 of the most common bryophyte species were determined. The *Cladonia* species were divided into two groups:

1. *C. cf. rangiferina*, which also included *C. impexa* and *C. silvatica*.
2. Other species of *Cladonia*.

Corresponding analyses from the *Calluna* heath inside the 0-parcel are shown in table 19, column 1-4.

Trees and shrubs

In 1979 the transects were placed in open areas, and after that time the areas were mechanically cleared. Therefore the analyses can only be used as a flora list and give no trustworthy statement of the frequency of the species in the whole area.

In 1979 the most widespread species were: *Betula pendula*, *Quercus robur*, *Pinus sylvestris*, and *Juniperus communis*. Furthermore *Frangula alnus*, *Lonicera periclymenum*, *Picea abies*, *Salix aurita* and *Sorbus aucuparia* were found in the transects. A minor stand of *Populus tremula* was found outside the transects.

Nearly all trees and shrubs were cut down, except *Juniperus* which was preserved.

New self-sown individuals of *Pinus*, *Quercus* and *Betula* were widespread throughout the study period, *Betula* almost only on bare soil.

Dwarf shrubs

Calluna vulgaris and *Vaccinium myrtillus* were the only dwarf shrubs in the *Calluna* heath. *Empetrum nigrum* was by no means frequent in the area, but was found sparsely on the outskirts of humid depressions with thicker soil layers.

Where the soil layer was ≥ 4 cm *Calluna* dominated (frequency $\geq 80\%$). However, the average degree of cover was highest (more than 70%) on soil ≥ 20 cm. On soil of 19-10 cm the cover was about 60%, and still lower on soil of 9-4 cm. On the thinnest layer of soil (3-0 cm) the frequency was only about 50% and the degree of cover was 20% in 1979/81 and 10% in 1984.

On soil layers of 10 cm or more, no significant change was found regarding the frequency and de-

gree of cover for *Calluna* (cf. table 18). On the other hand outside the 0-parcel the degree of cover decreased considerably on soil thinner than 10 cm, especially on soil of 3-0 cm, where the decrease was from more than 20% in 1979/81 to less than 10% in 1984. As mentioned above (page 32) this decrease was undoubtedly caused by the two dry summers in 1982 and 1983, when great areas of *Calluna* withered and died on the thin soil layers. The decrease in cover for *Calluna* was counterbalanced by an increase in cover of bare rock. Traffic of animals and people promoted erosion of the dried-up, thin layer of soil, so the rock became bared. Possibly this gives an explanation of the fact that, in the 0-parcel which was almost without traffic, there was no significant changes in the degree of cover for bare rock (cf. table 19). Furthermore the 0-parcel seemed to differ from the outside area as there was an increase in *Calluna* on the thin layers of soil. Unfortunately there were too few records in the 0-parcel (14) to prove this.

The other dwarf-shrub, *Vaccinium myrtillus*, was rather sparse in the area, but was characteristic of some of the north facing slopes in the heath. Furthermore it dominated several places in the not-analysed oak-birch forest on the western slope of Ravnedalen.

Herbs

Most of the herbaceous species occurred with only low frequencies in the *Calluna* heath. However, two of them: *Agrostis stricta* and *Deschampsia flexuosa* deserve some comments.

As can be seen in table 16, *Agrostis stricta* was most frequent on thin soil layers, where undoubtedly the competition is less than on thicker layers of soil, and the species seemed able to survive the dry summers. Table 16 shows that its main distribution was on soil of 9-0 cm. Frequently *Agrostis stricta* formed rather big stands in shallow depressions on top of the bared rocks (cf. fig. 20).

In 1979/81 *Deschampsia flexuosa* played only a minor role in the *Calluna* heath. The frequency was about 10% and the degree of cover about 1% in all

categories of soil thickness. In 1984 the frequencies had increased to between 30 % and 50 % and the degrees of cover to between 3 % and 10 %.

Deschampsia flexuosa increased mostly on soil layers of thickness between 9 and 4 cm, where the degree of cover rose from about 1 % to about 10 %, i.e. an increase corresponding to the decrease for *Calluna*. The slight increase of *Deschampsia* on soil ≥ 20 cm was also equal to the decrease of *Calluna*. However, on the thinnest soil layers of 3-0 cm, the increase in cover of *Deschampsia* (from about 1 % to about 3 %) was much smaller than the decrease of *Calluna* (from about 22 % to about 10 %). As mentioned above the reason for this was that much of the area covered by *Calluna* on thin soil turned into bare rock, where *Deschampsia* had few possibilities for growing.

The development of the relation between *Calluna* and *Deschampsia* from 1979 to 1984 seems to indicate that extremely dry summers increase the competitive power of *Deschampsia* against *Calluna*, at least where the layer of soil is thin.

Bryophytes

Most of the bryophytes occurred only with low frequencies in the *Calluna* heath. The only exception was *Hypnum cupressiforme*, which had its highest frequency and degree of cover on the thicker layers of soil. The frequencies and degrees of cover were almost unchanged from 1979 to 1984 on soils ≥ 20 cm and on soil of 3-0 cm. However, on soil of 19-4 cm outside the 0-parcels (cf. table 18) the species increased considerably both in frequency and degree of cover. Inside the 0-parcel bryophytes decreased considerably from 1979 to 1984.

Lichens

Both groups of *Cladonia* occurred on all categories of soil-thickness, but most frequently on soil ≤ 19 cm. Outside the 0-parcel no significant change could be found from 1979 to 1984. Inside the 0-parcel *Cladonia* spp. increased on soil ≤ 3 cm, possibly occupying some of the bare soil of 1979.

Areas without vegetation

These areas were found everywhere in the *Calluna* heath, but most frequently where the soil was thin. Tables 18 and 19 give the frequency and degree of cover of bare rock and bare soil. The older parts of "bare rock" were not really bare, as they were often overgrown with not investigated crustaceous lichens.

Bare soil was rather frequent (degree of cover 10-20 %) on soil of 19 cm or less, while bare rock was almost only found where the surrounding soil was ≤ 9 cm. Bare rock was common (degree of cover more than 30 %) especially on soil ≤ 3 cm.

Table 18 shows that on such thin soil there was a considerable increase in bare rock from 1979 to 1984 outside the 0-parcels. Inside the 0-parcel (table 19) bare rock was unchanged from 1979 to 1984, while there was a considerable decrease in the degree of cover for bare soil almost equalling the total increase of *Calluna* and *Cladonia* spp.

3. Clearing in former wooded area

Table 19, column 5 and 6, shows the results of the analyses of vegetation on an area which before 1979 contained a relatively dense stand of trees, mostly *Pinus sylvestris*.

In 1981 bare soil covered more than 50 % of the area, and the beginning re-establishment of the heath was represented only by 1-2 year old seedlings of *Calluna vulgaris*, i.e. plants germinated after the clearing in 1979. In places there was a dense growth of the small young plants. In 1981 the frequency was 70 % and the degree of cover 16 %.

In 1984 bare soil had diminished to a degree of cover of 10 % and *Calluna vulgaris* had increased to about 50. Furthermore several species of grasses, especially *Deschampsia flexuosa* had spread in the area, and *Deschampsia* now covered about 12 % of the area.

Rumex acetosella, mostly very sparse in Borrellyngen, had become rather frequent (frequency 39 % and degree of cover about 5 %).

The thickness of the soil is rather large in the

TABLE 19

Borrelyngen	Calluna heath in 0-parcel				Clearing in the N-S transect					
	≥20 cm		3-0 cm		1981		1984			
	1979	1984	1979	1984	1981	1984	1981	1984		
<i>Betula pendula</i>	-	-	-	-	-	-	9	1.8	-	-
<i>Frangula alnus</i>	+	12.0	+	3.6	-	-	4	0.1	9	0.8
<i>Lonicera periclymenum</i>	5	0.2	-	-	-	-	-	-	-	-
<i>Quercus robur</i>	5	13.3	4	0.1	-	-	4	0.1	4	0.9
<i>Agrostis canina</i>	-	-	-	-	-	-	-	-	4	0.1
<i>Agrostis tenuis</i>	-	-	-	-	-	-	-	-	9	0.3
<i>Calluna vulgaris</i>	100	78.8	96	68.3	29	10.6	57	24.8	74	47.4
<i>Carex pilulifera</i>	+	+	4	0.1	-	-	-	-	4	0.1
<i>Deschampsia flexuosa</i>	10	0.3	52	16.7	7	0.2	43	2.1	-	-
<i>Holcus lanatus</i>	-	-	-	-	-	-	-	-	9	0.9
<i>Juncus squarrosus</i>	-	-	4	0.1	-	-	-	-	-	-
<i>Luzula multiflora</i>	-	-	4	0.1	-	-	-	-	+	+
<i>Molinia coerulea</i>	-	-	-	-	-	-	-	-	4	0.1
<i>Polypodium vulgare</i>	-	-	-	-	7	0.6	7	0.2	+	+
<i>Rumex acetosella</i>	-	-	-	-	-	-	-	-	39	5.6
<i>Dicranum scoparium</i>	-	-	-	-	-	-	7	0.4	-	-
<i>Hypnum cupressiforme</i>	25	11.6	4	0.1	7	6.2	-	-	4	0.1
<i>Pleurozium schreberi</i>	25	2.0	-	-	14	3.4	-	-	-	-
<i>Pseudoscleropodium purum</i>	-	-	-	-	-	-	14	1.3	-	-
<i>Cladonia cf. rangiferina</i>	-	-	-	-	7	0.2	-	-	-	-
<i>Cladonia</i> spp.	-	-	-	-	-	-	36	4.9	-	-
Bare rock	-	-	-	-	57	39.4	57	42.4	-	-
Bare soil	-	-	-	-	21	17.2	21	1.9	65	55.7
n	20		23		14		14		23	
Number of species per 1/10 m ²		1.70		1.68		0.71		1.64		0.95
Soil thickness in cm, \bar{m}									32	34
Column no.		1		2		3		4		5
										6

Table 19. Frequency and degree of cover in the two periods of investigation in the *Calluna* heath inside the 0-parcel and in the clearing in the N-S transect. For explanation see text to table 18.

cleared area (mean value 32-34 cm). Undoubtedly this is the cause of the establishment of species like *Molinia coerulea*, *Agrostis canina* and *Holcus lanatus* which are all more hygrophileous than the species of the *Calluna* heath.

4. *Calluna-Molinia* communities

As mentioned above (page 35), *Molinia coerulea* was mainly distributed on localities where the soil layer was thicker than 20 cm (cf. table 15), and where the drainage was bad, so that the soil could retain its

humidity even in dry summers. Such places can be found in the low valleys which traverse the area or in depressions between the protruding rocks. Fig. 21 shows such a depression with a thick layer of soil. The transects show that the rock rises both north and south of the depression. Also to the east and the west the level of the rock is higher.

Areas of this kind are characterized by plant communities often dominated by *Calluna vulgaris* but also of *Molinia coerulea*. Furthermore they can be characterized by species preferring humid soil like *Agrostis canina*, *Carex echinata*, *C. panicea*, *Eriophorum angustifolium*, *Juncus bulbosus*, *J. effusus*, *Trichophorum caespitosum* and *Sphagnum spp.*

Table 20, column 1-8, contains analyses from 3 such communities:

1. The depression (bog) in and outside the northern border of the central 0-parcel.
2. A depression (valley) in the northern W-E transect dominated by *Calluna* and *Molinia*.

3. A depression (part of a valley) in the N-S transect containing a brooklet which drains the larger depression west of the transect and the 0-parcel.

The average thicknesses of soil in these three areas are 42.7, 43.1 and 42.0 cm.

The depression at the central 0-parcel (cf. fig. 21)

Table 20, column 1-4, shows the results of the analyses. Column 1 and 2 comprise the area outside the 0-parcel in 1979 and 1986 respectively. Column 3 and 4 give the corresponding results inside the 0-parcel.

Fig. 21. Two N-S transects through the depression with *Calluna* and *Molinia* at the northern border of the central 0-parcel. B7 cross the fence to the 0-parcel at 9 m east of the NW corner and B5 is placed 2 m west of B7. The soil thickness in the depression varies between 30 and 60 cm, while the soil layer in the surrounding *Calluna*-heath usually is thinner than 20 cm.

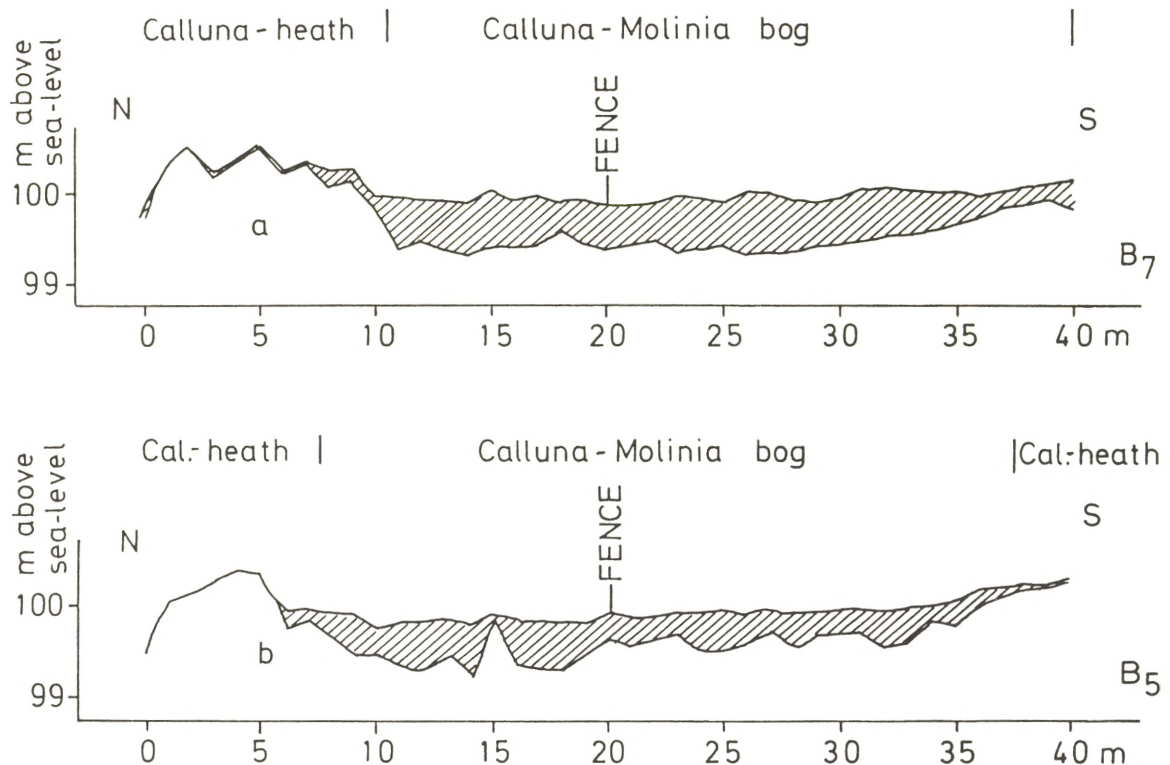


TABLE 20

	Calluna-Molinia				Calluna-Molinia		Calluna-Molinia-		Vaccinium-Molinia	
	outside		inside		in the northern		Juncus		Deschampsia	
	centr. 0-parcel		centr. 0-parcel		W-E transect		in the		in the	
Borrelyngen	1979	1986	1979	1986	1979	1984	1981	1984	1981	1984
<i>Betula pendula</i>	4 0.3	3 0.2	+ 5.4	17 2.4	- -	10 0.3	56 3.0	50 4.3	9 0.3	10 0.3
<i>Frangula alnus</i>	- -	- -	- -	- -	- -	- -	22 7.9	30 7.5	9 3.5	20 0.6
<i>Juniperus communis</i>	- -	- -	+ 1.2	8 1.1	- -	- -	- -	- -	9 0.8	20 2.2
<i>Pinus sylvestris</i>	2 0.1	5 0.6	+ 30.4	- -	- -	- -	- -	- -	- -	- -
<i>Quercus robur</i>	2 1.8	11 0.3	- -	4 0.1	- -	- -	- -	- -	9 0.3	10 0.3
<i>Salix aurita</i>	+ +	- -	- -	- -	- -	- -	- -	- -	- -	- -
<i>Agrostis canina</i>	- -	- -	- -	- -	- -	- -	22 0.7	70 9.1	- -	- -
<i>Calluna vulgaris</i>	100 79.7	100 78.1	100 69.8	96 71.4	100 84.3	100 76.8	78 6.1	70 13.4	27 6.3	30 12.8
<i>Carex echinata</i>	- -	- -	- -	- -	- -	- -	11 7.0	30 11.5	- -	- -
<i>Carex panicea</i>	2 0.1	- -	6 0.2	- -	- -	- -	- -	- -	- -	- -
<i>Carex pilulifera</i>	- -	- -	- -	- -	- -	- -	67 2.7	30 0.9	9 0.3	- -
<i>Deschampsia flexuosa</i>	- -	- -	- -	- -	- -	- -	33 2.3	30 3.1	27 6.8	100 16.0
<i>Empetrum nigrum</i>	+ +	3 0.2	- -	2 0.1	- -	- -	- -	- -	- -	- -
<i>Eriophorum angustifolium</i>	22 0.7	8 0.2	- -	- -	- -	- -	- -	- -	- -	- -
<i>Juncus bulbosus</i>	- -	- -	- -	- -	- -	- -	33 14.2	60 11.9	- -	- -
<i>Juncus effusus</i>	- -	- -	- -	- -	- -	- -	11 0.3	70 3.3	- -	- -
<i>Juncus squarrosus</i>	- -	- -	- -	- -	- -	- -	+ +	30 5.6	- -	- -
<i>Molinia coerulea</i>	16 2.3	24 5.5	33 2.2	35 3.6	56 2.3	60 7.5	44 1.3	90 5.9	36 1.1	60 8.7
<i>Polypodium vulgare</i>	- -	- -	- -	- -	- -	- -	- -	10 0.9	- -	- -
<i>Sieglingia decumbens</i>	- -	- -	- -	- -	- -	- -	11 0.3	- -	- -	- -
<i>Trichophorum caespitosum</i>	18 1.3	16 0.8	13 1.4	2 0.1	+ +	10 0.3	- -	- -	- -	- -
<i>Vaccinium myrtillus</i>	- -	- -	- -	- -	- -	- -	- -	10 0.3	64 12.4	70 27.6
<i>Dicranum scoparium</i>	- -	- -	- -	2 0.4	- -	- -	- -	- -	- -	- -
<i>Hypnum cupressiforme</i>	69 5.2	73 24.7	29 3.0	40 9.0	33 1.7	60 26.8	- -	- -	- -	- -
<i>Leucobryum glaucum</i>	- -	- -	4 1.3	2 0.1	- -	- -	- -	- -	- -	- -
<i>Sphagnum</i> spp.	10 0.3	11 1.1	6 0.2	- -	33 8.3	10 0.3	- -	- -	- -	- -
<i>Cladonia</i> cf. <i>rangiferina</i>	10 0.3	5 0.3	4 0.1	- -	- -	10 0.3	- -	- -	- -	- -
Bare rock	- -	- -	- -	- -	- -	- -	- -	- -	9 7.9	10 0.9
Bare soil	- -	- -	- -	- -	- -	10 3.8	44 12.2	- -	9 7.9	20 2.2
n	49	37	55	52	9	10	9	10	11	10
Number of species per 1/10 m ²	2.55	2.59	1.95	2.08	2.22	2.60	3.88	5.80	1.99	3.20
Thickness of soil in cm, \bar{m}	42.7				43.1		42.0		29.1	
Column no.	1	2	3	4	5	6	7	8	9	10

Table 20. Frequency and degree of cover in *Calluna-Molinia* communities (column 1-8) and the *Vaccinium-Molinia-Deschampsia* community in 1979/81 and in 1984/86. For explanation see text to table 18. Apart from the species listed, also the following were present with the stated frequencies and degree of cover: Column 4: *Picea abies* 6, 4.1; Column 7: *Chamaenerion angustifolium* 11, 0.3, Bryophytes 67, 7.2; Column 8: *Rubus fruticosus* 10, 0.3, *Holcus lanatus* 10, 0.3; Column 9: *Sorbus aucuparia* 9, 0.3; and Column 10: *Hypochoeris radicata* 10, 0.3.



The depression was dominated by *Calluna vulgaris*, but *Molinia coerulea*, *Trichophorum caespitosum* and *Hypnum cupressiforme* were also important.

In 1979 a small stand of *Empetrum nigrum* was found near the fence, in 1986 it was somewhat bigger.

Outside the 0-parcel *Eriophorum angustifolium* had a frequency of 22% in 1979, but the stand had decreased in 1986. Inside the 0-parcel *Eriophorum* was not found in the analyses.

Sphagnum spp. was of smaller importance in this depression and was not found inside the 0-parcel in 1986. In other depressions several species of *Sphagnum* were frequent, e.g. in the depression shown in fig. 22.

Apart from what is mentioned above, very few changes took place from 1979 to 1986. Even in summertime the area was wet and the traffic was

Fig. 22. Borrellyngen 23/7 1982. The N-S running valley from the depression west of the central 0-parcel (left foreground) towards NNE (right background). The depression is characterized by *Sphagnum spp.*, *Juncus effusus*, *J. bulbosus* and *Molinia coerulea*. V. M. phot.

without importance, even the sheep avoided the part outside the fence of the 0-parcel. The changes in frequency for the trees and shrubs were caused by the fact that the whole area was cleared in 1979, and only the part outside the 0-parcel the following times.

The *Calluna-Molinia* community in the northern W-E transect

About 70 m northeast of the central 0-parcel the transect crossed an approximately 5 m broad, N-S running valley with a rather thick layer of soil (cf. fig. 13).



Fig. 23. *Frangula alnus*. The leaves and the young shoots are eaten by the sheep. The *Calluna-Molinia-Juncus* community in the N-S transect in Borrellyngen. August 1982. V. M. phot.

Table 20, column 5-6, shows that *Calluna vulgaris* dominated this community also, and that both *Molinia coerulea* and *Hypnum cupressiforme* were important. *Trichophorum caespitosum* and *Sphagnum* were present.

The changes from 1979 to 1984 were small. A decrease in *Sphagnum* and a corresponding increase in *Hypnum cupressiforme* could possibly indicate some drying out of the area.

The *Calluna-Molinia-Juncus* community in the N-S transect

The area contains a brooklet draining the depression shown in fig. 22 and is very wet throughout the

year. To the north the depression was bordered by a rather dense stand of *Betula pendula* and *Frangula alnus*. The last species was heavily browsed by the sheep during the first years of grazing (cf. fig. 23).

Populus tremula and *Frangula alnus* were preferred by the sheep rather than *Quercus robur* and *Betula pendula*. However, the latter were also browsed.

During the mechanical clearing in the period between 1981 and 1984 *Betula* and *Frangula* were felled, but both species regenerated vigorously, because sheep grazing was missing toward the end of the period. The degree of cover for these species was unchanged from 1981 to 1984.

Table 20, column 7 and 8, shows that *Calluna vulgaris* formed an important part of the vegetation both years. Also *Deschampsia flexuosa* and *Carex pilulifera* were rather frequent.

The presence of several species preferring humid soil: *Agrostis canina*, *Carex echinata*, *Juncus bulbosus*, *J. effusus* and *Molinia coerulea* was characteristic of the community. The frequency and degree of cover increased for all these species from 1981 to 1984. *Juncus squarrosus* was present in 1981 and became rather frequent during the following years. *Carex pilulifera* was common, but not dominating, neither in this community nor in the *Calluna* heath. In 1984 it had decreased in the discussed community.

The area was cleared in 1979 and in 1981 there was still bare soil on 12 % of the area. In 1984 the whole area was covered by vegetation.

The increase in frequency and cover of the species preferring humid soil and the decrease of *Carex pilulifera* may indicate an increase in the

humidity in the area. This may have been caused by the cutting down of the rather numerous birch trees in the depression drained by the brooklet. This depression was not analysed, but locally *Sphagnum* and *Juncus bulbosus* increased very much from 1979 to 1984.

5. *Vaccinium-Molinia-Deschampsia* community

In Borrellyngen *Vaccinium myrtillus* were found mostly either on north facing slopes in the *Calluna* heath or in the oak and birch forest on the western border of Ravnedalen. In the N-S transect a small area is covered by a community characterized by *Vaccinium myrtillus*, *Molinia coerulea* and *Deschampsia flexuosa*. Vegetation as well as thickness of the soil was rather inhomogeneous in this community. As elsewhere in the area, *Molinia* was found only on a rather thick layer of soil while the other species were found on all kinds of soil thickness.

In 1981 no single species was dominant, but *Calluna vulgaris*, *Deschampsia flexuosa*, *Molinia coerulea* and *Vaccinium myrtillus* were important components of the vegetation (table 20, column 9).

Column 10 in table 20 shows that in 1984 *Deschampsia flexuosa* had become a dominant and covered 16 % of the area. Likewise the other species mentioned increased in degree of cover. Bare rock as well as bare soil decreased during the period from a degree of cover of 7.9 % to 0.9 and 0.2 respectively. This depicts the reestablishment of the community after the felling of trees and shrubs.

VIII General conclusions

1. The influence of climate and man on the vegetation

The development of vegetation in Borrelyngen during the first millenia of the forest period is unknown but undoubtedly it followed the same pattern as elsewhere in Denmark. The pollen diagram (fig. 3) tells us that from about 4000 BC to about AD 1200 the area was more or less covered by forest of oak and birch. Human influence was slight, but in the outskirts of the part of Borrelyngen which now belongs to the State Forest District of Bornholm some cultivation took place from Late Bronze Age to the last century BC.

While climate was the main determining factor for the development of vegetation before AD 1200, the human influence became more prominent in the following centuries. From AD 1200 to about AD 1900 Borrelyngen was used for common grazing for sheep and other livestock. Heather, peat and wood were collected for fodder and fuel. This caused a change in the vegetation from forest to heath and grassland. This common was not an unbroken cover of heather and grass. Hard grazing and traffic of animals produced areas of bare rock, and in the depressions shrubs and trees grew, especially in the valleys where the soil was deeper.

After AD 1900 this exploitation of Borrelyngen diminished very much and around 1920 grazing stopped completely. Apart from a short period during the second world war the other forms of exploitation stopped also, and the invasion of trees and shrubs in the heath began. The trees and shrubs in the valleys formed shelter belts which later promoted the total overgrowth.

During the first decades after the war, part 690 was rather open but from about 1961 the speed of the overgrowing accelerated. Many of the formerly bare rocks became overgrown by lichens and bryophytes. In combination with the litter from the shrubs these formed a thin layer of soil making low

vegetation possible. In 1977, when the State Forest District of Bornholm acquired the area, it was very much overgrown and it would not have lasted long before the shade of the trees and shrubs would have killed the heather, and the forest on the area would have been reestablished. This forest would have contained many conifers, especially *Pinus sylvestris*, contrary to the oak-birch forest before AD 1200.

In 1979 the trees and shrubs were cut down and sheep were introduced in the now open heath. Unfortunately there were too few sheep and they could not keep the prolific shoots from the stumps of oak and birch down. Numerous seedlings of oak and pine also appeared and mechanical clearing became necessary.

The sheep caused a change toward the heath vegetation of the centuries before 1900. During the very dry summers of 1982 and 1983 much of the heather on the very thin soil died, and passage of sheep promoted erosion and bare rock reappeared.

2. The *Calluna* heath in 1979/81 and in 1984

The clearing of the area in 1979 produced light conditions which favoured *Calluna*, and many of the places where the stands of trees and shrubs had been dense were left more or less without vegetation. In these places new seedlings of heather germinated. On the other hand much of the heather in the area was however rather old, approaching the senile stage. These factors, as well as climate and sheep grazing, influenced the development of the heath.

Table 21 shows the average degree of cover in % in the *Calluna*-heath outside the 0-parcels. The table lists the more important species, groups of species, and bare soil and rock. The values are averages for all types of soil thickness in the area in contrast to the tables 18-19.

TABLE 21

Calluna heath	Degree of cover in %	
	1979/81	1984
Trees and shrubs	0.9	0.9
<i>Calluna vulgaris</i>	48.9	42.6
<i>Deschampsia flexuosa</i>	0.8	5.0
Other herbs	0.7	0.5
Bryophytes	3.7	6.5
Lichens	1.2	1.2
With vegetation	56.2	56.7
Bare rock	11.2	14.7
Bare soil	10.6	11.9
Without vegetation	21.8	26.6
Number of samples	330	331

Table 21. Average values of degree of cover of the main components of the *Calluna* heath outside the 0-parcels. All analyses both on thick and thin soil layers are used.

On the heath as a whole the degree of cover for *Calluna vulgaris* decreased from 48.9 in 1979/81 to 42.6 in 1984. However, the decrease was not general for all types of soil thickness. As is shown in table 18, *Calluna* remained nearly constant on soil layers ≥ 10 cm, but decreased considerably on thinner soil. So the decrease in the area as a whole was heavily influenced by the considerable decrease on the thinner soils where the influence of the dry summers was strongest (cf. page 33). The decrease could also have been influenced by acid precipitation which has been reported to change soil pH in forests elsewhere in Europa. Measurements of pH in the soil in the area in 1979 and 1984 (cf. table 2) showed, however, that this has not been the case here, as the soil did not become more acid. Undoubtedly the lack of moisture has been too severe for *Calluna* on thin layers of soil during the dry summers of 1982 and 1983.

Deschampsia flexuosa covered 0.8% in 1979/81 and increased to 5% in 1984. As table 18 shows, *Deschampsia* increased in all groups of soil thickness, but the greatest increase was on soil layers of be-

tween 4 and 19 cm. As *Deschampsia* also increased on soils where *Calluna* remained constant, the increase for *Deschampsia* was not caused only by *Calluna* being damaged by drought. Another factor causing the increase of *Deschampsia* could be the diminishing sheep grazing during the last years of the period of investigation. The sheep which graze other parts of Borrellyngen do not eat *Deschampsia* very much, and avoid it as long as there are alternative fodder plants. However, some unpublished experiments in the heath of Hammeren (3.5 km N of Borrellyngen) showed a great difference between the frequency of *Deschampsia flexuosa* in the grazed heath and the ungrazed 0-parcels. In the 0-parcels straws of *Deschampsia* were common while no straws could be seen in the grazed area. Even if the sheep on Hammeren were much more hungry than the sheep now grazing in Borrellyngen, this observation seems to indicate that sheep grazing has a restrictive influence on the growth of *Deschampsia flexuosa*.

The total cover for other herbs, lichens, and bare soil showed no essential changes from 1979/81 to 1984, but bryophytes increased. There was, however, a significant increase in the degree of cover of bare rock. During the period several protruding rocks have been bared. The newly bared rocks were whitish and without any vegetation, while the older ones were grey from crustaceous lichens (cf. fig. 11).

Primarily the increase of bare rock was caused by the dry summers which killed the heather on the thin soil. Traffic of animals and people also played a great role. The dried out soil crumbled and was washed down into the surrounding depressions. In these the bare soil formed a bed for young seedlings of heather. The intensity of sheep grazing in Borrellyngen was however, too low to produce bare rock in such dimensions as can be seen in another grazed heath 1.5 km to the west or as was common on Bornholm at the end of the last century according to old photos.

3. Nature conservancy

Because of the combination of areas where the soil

layer is very thin with depressions and small valleys with deeper and more humid soil the *Calluna* heath in Borrelyngen is a very sensitive kind of nature. The valleys especially are very good nuclei for overgrowing with shrubs and trees. When a kind of shelter belts is formed in these valleys they promote a general spread of the trees and shrubs. This overgrowth can be limited by mechanical clearing. Several of the deciduous tree species in the area, however, form proliferous shoots from the stumps, and *Quercus robur* and *Pinus sylvestris* produce lots of seedlings in the area. Therefore mechanical clearing has to be repeated every few years.

A not yet concluded investigation of the development of shoots from stumps in another part of Borrelyngen grazed by sheep has shown that sheep have a preference for young shoots from stumps of oak and birch. However, when shoots of birch are 1 m tall or more the sheep avoid them. If the shoots are browsed every year, birch will die in the course of a few years. Oak keeps alive somewhat longer but most of the oaks felled in 1981 were dead in 1988 and none had shoots taller than 0.5 m. Also shoots of other trees in the area, e.g. *Carpinus betulus*, *Populus tremula*, *Prunus avium*, *Salix caprea*, *Sorbus aucuparia* and *S. intermedia* were browsed by sheep, and none of the stumps have developed a new tree. So a rather slight sheep grazing will keep the overgrowth down. However, it is important that the sheep are

kept in the area when the shoots are young, as the sheep do not seem to like old shoots.

In part 690 there has been periodically some sheep since 1985, but too late in the year. At least the shoots of birch were too long and old to be of any interest for the sheeps.

Sheep grazing in the *Calluna* heath seems to promote *Calluna vulgaris* rather than *Deschampsia flexuosa*. In part 690 of Borrelyngen, however, the sheep grazing has not been adequate. The investigation indicates that *Deschampsia* increases when *Calluna* dies because of climatic stress or in other heaths when *Calluna* reaches its maximum age. Undoubtedly in Borrelyngen as well as in the neighbouring heath on Hammeren sheep grazing will reduce *Deschampsia* and favour *Calluna*. Furthermore the sheep will promote the appearance of more bare rock which will look well in the scenery.

The nature conservancy management of the State Forest District of Bornholm has produced a good-looking and attractive landscape where, at least for some time, the *Calluna*-heath is the dominant element. However, undoubtedly continued sheep grazing will be necessary if the heath shall be preserved. A combined grazing of goats and sheeps which takes place in another part of the District is undoubtedly better, but unfortunately in regard to economy not so good, because of more expensive fences and because the goats give lower income.

IX Acknowledgements

Grants from the Danish Natural Science Research Council have made this investigation possible. Gerda Mikkelsen has assisted in all the work in the field. Forest ranger Bent Hansen, forest supervisor the late B. Engberg and forest supervisor Tom Nielsen have been extremely helpfull during the investigation. The department of Nature conservancy of the County of Bornholm has provided some aerial photos and information from the archives. During the preparation of this paper I have received valuable help from the Department of Botany, Roy-

al Veterinary and Agricultural University, Copenhagen. The soil analyses were made there, prof., dr. K. Hansen has kindly provided me with some unpublished data from his investigations on Bornholm, Kaj Svendsen has drawn most of the figures. I have had good discussion with lic. agro. Anne Bülow-Olsen, who together with James Chalmers, B.Sc. have revised my English manuscript. Ole Lansø typed the manuscript. My sincere thanks are due to all for their kind and valuable help.

X References

- Hansen, Helmer 1988: Husdyrbruget på Bornholm. – Bornholmske Samlinger III, 2. bd. Rønne. 199-227.
- Hansen, K. 1979: Ecological Studies in Danish Heath Vegetation. – Dansk Botanisk Arkiv 31, nr. 2. 118 pp.
- Jørgensen, J. A. 1900 and 1902: Bornholms Historie I-II. – Rønne. Genoptrykt 1980. 256 + 352 pp.
- Mikkelsen, Vald. M. 1954: Studies on the sub-atlantic history of Bornholms vegetation. – D.G.U. II række, nr. 80. 210-229.
- Mikkelsen, Vald. M. 1963: Beech as a natural forest tree in Bornholm. – Bot. Tidsskrift 58:253-280.
- Mikkelsen, Vald. M. 1966: Bornholms natur, beboere og naturfredning gennem tiderne. – Bornholmske Samlinger II, 2. bd. Rønne. 9-47.
- Mikkelsen, Vald. M. 1986: Borup. Man and Vegetation. – The National Museum of Denmark. Copenhagen. 42 pp.
- Mikkelsen, Vald. M. 1989: Borrelyngen. Udnyttelse af og bevoksning på en bornholmsk udmark fra Oldtid til Nutid. – Bornholmske Samlinger III, 3. bd. Rønne. 83-102.
- Pontoppidan, E. 1767: Danske Atlas, bd. III. – København.
- Resen, Peder Hansen (MS): Atlas Danicus Bornholm i dansk oversættelse ved Johannes Knudsen. – København 1925. 81 pp.
- Skovgaard, P. N. 1804: Beskrivelse over Bornholm. – Genudgivet 1975. København. 411 pp.
- Thamdrup, H. M. 1939: Studier over jyske heders økologi (Summary in English). – Acta Jutlandica XI, supplementum. Aarhus. 1-89.
- Thura, Laurids de 1756: Omstændelig og tilforladelig Beskrivelse over ... Bornholm og ... Christiansø ... – København. Genoptrykt 1968. 288 pp.
- Zartmann, M. K. 1934: Borringholmerens Historiebog I-II. – Rønne, 300 pp.
- Zarthammn M. K. 1935: Borringholmerens Historiebog III-IV. – Rønne. 332 pp.

Submitted to the Academy November 1989.

Published February 1991.

Title. – Titles should be kept as short as possible and with an emphasis on words useful for indexing and information retrieval.

Abstract, Summary. – An abstract in English is compulsory. It should count 10-15 lines, outline main features, stress novel information and conclusions, and end with the author's name, title, and institutional and/or private postal address. – Papers in Danish may be provided with a summary in another language by agreement between author and editor.

Typescript. – Page 1 should contain title, author's name and the name of the Academy. Page 2: Abstract, author's name and address. Page 3: Table of contents if necessary. Captions should be delivered on separate sheets. Footnotes should be avoided if at all possible; if indispensable, they, too, should be typed on separate sheets. Consult a recent issue of the series for general layout.

Typewrite with double space throughout and leave a 4 cm margin *right*. Indicate desired position of illustrations and tables with pencil in margin *and repeat it in the galley proof*.

Use three or fewer grades of heading unless more are indispensable. Avoid long headings. Indicate clearly the hierarchy of headings.

Figures. – Please submit two copies of each graph, map, photograph, etc., all marked with the author's name. Whenever possible all figures will be placed within the text; the nature of the illustrations will govern the editor's choice of paper quality.

All figures, also line drawings, must be submitted as glossy, photographic prints suitable for direct reproduction. Prints fitting the indicated printed area are preferred, but the final size is the responsibility of the editor. The scale should be indicated in the caption or, preferably, on the illustration itself.

Fold-out figures and tables should be avoided. Use distinct (but not dominant) capital letters for the items in composite figures. For transfer lettering use simple, semi-bold typefaces. The size of the smallest letters should not be less than 1.5 mm. Intricate tables are often more easily reproduced from line-drawings or from technically perfect original computer or type processor output.

References. – In general, the editor expects all references to be formally consistent and in accordance with accepted practice within the particular field of research. Bibliographical references should preferably be given as, e.g., Shergold 1975, 16, the latter figure indicating the page number unless misunderstandable.

Correspondence

Manuscripts should be sent to the Editor, Det Kongelige Danske Videnskabernes Selskab, H. C. Andersens Boulevard 35, DK-1553 Copenhagen V, Denmark (tlf. +45.1.11 32 40). Questions concerning subscription to the series should be directed to the publishers.

Publisher

Munksgaard Export and Subscription Service
Nørre Søgade 35, DK-1370 Copenhagen K, Denmark

Editor: Poul Lindegård Hjorth

© (Year) Det Kongelige Danske Videnskabernes Selskab. All rights reserved. No part of this publication may be reproduced in any form without the written permission of the copyright owner.

Biologiske Skrifter

Biol. Skr. Dan. Vid. Selsk.

Priser excl. moms/Prices abroad in Danish Crowns

Vol. 23

1. NIELSEN, ANKER: A Comparative Study of the Genital Chamber in Female *Trichoptera*. 1980 200.-
2. BÖCHER, TYGE W.: Evolutionary Trends in Ericalean Leaf Structure. 1981 90.-
3. LARSEN, TORBEN B.: The Butterflies of Yemen Arab Republic. With a Review of Species in the *Charaxes viola*-Group from Arabia and East Africa by A. H. B. RYDON. 1982 120.-
4. BÖCHER, TYGE W.: A Developmental Analysis of the Photosynthesizing Organs in *Prosopis Kuntzei*. 1982 90.-
5. SALOMONSEN, FINN: Revision of the Melanesian Swiftlets (*Apodes, Aves*) and their Conspecific Forms in the Indo-Australian and Polynesian Region. 1983 200.-

Vol. 24

1. ANDERSEN, SVEND TH.: Forests at Løvenholm, Djursland, at present and in the past. 1984 200.-
2. NILSSON, JYTTE R.: Dose- and Time-dependent Effects of Actinomycin D on *Tetrahymena* with Special Reference to Nucleolar Changes. 1985 40.-
3. FRIIS, ELSE MARIE: Angiosperm Fruits and Seeds from the Middle Miocene of Jutland (Denmark). 1985 160.-

Vol.

- 25** Six Papers in the Biological Sciences, being Part Two of *Sixteen Research Reports* by the Niels Bohr Fellows of the Royal Danish Academy of Sciences and Letters, published on the Occasion of the Centenary of Niels Bohr. 1985 200.-
(*Sixteen Research Reports* Part One is identical with: Ten Papers in the Exact Sciences and Geology, *Matematisk-fysiske Meddelelser* 41. 1985, 400.-)

- 26** JENSEN, HANS ARNE: Seeds and other Diaspores in Soil Samples from Danish Town and Monastery Excavations, dated 700-1536 AD. 1986 200.-
- 27** NILSSON, JYTTE R.: The African Heterotrich Ciliate, *Stentor andreseni* sp.nov., and *S.ametysthinus* Leidy. A Comparative Ultrastructural Study. 1986 100.-
- 28** WUNDERLIN, RICHARD; LARSEN, KAI; and LARSEN, SUPPEE SAKSUWAN: Reorganization of the *Cercidae* (*Fabaceae: Caesalpinioideae*). 1987 80.-
- 29** JENSEN, HANS ARNE: Macrofossils and their Contribution to the History of the Spermatophyte Flora in Southern Scandinavia from 13000 BP to 1536 AD. 1987. 200.-
- 30** DYCK, JAN: Structure and Light Reflection of Green Feathers of Fruit Doves (*Ptilinopus spp.*) and an Imperial Pigeon (*Ducula concinna*). 1987 100.-
- 31** FRIIS, ELSE MARIE; CRANE, PETER R.; PEDERSEN, KAJ RAUNSGAARD: Reproductive Structures of Cretaceous Platanaceae. 1988 100.-
- 32** WINGSTRAND, K. G.: Comparative Spermatology of the Crustacea Entomostraca 2. Subclass Ostracoda. 1988. 250.-
- 33** MIKKELSEN, VALD. M.: The Commons of Rejnstrup, Denmark. 1989 50.-
- 34** ØLLGAARD, BENJAMIN: Index of the *Lycopodiaceae*. 1989 150
- 35** SRINIVASAN, VIJAYALAKSHMI, FRIIS, ELSE MARIE: Taxodiaceous conifers from the Upper Cretaceous of Sweden. 1989 100.-
- 36** FRIIS, ELSE MARIE: *Silvianthemum sneicum* gen. et sp. nov., a new saxifragalean flower from the Late Cretaceous of Sweden. 1990 70.-
- 37** MOESTRUP, ØJVIND; THOMSEN, HELGE A.: *Dictyochoa speculum* (Silicoflagellata, Dictyochophyceae), studies on armoured and unarmoured stages. 1990 100.-
- 38** MIKKELSEN, VALD. M.: Borrelyngen on Bornholm, Denmark. 1991 100.-