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INVESTIGATIONS ON THE ECOLOGY AND PHENOLOGY OF THE MACROMYCETES IN THE ARCTIC

BY

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WITH 23 FIGURES AND 25 TABLES

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Abstract

The macromycete flora at Godhavn, Disko, West Greenland (69°14'N, 53°31'W) has been studied over a three year period, 1970-72. 170 permanent quadrates of 1 square meter each, distributed over 16 sites, were inspected four times a month throughout the growing season. The number of fruit bodies present, as well as the number produced since the last inspection, was recorded. On the basis of these data, the phenology of the macromycete flora in the area is described, and the differences in this respect between the three years are stated. In Godhavn, the fungus season may be divided into a vernal, an aestival and a seasonal aspect; the peak of the season occurred in the first half of August. During the growing season, several variable environmental factors have been measured (precipitation, solar radiation, soil moisture content, soil temperature, and the phenology of the deciduous mycorrhiza associates). An attempt has been made to correlate the fructification of the macromycetes with these factors. There was a high degree of accordance between fructification and solar irradiance as well as soil temperature. It is demonstrated that the soil temperature, as expressed by the daily temperature sum, is positively correlated with the daily solar irradiance. It seems evident that low soil temperatures may delay the growth and development of the macromycete mycelia so much that there is insufficient time left for fructification before the definitive decrease of the soil temperature in the autumn. - Locally, the brevity of the frost free period, as well as a low soil water content may have been limiting in some of the years.

A comparison is made between the macromycete flora in the Arctic and in the temperate forest zone, mainly on the basis of the present investigation and the paper of LANGE (1948a} on the Agarics of Maglemose (in Denmark). It is stated that in the Arctic, the number of species is lower, the individual species of a more sporadic occurrence, and the ratio of litter decomposers to mycorrhiza forming species lower than in the temperate forest zone. The causes of these differences are discussed.

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Макромицетовая флора была изучена в районе Годхавна (о.Диско, $3a\pi$. Гренландия: 69°14'с. m ., 53°31'з.д.) в течение трех лет с 1970 по 1972 гг. Наблюдение проводилось четыре раза в месяц во время периода роста на 170 постоянных квадратах площадью $1M^2$ каждый, расположенных на 16 участках. Регистрировалось число наличествующих плодовых тел и тел, образованных со времени предыдущего наблюдения. На основании этих панных была описана фенология макромицетовой флоры и выявлено ее различие в течение трех лет. В районе Годхавна грибной сезон может быть разp;eJieH Ha BeCeHHHil:' JieTHHil: **H** rJiaBHhlfi acneRTbl; BepIIIHHa ceaoHa nap;aeT Ha первую половину августа. В течение периода роста были замерены переменные факторы среды: атмосферные осадки, солнечная радиация, влажность и температура почвы и фенология листопадных, ассоциирующих с микоризовыми. Была сделана попытка соотношения плодоношения макромицетовой флоры с этими факторами. Выяснилось, что степень плодоношения тесно связана с солнечной радиацией и температурой почвы. В работе показано, что температура почвы, выраженная в суммарной дневной температуре, положительно сочетается с дневной солнечной иррадиацией; таким образом, низкие температуры почвы могут задержать рост и развитие макромицетовых мицелий настолько, что до определяющего снижения температуры почвы может не остаться времени для плодоношения. Местами, в отдельные годы, плодоношение могло быть ограничено краткостью безморозного периода и недостатком почвенной воды.

На основании настоящих исследований и работы Ланге по пластинчатым грибам района Маглемозе в Дании (1948 a) проведено сравнение макромицетовой флоры Арктики и зоны "умеренного" леса. Отмечено, что в Арктике видовое количество ниже, отдельные виды появляются спорадически и соо-THOIIIeHHe BH}];OB, paaJiara1011.111:x nop;CTHJIRY **H** 06paay1011.111:x MHROpH8bI, HHlRe, чем в зоне "умеренного" леса. Причины, обусловливающие эти различия, также обсуждаются в работе.

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INTRODUCTION

In recent decades, biologists have become increasingly interested in the Arctic, first and foremost because of the nature relatively unchanged by Man, but also due to the easier access to hitherto closed areas. The interest of the mycologists has in most cases resulted in short forays with the aim of floristic, plant geographical, and taxonomical studies.

The abundance of fruit bodies of macromycetes at the end of the growing season has often been noted. On the other hand, fluctuations in the intensity of fructification from year to year have also been reported (VAsSILKov, 1967), fluctuations which may be difficult to explain on the basis of short stays only.

A three year working period at the Arctic Station in Godhavn on Disko, West Greenland, made it possible to investigate the phenology of the macromycetes in relation to a number of environmental factors, as well as various other aspects of the ecology of the macromycetes in an arctic area.

ACKNOWLEDGEMENTS

The present author is greatly indebted to a number of persons and institutions who have contributed to the investigation. First of all, I want to thank Mr. HARRY CHRISTENSEN, Godhavn, Manager of the Arctic Station, for his kindness and great help during may stay, not only in connection with the investigations, but also personally. The board of the Arctic Station is thanked for making my three years stay possible.

The following institutions and persons have provided material of different kinds:

The Geophysical Observatory, Godhavn (measurements of air temperature and precipitation).

The Hydrotechnical Laboratory, The Royal Veterinary and Agricultural College, Copenhagen (radiation measurements from Denmark). The Meteorological Institute, Copenhagen (climatological data).

MARTIN LEWIS, Ph.d. (radiation measurements from Godhavn for 1970). BoY OVERGAARD NIELSEN, M.Sc. (unpublished data from the Danish IBP-project, section PT).

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ERIC STEEN HANSEN, M.Sc., has identified the lichens and GERT STEEN MOGENSEN, M.Sc., some of the mosses. Professor MORTEN LANGE, Dr. phil., and PETER VESTERGAARD, M.Sc., kindly read the manuscript and offered many valuable suggestions. Finally, CHERRY NIELSEN, B.Sc., has revised the English translation, and A. DEMINA, engineer of mining geology, kindly translated the abstract into Russian.

PREVIOUS WORKS

Most of the investigations on the macromycetes in arctic-alpine areas have been floristic, but a few include valuable sections on their ecology. This applies to the papers of FAVRE (1955), LANGE (1957), and OHENOJA (1971). VAsSILKOV (1967) has given a general account of the ecology of the macromycetes in the Soviet Arctic, and the present author has published a paper on the fireplace fungi of middle West Greenland (P. MILAN PETERSEN, 1974).

GENERAL DESCRIPTION OF THE INVESTIGATION AREA

The investigation area, approximately four square km, is situated around the Arctic Station in Godhavn on Disko, West Greenland (69°14' N, 53°31' W). The area is at the foot of the 800 m high Lyngmarksfjeld, facing Disko Bugt to the south.

The bedrock is partly tertiary basalt—as in almost all other parts of Disko-and partly gneissic rock. A wide range of plant communities occurs in the area: almost naked fell-fields and solifluction slopes, fens, heaths with a thick raw humus layer, snow-bed communities with a mull-like soil, and luxuriant willow scrubs. Neither where the vegetation nor where the soil is concerned is there a distinct limit corresponding to the borderline between the two types of bedrock. This is because part of the gneiss area is influenced by material carried by wind and water from the neighbouring basalt area.

Fig. 1 shows the investigation area as seen when looking southward from the top of Lyngmarksfjeld.

A summary of the temperature and precipitation conditions in the period 1962-69 is given in Table 1. The winter, characterized by temperatures mainly below 0°C, comprises eight months, October-May. The coldest month is February or March. In July and August, the warmest months, air frost does not occur even during the night. However, on nights with clear skies, frost may occur locally at the soil surface at any time during the summer. Conversely, on days with strong insolation, temperatures in the air layer just above the ground may rise considerably above the values measured in a meteorological screen.

The annual precipitation varies from approx. 350 to approx. 670 mm. However, between individual years the distribution of precipitation differs considerably. Generally precipitation is high between July and November.

Fig. 1. View over the investigation area at Godhavn, as seen from Lyngmarksfjeld towards south. The Arctic Station is situated in the middle of the picture (below the two large icebergs). The gneiss area, characterized by the rugged forms, is situated in the middle and to the right. The basalt area, characterized by a more soft relief, is situated to the left.

		Precipitation			Mean min. temperature			Mean max. temperature	
Month	lowest value	mean	highest value	lowest value	mean	highest value	lowest value	mean	highest value
January	6.7	21.0	55.0	-16.6	-12.7	-9.1	-12.0	-6.5	-1.3
February	3.8	40.4	159.6	-18.3	-13.9	-8.2	-10.2	-6.3	-1.2
$March \dots \dots \dots \dots$	6.7	23.2	53.1	-21.7	-17.3	-7.3	-15.0	-10.1	-1.4
$\operatorname{April.}\dots\dots\dots\dots$.	8.3	19.8	65.3	-13.8	-10.8	-7.5	-8.0	-3.9	-0.2
May.	1.8	21.8	68.5	-5.1	-3.0	-1.1	0.4	2.8	5.6
$June \ldots \ldots \ldots$	0.9	28.2	46.3	0.7	1.3	1.9	6.3	7.1	8.5
$July \dots \dots \dots \dots$	9.6	56.0	80.3	2.6	4.3	6.0	7.9	10.2	11.9
August.	0.8	42.4	78.6	3.5	4.6	5.6	8.7	9.9	10.8
$September. \dots.$	24.8	80.7	239.8	-0.1	0.7	1.5	4.1	5.0	5.9
$October \ldots \ldots$	8.9	37.7	81.3	-5.2	-3.7	0.0	-1.6	0.4	4.2
$\texttt{November} \dots \dots \dots$	16.2	61.5	167.6	-9.7	-7.5	-5.0	-4.8	-2.7	0.3
$December \ldots \ldots$	15.3	32.4	53.8	-13.8	-10.7	-8.4	-8.4	-5.6	-2.4
year.	351.5	465.1	668.1						

Table 1. Monthly precipitation (mm), mean minimum and mean maximum temperatures ($^{\circ}$ C) in Godhavn in the eight year period 1962-69.

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From October to May practically all the precipitation is in the form of snow. The thickness of the snow cover is not equal throughout the area. The frequent eastern and western winds blow the snow away from exposed sites and deposit it in the lee of cliffs, in small valleys etc. The considerable differences in the depth of the snow result in a large local variation in the time of the commencement of the snow free period. In the spring, the melting of the snow is negligible during the months March-May, even though the solar irradiance is relatively high in this period. Extensive melting does not take place until the air temperature rises above 0° C; it is accelerated by rain.

METHODS

The main objective of the investigation has been to study the development of the macromycete flora in the three years 1970-72. Concomitantly, a number of variable environmental factors was measured (see p. 32-44 and 53-63).

In June-July 1970, as soon as the snow had disappeared and before any macromycetes had appeared, 16 sites within the investigation area were selected. The position of these sites is shown on Fig. 2. The sites included the most important plant communities in the area and showed as wide a variation as possible as regards edaphic and microclimatic conditions. 5, 10 or 15 permanent quadrates of 1 square meter each were placed at each site, giving a total of 145 quadrates. In the spring of 1971, 25 additional quadrates were marked out so that the minimum number of quadrates at each site became 10.

The size of the quadrates, 1 square meter, was determined partly by the fact that it was difficult to find larger areas with homogeneous vegetation, partly by the necessity of being able to examine the quadrates in detail through a three year period without causing damage to the rather susceptible vegetation.

Each quadrate was marked with a wooden peg in each of the four corners. All the quadrates were inspected on the same day, four times a month in the period May-September, except in the spring when the interval between two inspections was about ten days. Table 2 gives the exact dates of the inspections. At each inspection, the macromycetes occurring in the quadrates were identified and listed, the fruit bodies were counted, and an estimate was made of the number of fruit bodies produced since the preceding inspection. It was attempted not to remove any fruit bodies from the quadrates, but in a few cases it was necessary to do this in order to ensure the correct identification of a species. The use of a wooden frame made it possible to survey exactly the same

Fig. 2. Position of the sites in the investigation area. For explanation of the abbreviations see p. 14-24. The broken line indicates the limit between the basalt (to the north and to the east) and the gneiss. Scale 1: 20,000, interval between contours represents 25 m height difference.

area of a quadrate at each inspection. Finally, a list was made of the macromycetes occurring at the sites, but only outside the quadrates.

The arrangement and the method of inspection of the quadrates was identical with that of LANGE (1948a) in his investigation of the Agarics of Maglemose in Denmark, a fact which makes it possible for a direct comparison of the results (see p. 67-70).

The vegetation in the permanent quadrates was analyzed in July 1971, according to the modified Hult-Sernander method (cp. p. 14

Month	1970	Year 1971	1972
$May \ldots \ldots \ldots \ldots$		1, 11, 22	2, 11, 22
$June \dots \dots \dots \dots \dots$	11, 20	1, 9, 16, 23	1, 8, 16, 23
$July \ldots \ldots \ldots \ldots \ldots$	1, 8, 16, 24	1, 8, 16, 24	1, 8, 16, 24
$August \ldots \ldots \ldots \ldots$	1, 9, 16, 24	1, 9, 16, 24	2, 9, 18, 25
$September \ldots \ldots \ldots$	1, 8, 15, 26	1, 7, 12	2, 9, 18, 25

Table 2. Dates of inspection of the permanent quadrates in Godhavn.

below). All vascular plants were included in the analysis, whereas mosses and lichens were only considered in so far as they were quantitatively important and the species could be distinguished from each other in the field. Owing to considerations of space, the analyses have not been published in detail, but in Tables 3-18, the frequency and the degree of cover has been given for all the dwarf shrubs and for the herbs, mosses and lichens which occurred in more than half of the quadrates at the individual sites.

SPECIES LIST

The present investigation takes into account the macromycetes, i.e. the orders *Agaricales, Gasteromycetales, Aphyllophorales,* and *Pezizales.* The family *Sclerotiniaceae* and the genus *Mitrula,* both belonging to the inoperculate *Discomycetes,* were also listed. The fruit bodies of some of the species of the two last mentioned taxa are rather small, but they were considered important, qualitatively and quantitatively.

In the list given below, all the macromycetes which have been determined to species level and which occurred at the sites have been noted, a total of 77 species. For comparison, the total number of species found at Godhavn in the period 1970-72 amounts to ea. 140. - Species concept and nomenclature is in most cases in accordance with the literature available at the time of the investigation, that is GULDEN & LANGE (1971) (species marked with one asterisk) and MosER (1963, 1967) (species marked with two asterisks). In a few cases it has been possible to refer the finds to species which have been described more recently, Lactarius dryadophilus and *L. salicis-herbaceae* (KÜHNER, 1975). Probably forthcoming and future research will show that the species concept used in the present investigation is in many cases too broad. The collections referred to as *Hebeloma crustuliniforme, H. mesophaeum,* and *Rhodophyllus sericeus* showed a high degree of variation and probably represent a larger number of species. - A number of small *Cortinarii* found at the sites offered a special problem. Even if an exhaustive key

to the species had existed, it would in many cases have been impossible to determine the specimens, due to alterations of the fruit bodies caused by drought, rain, and frost.

Helotiales

Ciboria amentacea (BALBIS ex FR.) FucK.** *C. aschersoniana* (HENN. & PLOTT.) WHETZEL** *C. betulae* (WoRONIN} WHITE** *C. polygonum-()i()ipari* EcKBL. *Mitrula gracilis* KARST.** *Monilinia megalospora* (WoRONIN} WHETZEL** *M. rhododendri* (FISCHER} WHETZEL** $Sclerotinia$ *vahliana* Rostra.*

Pezizales

Microstoma protracta (FR.) KANOUSE** *Sepultaria arenosa* (FucK.} MAss.**

Aphyllophorales

Cla()ulina cinerea (FR.) ScHROET. * *Thelephora radiata* HoLMSK. ex FR.

Agaricales

Amanita ()aginata (BuLL. ex FR.) VITT. forma *Arrhenia auriscalpium* FR.** *Clitocybe diatreta* FR. ss. J. E. LANGE *C. lateritia* FAVRE* Collybia cirrhata (SCHUM. ex FR.) KUMM.* C. dryophila (BULL. ex FR) KUMM.* *C. obscura* FAVRE* *Cortinarius cinnamomeoluteus* ORTON* *C. alpinus* Boun. ss. FAVRE* *C. anomalus* (FR. ex FR.) FR.* *C. hemitrichus* (PERS.) FR. *C. mucosus* (BuLL. ex FR.) FR.** *C. obtusus* FR.** $C.$ *subtorqus* LAMOURE* $Galerina heterocystis$ (ATK.) KÜHN.* *G. moelleri* BAs* *G. ()ittaeformis* (FR.) SING.* *Gerronema fibula* (BULL. ex FR.) SING.* *Hebeloma crustuliniforme* (BuLL. ex ST-AMANS} QuEL.*

H. mesophaeum (PERS.) QuEL. * *H. pusillum* J. E. LANGE* *Hygrophorus lilacinus* (LAEST.) M. LANGE* *H. turundus* (FR. ex FR.) FR.* *Inocybe calamistrata* (FR.) GILL.* *I. decipiens* BRES. var. *mundula* FAVRE* *I. dulcamara* (ALB. & SCHW. ex PERS.) KUMM.* *I. fastigiata* (SHAEFF. ex FR.) OUEL.* *I. gausapata* KÜHN.** *I. griseolilacina* J.E. LANGE** *I. lacera* (FR.) KUMM.* *I. cfr. ovalispora* KAUFF. var. *brunneola* FAVRE *Laccaria altaica* SING. ex SING.* *L. laccata (Scop.* ex FR.) BERK. & BROOME** Lactarius dryadophilus KüHN. *L. mitissimus* FR.** L. salicis-herbaceae Kü_{HN.} *L. torminosus* (SCHAEFF. ex FR.) S. F. GRAY* *L. uvidus* (FR. ex FR.) FR.* *Leccinum rotundifoliae* (SING.) SMITH *et al.* Leptoglossum lobatum* (PERS. ex FR.) RICKEN $Marasmius$ epidryas KüHN.** *M. epiphyllus* (PERS. ex FR.) FR.** *Mycena aetites* (FR.) QuEL.** *M. citronomarginata* GILL** M. griseogilva HORAK* *M. permixta* (BRITZ.) SACC.** *M. psammicola* BERK. & BROOME *M. urania* (FR.) GILL.* *Mycenella salicina* (VEL.) SING.** $Ombalia$ striatula (KÜHN.) KÜHN. & ROMAGN.** *0mphalina acerosa* (FR.) M. LANGE* *0. ericetorum* (PERS.) M. LANGE* *0. rustica* (FR.) QuEL.* *O. velutina* (QuÉL.) QuÉL.* *Psathyrella trepida* (FR.) GILL* Psilocybe montana (PERS. ex FR.) KUMM.* $Rhodophyllus juncinus$ KÜHN. & ROMAGN.** *R. sericeus* (BULL. ex MÉRAT) QUÉL.* *Russula aeruginea* LINDBL. ex FR.* *R. alpina* (BLYTT) MoELL. & J. ScHAEFF.* *R. delica* FR.** *R. obscura* RoM. *

R. oreina SING.*

R. sphagnophila KAUFF. var. *heterosperma* SING.*

Gasteromycetales

Calvatia cretacea (BERK.) LLOYD

In the following pages, the species have been grouped into *Sclerotiniaceae,* litter decomposers, and mycorrhiza forming species.

The *Sclerotiniaceae* is taxonomically defined. Biologically this group is characterized by the sclerotia which survive the winter and out from which one or several fruit bodies grow the following spring.

The delimitation of the group of mycorrhiza forming species from the litter decomposers has been made on the basis of information about the biology of the genera, but field evidence has also been taken into consideration. Thus, *Rhodophyllus sericeus* and the *Laccaria* spp. are considered mycorrhiza forming species, in addition to the genera *Amanita, Cortinarius, Hebeloma, Inocybe, Lactarius, Leccinum,* and *Russula.* A few species of these genera (e.g. *Hebeloma crustuliniforme, H. mesophaeum,* and *Inocybe dulcamara)* sometimes occurred on frost ground devoid of vegetation, probably as decomposers of dead roots of *Salix glauca* and other dwarf shrubs.

The litter decomposers comprise the genera Arrhenia, Calvatia, *Clitocybe, Collybia, Galerina, Hygrophorus, Leptotus, M arasmius, M itrula, Mycena, Mycenella, Omphalina, Plectania, Psathyrella, Psilocybe, Ramaria, Scutellinia, Sepultaria,* and *Thelephora.*

THE SITES AND THEIR MACROMYCETE FLORA

Of the sixteen sites selected as representative of the investigation area, one was dominated by *Dryas* and *Rhododendron,* six by *Betula nana* and four by *Salixglauca.* Two sites could be characterized as wet and three as snow-bed communities, dominated by *Salix herbacea.* It would have been desirable if each individual site or at least each individual quadrate had been covered with only one of the shrubs forming ectotrophic mycorrhiza *(Betula nana,* the *Salix* spp., *Dryas integrifolia,* cfr. KATENIN (1964)) and far enough from any of the other species to exclude root interference; but this was impossible. At best the quadrates could be placed in such a way that they were dominated by one of the shrubs mentioned. Especially *Salix glauca,* which has a broad ecological amplitude, occurred practically everywhere either within or just outside the quadrates.

Fig. 3. In the middle distance southwest-exposed slope (Site DR) dominated by *Dryas integrifolia* (to the right) and *Rhododendron lapponicum* (to the left). The site is situated on basalt, just at the border to the gneiss area north of Godhavn. In the background is Lyngmarksfjeld (802 m).

In the following pages, the individual sites and their macromycete flora are described. For clarity, some of the site characteristics and the methods by which they have been measured are discussed separately on p. 31-44.

Site dominated by *Dryas integrifolia* **and** *Rhododendron lapponicum:*

DR: Southwest-exposed slope dominated by *Dryas integrifolia* and *Rhododendron lapponicum* (Fig. 3 and Table 3). Slope approx. 30°, altitude 100 m. A relatively stable scree with a fairly close vegetation.

Explanation to Tables **3-18:** The head of the table gives the quadrate numbers and the investigation period, also a short characteristic of the site, and reference to a more detailed description. The vegetation analysis gives the frequency in percent, and the range of the degree of cover (to the left and right of the inclined quoin respectively), for all the dwarf shrubs, and for the herbs, mosses and lichens occurring in more than half of the quadrates. 6 corresponds to a degree of cover from 1 to $3/4$; 5 to a degree of cover from $3/4$ to $1/2$; 4 to a degree of cover from $1/2$ to $1/4$; 3 to a degree of cover from $1/4$ to $1/8$; 2 to a degree of cover from $1/8$ to $1/16$; and 1 to a degree of cover less than $1/16$. $-$ The nomenclature of the vascular plants is in accordance with Böcher, HOLMEN & JAKOBSEN (1966). The mosses have been identified following the floras of GROUT (1928-40) and NYHOLM (1954-69) and their nomenclature is in accordance with W1JK *et al.* (1959-69). The nomenclature of the lichens is taken from HALE & CULBERSON (1970).

Because of the exposure this site was covered with only a thin snow layer in the winter. Consequently the snow disappeared very early in the spring. DR was the warmest of the sites investigated. In 1971 the highest temperature at the soil-litter interface, 31°C, was measured here. DR was also one of the driest sites, though the moisture conditions varied somewhat along the slope. In the spring, the western part was kept moist by seepage water for a longer period of time than the eastern. This had resulted in some variation in the soil conditions (cp. Fig. 9, DR_I from the western part of the slope, DR_{II} from the eastern part). *Rhododendron lapponicum* dominated the moister part; *Dryas integrifolia* the drier part of the slope. 15 quadrates were marked out in June 1970:

Table 3. DR 1-15, 1970-72. The macromycetes occurring in 15 quadrates on a slope dominated by *Dryas integrifolia* and *Rhododendron lapponicum* (p. 14). No fruit bodies occurred in Quadrate 7. Vegetation analysis: *Dryas integrifolia:* DR 1-10: 100/3-6, DR 11-15:0/0; *Rhododendron lapponicum:* DR 1-5:0/0; DR 6-15:100/3-5. DR 1-15: *Vaccinium uliginosum:* 100/1-3; *Polygonum viviparum:* 93/0-2; *Carex rupestris:* 80/0-3; *Salix glauca:* 67 /0-£,.; *Pyrola minor:* 53/0-1. *Stereocaulon* sp.: 100/1-3; *Alectoria ochroleuca:* 100/1-2; *Cetraria nivalis:* 87 /0-1.

									Quadrate no.							bodies produced		number of fruit constancy	$\frac{0}{0}$, 1970–72
Species	$\mathbf 1$	$\overline{2}$	3	4	5	6	8	9	10									12 13 14 15 1970 1971 1972 DR1-10 DR6-15	
Cortinarius sp. \dots +		$^{+}$				$^{+}$			$^{+}$						13	1	5	40	40
$C.$ anomalus		$^{+}$			$^{+}$	$+$	$^{+}$		$^{+}$		$^+$				19	5	2	50	40
Monilinia rhododend.			$^{+}$				$^{+}$	$^{+}$		$^{+}$	$+$	$^{+}$				17	$\mathbf{1}$	30	50
$Mycena$ aetites					$^{+}$	$^{+}$			$^{+}$				$^{+}$		3		1	30	30
Inocybe dulcamara		$^{+}$		$^{+}$							$^{+}$				3	$\overline{2}$	7	20	10
$I.$ ovalispora		$+$	$^{+}$						$^{+}$						$\mathbf{3}$		1	30	10
Omphalina velutina.							$^{+}$			$^{+}$				$^{+}$		$\mathbf{1}$	12	10	30
Hebeloma mesophaeum						$^{+}$					$^{+}$				$\overline{2}$	$\mathbf{1}$	$\mathbf{1}$	10	20
Inocybe griseolilacina		$+$				$^{+}$									4			20	10
Rhodophyllus sericeus				$^{+}$								$^{+}$				$\overline{2}$		10	10
Arrhenia auriscalpium														$^{+}$			$\overline{2}$		10
Clavulina cinerea						$^{+}$											5	10	10
Clitocybe lateritia					$+$													10	
Cortinarius cinnamo.						$^{+}$									$\overline{2}$			10	10
Galerina moelleri														$^{+}$		1			10
Inocybe gausapata				┿											1			10	
Marasmius epidryas		$\hspace{0.1mm} +$													3		6	10	
Total number of $species \ldots \ldots \ldots$		6	2	3	3	7	3	1	4	3	5	$\overline{2}$	1	3					

Species occurring outside the quadrates: *Collybia obscura, Cortinarius subtorvus, Hebeloma crustuliniforme, Lactarius dryadophilus, Leccinum rotundifoliae, Thelephora radiata.*

Table 4. BSi 1-10, 1970-72. The macromycetes occurring in 10 quadrates in a heath with *Betula nana* and *Silene acaulis* (p. 16). No fruit bodies occurred in Quadrates 1, 3, 9, or 10. Vegetation analysis: *Betula nana:* 100/4–6; *Vaccinium uliginosum*: 100/3-5; *Salix glauca:* 60/0-3; *Empetrum hermaphroditum:* 50/0-3; *Dryas integrifolia:* 20/0-1. *Carex rupestris:* 100/1; *Silene acaulis:* 100/1; *Polygonum Piviparum:* 90/0-1; *Pyrola minor:* 60/0-2. *Hylocomium splendens:* 90/0-i; *Aulacomnium turgidum:* 80/0-3; *Dicranum majus:* 60/0-3; *Polytrichum juniperinum:* 60/0-1. *Stereocaulon* sp.: 80/0-2; *Cetraria cucullata:* 60/0-1.

Species occurring outside the quadrates: *Arrhenia auriscalpium, Collybia obscura, Cortinarius subtorvus, Lactarius dryadophilus, Omphalina velutina, Thelephora radiata.*

DR 1-5 dominated by *Dryas,* DR 6-10 with both *Dryas* and *Rhododendron,* and DR 11-15 dominated by *Rhododendron.* This site had the highest number of species of macromycetes.

Sites **dominated by** *Betula nana:*

BSi: heath with *Betula nana* and *Silene acaulis* (Table 4). A level plain 35 m a.s.l., covered with a mosaic of *Carex rupestris* and *Betula nana.* 10 quadrates dominated by *Betula nana* were marked out in June 1970. The site was covered by only a thin layer of snow in the winter and therefore became free of snow relatively early in the spring. The soil conditions favouring drainage and the relatively low content of organic matter resulted in high soil temperatures in the summer.

Bf: fell-field with *Betula nana* (Fig. 4 and Table 5). A gravelly, slightly south sloping area with scattered rocks, stone polygons and stripes, 125 m a.s.l. Scattered patches of low-growing *Betula nana, Dryas integrifolia,* and *Salix glauca.* In the winter it was covered by only a thin snow layer and was hence free of snow relatively early in the spring. Ten quadrates dominated by *Betula nana* were marked out in June 1970.

Fig. 4. The basalt plateau, fell-field with Betula nana (Site Bf). In the background to the left, Skarvefjeld (860 m). In the distance to the right, Disko Bugt.

Table 5. Bf 1-10, 1970-72. The macromycetes occurring in 10 quadrates on a fell field with *Betula nana.* No fruit bodies occurred in Quadrates 1, 3, 6, 8 or 9. Vegetation analysis: *Betula nana:* 100/4-5; *Vaccinium uliginosum:* 100/2-4; *Dryas integrifolia:* 80/0-2; *Salix glauca:* 60/0-1; *Empetrum hermaphroditum:* 20/0-3; *Diapensia lapponica:* 10/0-1. *Luzula confusa:* 80/0-1; *Polygonum r,ir,iparum:* 60/0-1. *Alectoria ochroleuca:* 100/1-3; *Stereocaulon* sp.: 100/1-2; *Cetraria cucullata:* 90/0-1.

	Quadrate no.				1970 1971 1972		number of fruit constancy $\frac{0}{0}$ bodies produced 1970–72
			-10				
<i>Cortinarius</i> sp. \ldots + $Rhodophyllus$ sericeus Collybia cirrhata $+$ $Marasmius epidryas +$				3 1	$\mathbf 2$	3	20 20 10 10
$The lephora \, radiata \ldots \ldots$			+				10
Total number of species 3	1						

Species occurring outside the quadrates: *Collybia obscura, Cortinarius anomalus,* C. *subtorvus, lnocybe dulcamara, Lactarius dryadophilus, Leccinum rotundifoliae.*

Fig. 5. Lyngmarken, part of the gneiss area north of Godhavn. In the foreground heath with *Betula nana* and *Ledum palustre* (Site BLe).

BCS: heath with *Betula nana, Cassiope tetragona,* and *Salix glauca* (Table 6). A slightly south sloping area 75 m a.s.1., in a somewhat hilly terrain. Considerable amounts of snow accumulate in winters of high precipitation, e.g. in the winter 1969-70. The moss carpet was thick, due to the occurrence of seepage water. Many dead shoots of *Betula nana* occurred in the quadrates BCS 1, 4, 7 and 10.

BA: vegetation dominated by *Betula nana* and *Aulacomnium turgidum* (Table 7). A very slightly southwest sloping sandy plain, 30 m a.s.l. The vegetation here was poor, except along a small watercourse where a relatively luxuriant vegetation had developed, consisting mainly of *Aulacomnium turgidum* and *Betula nana.* Many dead shoots of *Betula nana* occurred in the quadrates BA 8, 9 and 10. The thickness of the moss layer was considerable. The watercourse originated in a small pond and the height of water was variable; high during the snow melt and after periods of rain, low in periods of drought. This resulted in a corresponding variation in the water content of the soil along the watercourse.

Five quadrates were marked out in June 1970, and five more in June 1971.

BLe: heath with *Betula nana* and *Ledum palustre* (Fig. 5 and Table 8). On a level area, 35 m a.s.l. A mosaic of hummocks with dwarf shrub

Table 6. BCS 1-10, 1970-72. The macromycetes occurring in 10 quadrates in a heath with *Betula nana, Cassiope tetragona,* and *Salix glauca* (p.18). No fruit bodies occurred in Quadrates 1, 2, 4, or 6-10. Vegetation analysis: *Betula nana:* 100/4-5; *Vaccinium uliginosum:* 100/3-5; *Salix glauca:* 100/2-4; *Cassiope tetragona:* 100/1-4; *Empetrum hermaphroditum:* 100/1-4; *Dryas integrifolia:* 10/0-1. *Carex rupestris:* 100/1-2; *Polygon um PiPiparum:* 60/0-1; *Pyrola grandiflora:* 60/0-1. *Hylocomium splendens:* 70/0-3; *Tomenthypnum nitens:* 60/0-5; *Dicranum* sp.: 60/0-3. *Stereocaulon* cfr. *paschale:* 70/0-2; *Cetraria crispa:* 60/0-1.

Species occurring outside the quadrates: *Cortinarius mucosus, C. subtorcus, Hebeloma crustuliniforme, Lactarius torminosus, L. uc,idus, Leccinum rotundifoliae, Russula alpina.*

Table 7. BA 1-5, 1970-72; BA 6-10, 1971-72. The macromycetes occurring in 10 quadrates in vegetation dominated by *Betula nana* and *Aulacomnium turgidum* (p. 18). No fruit bodies occurred in Quadrate 8. Vegetation analysis: *Betula nana:* 100/4-5; *Vaccinium uliginosum:* 100/2-4; *Salix arctophila:* 90/0-4; *Empetrum hermaphroditum:* 90/0-3; *Salix herbacea:* 40/0-4. *Polygonum viviparum:* 100/1-2; *Carex bigelowii:* 90/0-2; *Poa pratensis:* 80/0-2; *Pyrola grandiflora:* 70/0-1. *Aulacomnium turgidum:* $100/3 - 6$.

Species occurring outside the quadrates: *Hebeloma mesophaeum, Leccinum rotundifoliae.*

 $2*$

heath and hollows with mineral soil almost devoid of vegetation. The soil at this and the following site (BCa) was characterized by the low **pH.** Ten quadrates were laid out on the hummocks in June 1970.

BCa: moist heath with *Betula nana* and *Carex rariflora* (Table 9). A small valley in the gneiss area, 20 m a.s.1. The vegetation consisted of a mosaic of low hummocks with dwarf shrub heath and hollows with *Carex rariflora* and *Eriophorum angustifolium.* Many dead shoots of *Betula nana* occurred in the quadrates BCa 1 and 10. The soil was wet except during the driest period in the middle of the summer. In the winter 1969-70 considerable amounts of snow had accumulated so that the growing season in -70 began rather late, but this seemed to be exceptional. Ten quadrates were laid out on the hummocks in June 1970.

Table 8. BLe 1-10, 1970-72. The macromycetes occurring in 10 quadrates in heath with *Betula nana* and *Ledum palustre* (p. 18). No fruit bodies occurred in Quadrate 3. Vegetation analysis: *Betula nana:* 100/3-5; *Empetrum hermaphroditum:* 100/3-5; *Vaccinium uliginosum:* 100/3-4; *Ledum palustre* ssp. *decumbens:* 100/1-3; *Salix arctophila:* 90/0-3; *S. herbacea:* 30/0-1. *Carex bigelowii:* 100/1-2; *Luzula confusa:* 70/0-1. *Polytrichum affine:* 100/1-2; *Aulacomnium turgidum:* 90/0-2; *Dicranum majus:* 90/0-2.

						Quadrate no.					number of fruit bodies produced		constancy $\frac{0}{0}$
Species	$\mathbf{1}$	$\mathbf{2}$	4	5	6	7	8	9	10	1970	1971	1972	1970-72
$Clitocube$ diatreta		$+$		$^{+}$				\div	$^{+}$	8			50
$Ombalina$ ericetorum $\dots \dots$ +			$^{+}$		$+$	$^{+}$	$^{+}$			16	7	3	50
$Mycena$ aetites +				$^{+}$		$\ddot{}$			$^{+}$	1			40
$\textit{Collybia}$ cirrhata		$^{+}$					$^{+}$	$+$				17	30
$Mycena urala \ldots \ldots$					$^{+}$	$^{+}$			$^{+}$	6		3	30
$Galerina$ vittaeformis		$^{+}$					\pm					2	20
<i>Leccinum rotundifoliae</i> $+$ +											3		20
Omphalina rustica $+$ +										8	$\overline{2}$	$\overline{2}$	20
$Ciboria$ amentacea								\pm			$\overline{2}$		10
$C. \, \text{betulae} \ldots \ldots \ldots \ldots \ldots +$													10
$\textit{Cortinarius}$ sp. $\dots \dots \dots \dots$	\pm											$\overline{1}$	10
Hy grophorus lilacinus +											1		10
$H.$ turundus	$^{+}$										$\overline{2}$		10
$Inocybe$ lacera +											3		10
$Mycena\ griseogilva \ldots$		$^{+}$									$\mathbf{1}$		10
$M.~psammicola. \ldots \ldots \ldots$									$^{+}$				10
					$^{+}$						$\overline{2}$		10
Total number of species	9	5		$\mathbf 2$	3	3	4	3					

Species occurring outside the quadrates: *Gerronema fibula, Hebeloma mesophaeum, Russula obscura.*

Table 9. BCa 1-10, 1970-72. The macromycetes occurring in 10 quadrates with *Betula nana* and *Carex rariflora* (p. 20). No fruit bodies occurred in Quadrates 3 or 9. Vegetation analysis: *Betula nana*: 100/4-6; *Vaccinium uliginosum*: 100/2-4; *Empetrum hermaphroditum:* 100/1-3; *Salix arctophila:* 80/0-2; *Salix glauca:* 10/0-1. *Carex rarifiora:* 100/1-t.; *Eriophorum angustifolium:* 100/1-3; *Polygonum viviparum:* 100/1-2. *Aulacomnium turgidum:* 100/1-t.; *Polytrichumjuniperinum:* 80/0-1. *Cetraria delisei:* 90/0-2; *C. cucullata:* 80/0-1; *C. nivalis:* 60/0-1.

Species occurring outside the quadrates: *Cortinarius alpinus, C. mucosus, Hebeloma crustuliniforme, Lactarius torminosus, Omphalina umbellifera.*

Sites **dominated by** *Salix glauca:*

S: *Salix glauca* scrub (Fig. 6 and Table 10). A level area 70 m a.s.l., traversed by a network of watercourses originating in the neighbouring basalt area, resulting in a relatively high soil water content throughout the summer. The luxuriant willow scrub (0.5-1.0 m high) was covered every winter by a thick layer of snow or ice. In the spring, the snow disappeared rather early, but it took a long time before the soil thawed. The undergrowth in the scrub varied a great deal according to the local moisture and shade conditions, from a thick moss carpet to almost none, the soil surface then being covered with a thick litter layer. Ten quadrates were marked out in June 1970.

SHy: heath with *Salix glauca* and *Hylocomium splendens* (Fig. 6 and Table 11). A level area 70 m a.s.l., situated on the lower part of an old alluvial fan, covered with a thick moss carpet and *Salix glauca,* 10-15 cm high. Ten quadrates were marked out in June 1970.

SE: heath with *Salix glauca* and *Empetrum hermaphroditum* (Fig. 6 and Table 12). Adjacent to the preceding site, but somewhat drier and free of snow a little earlier. Ten quadrates were marked out in June 1970. This and the following site had the lowest number of species and fruit bodies of macromycetes.

Fig. 6. Valley just north of the Arctic Station. A cliff, approx. 30 m high, bordered by a scree (\emptyset sterlien) with willow scrub, flushes, and herb slope vegetation, forms the limit between the gneiss area (in the foreground) and the basalt area. - In the middle distance, on the flat area, a *Salix herbacea* snow-bed with some *Salix glauca,* moist and relatively early free of snow (Site Shb}. A little to the left, a heath with *Salix glauca* and *Hylocomium splendens* (Site SHy). A little further to the left, a heath with *Salix glauca* and *Empetrum hermaphroditum* (Site SE). At the base of the scree, a 0.5-1.0 m high *Salix glauca* scrub (Site S).

Sf: fell-field with *Salix glauca, S. herbacea,* and *Empetrum hermaphroditum* (Fig. 7 and Table 13). A fell-field with small patches of shallow soil between the stones, 70 m a.s.l. The site was very dry. Ten quadrates were marked out in June 1970, five (Sf 1-5) in pure *Empetrum hermaphroditum* and five (Sf 6-10) in vegetation dominated by *Salix glauca.* In 1971, five additional quadrates (Sf 11-15) were marked out in vegetation dominated by *Salix glauca.*

Wet sites:

A: fen with *Aulacomnium palustre* (Table 14). A fen, 35 m a.s.l., along a watercourse originating from the basalt area. The soil was constantly soaked, two of the quadrates (A 5 and 8) even occasionally flooded. Five quadrates were marked out in June 1970, five additional ones in 1971. This site had the highest mean number of species and fruit bodies of macromycetes per quadrate.

Ca: fen with *Carex rarifiora* (Fig. 8 and Table 15). A fen in the gneiss area, 25 m a.s.l., waterlogged throughout the summer and domi-

nated by mosses, mainly *Oncophorus wahlenbergii.* Five quadrates were marked out in June 1970, five more in 1971. The first five were the richest, both in species and fruit bodies. The explanation may be that in 1971, after the last five quadrates had been marked out, the moss layer in that part of the fen dried up before the ice underneath had melted. This dry moss layer formed an insulating mat, which delayed the melting of the ice beneath. As a result the last five quadrates remained 10-20 cm above the level of the rest of the fen for most of the summer.

Snow-bed communities dominated by *Salix herbacea:*

Sha: *Salix herbacea* snow-bed, dry and free of snow early (Table 16). Situated in the gneiss area, 25 m a.s.1., slightly south sloping. Large stones and boulders with interspersed fragments of *Salix herbacea*vegetation, in the winter covered with up to two meters of snow. However, the site became free of snow early in the summer, and the soil was

Table 11. SHy 1-10, 1970-72. The macromycetes occurring in a heath with *Salix glauca* and *Hylocomium splendens* (p. 21). Vegetation analysis: *Salix glauca:* 100/5-6; *Vaccinium uliginosum:* 50/0-3; *Salix herbacea:* 20/0-2; *Empetrum hermaphroditum:* • 10/0-1. *Pyrola grandiflora:* 100/1-4; *Poa pratensis:* 90/0-2; *Polygonum viviparum:* 90/0-2; *Equisetum arvense:* 70/0-1. *Dicranum fuscescens:* 100/1-3; *Hylocomium splendens:* 90/0-4; *Aulacomnium turgidum:* 70/0-3. *Stereocaulon alpinum:* 90/0-1; *Cetraria crispa:* 60/0-1; *C. cucullata:* 60/0-1.

Species occurring outside the quadrates: *Cortinarius subtorvus, Lactarius dryadophilus, Russula alpina, R. delica, R . oreina.*

dry and warm. Five quadrates, Sha 1-5, were marked out in June 1970. In the spring of -71, Sha 3 was destroyed by a picnic party and had to be moved. At the same time, five additional quadrates were marked out, Sha 6-10.

Shb: *Salix herbacea* snow-bed with some *Salix glauca,* moist and free of snow relatively early (Fig. 6 and Table 17). Situated 70 m a.s.l., close to SHy. In periods throughout the summer, the soil was moist from seepage water, originating in a small lake. Ten quadrates were marked out in June 1970, in vegetation dominated by *Salix herbacea* and with scattered *Salix glauca,* approx. 5 cm high.

She: *Salix herbacea* snow-bed, free of snow late (Table 18). Situated in a narrow cleft in the basalt plateau, 140 m a.s.l. In the winter the snow cover had a thickness of approx. 2 m, and the vegetation normally did not appear until late in the summer. Due to seepage water, the soil did not dry up even in periods of drought. Ten quadrates were marked out in July 1970.

Fig. 7. The gneiss area north of Godhavn. Fell-field with *Salix glauca, S . herbacea,* and *Empetrum hermaphroditum* (Site Sf). In the background (to northwest) Apostelfjeld (748 m).

Table 12. SE 1-10, 1970-72. The macromycetes occurring in 10 quadrates in a heath with *Salix glauca* and *Empetrum hermaphroditum* (p. 21). No fruit bodies occurred in Quadrates 1-5, 7, 9, or 10. Vegetation analysis: *Empetrum hermaphroditum:* 100/3-4; *Salix glauca:* 100/3-4; *Vaccinium uliginosum:* 100/2-4. *Pyrola minor:* 100/1-3; *Equisetum arvense:* 90 /0-2 ; *Poa pratensis:* 80 /0-1 ; *Polygonum viviparum:* 80 /0-1 ; *Luzula confusa:* 70/0-1; *Pedicularis hirsuta:* 60/0-1. *Dicranum fuscescens:* 100/1-2; *Aulacomnium turgidum:* 80/0-3; *Hylocomium splendens:* 80/0-2; *Oncophorus wahlenbergii:* 70/0-2. *Psoroma hypnorum:* 90/0-1.

Species occurring outside the quadrates: *Clitocybe diatreta, Cortinarius mucosus, Lactarius dryadophilus, Omphalina rustica.*

Fig. 8. Lyngmarken in the gneiss area north of Godhavn. Fen with *Carex rariflora* (Site Ca).

Table 13. Sf 1-10, 1970-72; Sf 11-15, 1971-72. The macromycetes occurring in 15 quadrates on a fell-field with *Salix glauca, S. herbacea* and *Empetrum hermaphroditum* (p. 22). No fruit bodies occurred in Quadrates 1-8 or 10-12. Vegetation analysis: *Empetrum hermaphroditum:* Sf 1-5: 100/3-6; Sf 6-10: 100/4-5; *Salix herbacea:* Sf 1-5: 100/1-2; Sf 6-10: 40/0-2; *Salix glauca:* Sf 1-5: 20/0-1; Sf 6-10: 100/4-5; *Vaccinium uliginosum:* Sf 1-5: 20/0-2; Sf 6-10: 0/0. *Pyrola minor:* 100/1-2; *Polygonum viviparum:* 60/0-1. *Dicranum scoparium:* 90/0-3; *Polytrichum piliferum:* 90/0-1; *Ceratodon purpureus:* 70/0-1.

Species occurring outside the quadrates: *Cortinarius mucosus, Omphalina rustica.*

Table 14. A 1-5, 1970-72; A 6-10, 1971-72. The macromycetes occurring in 10 quadrates in a fen with *Aulacomnium palustre* (p. 22). Vegetation analysis: *Salix glauca:* 100/3-4; *Empetrum hermaphroditum:* 10/0-2; Vaccinium uliginosum: 10/0-2. *Carex stans:* 100/2-4; *Pedicularis hirsuta:* 100/1-3; *Polygonum c,iviparum:* 100/1-3; *Equisetum variegatum:* 100/1-2; *Equisetum arcense:* 90/0-2; *Poa pratensis:* 90/0-2; *Eriophorum angustifolium:* 70/0-3; *Luzula parc,iflora :* 60/0-1; *Stellaria longipes:* 60/0-1. *Aulacomnium palustre:* 100/2-6; *Drepanocladus uncinatus:* 90/0-4; *Hylocomium splendens:* 80/0-1. *Peltigera aphthosa:* 100/1-4.

Tables 3-18 show that there was a great variation in the number of species encountered at the sites. The maximum was 23 (DR), the minimum 6 species (She). Also the number of species per quadrate varied considerably, both between and within the sites. The mean for all 144 quadrates was 2.0, hut at the individual sites, the mean varied from 0.1 (Sf) to 10.6 (A). The highest number of species found in a single quadrate was 14 (A 5), but in about one third of the quadrates there occurred no macromycetes at all. It was characteristic that at several of the sites, one or a few quadrates without any obvious reason yielded quite a number of species (e.g. DR 2 and 6, BLe 1, S 8, SHy 9, and Ca 5) whereas in the rest of the quadrates only a few or none at all

Table 15. Ca 1-5, 1970-72; Ca 6-10, 1971-72. The macromycetes occurring in 10 quadrates in a fen with *Carex rariflora* (p. 22). No fruit bodies occurred in Quadrates 4., 6, 7, or 9. Vegetation analysis (Ca 1-5): *Salix arctophila:* 100/3-4.; *Vaccinium uliginosum: 20/0-1. Carex rariflora: 100/4; Eriophorum angustifolium: 100/2-4. Oncophorus wahlenbergii:* 100 /4.-6; *Calliergon sarmentosum:* 100 /1-3; *Polytrichum alpinum:* 100/1-2.

Species occurring outside the quadrates: *Lactarius salicis-herbaceae.*

were found. This is despite the fact that the vegetation in the quadrates at the individual sites was fairly homogeneous. Except at site A, the constancy percentages were low, i.e. most of the species occurred only in a few quadrates at each site.

It is also characteristic that there were relatively few litter decomposers as compared to mycorrhiza forming species. The ratio litter decomposers: mycorrhiza forming species ranged from $2:16 = 0.13$ (at SHy) to $4:2 = 2.0$ (at SE).

In order to obtain a rough estimate of the dry weight of the fruit bodies produced per unit area, 2-10 representative herbarium specimens of each species were weighed and the mean dry weight per fruit body was found. The mean values were used to calculate the dry weight of the fruit bodies produced per square meter at each individual site, in each of the three years. Due to considerable variation in size of the fruit bodies of the individual species, the values given below will only represent the order of magnitude.

The mean dry weight produced per square meter for all the 144 quadrates was 375 mg in 1970, 600 mg in -71 , and 190 mg in -72 . There was a large variation between the sites. The dry weight of fruit bodies produced per square meter per year, as a mean of three years was for

Table 16. Sha 1, 2, 4, and 5, 1970-72; Sha 3a, 1970; Sha 3b and 6-10, 1971-72. The macromycetes occurring in 10 quadrates in *Salix herbacea* snow-bed, dry and early free of snow (p. 23). No fruit bodies occurred in Quadrates 4 or 6. Vegetation analysis (Sha 1-5): *Salix herbacea:* 100/6; *Vaccinium uliginosum:* 60/0-1. *Carex bigelowii:* 80/0-3; *Polygonum viviparum:* 80/0-2; *Luzula confusa:* 80/0-1; *Trisetum spicatum:* 60/0-1. *Stereocaulon* sp.: 100/1-2.

				Quadrate no.						number of fruit bodies	constancy $\frac{0}{0}$			
Species	1			2 3a 3b		5 7	8				produced	9 10 1970 1971 1972 1971 1972	Sha $1, 2, 4, 5$ Sha $3b, 6-10$	Sha $1,2,4,5$ 1970-72
Clitocybe diatreta + +									5					50
$Cortinarius$ sp +				$^{+}$		$+$		$+ +$	10		7	5	5	50
$C. subtorous \ldots \ldots \ldots +$		$+$			$^{+}$				4					50
$Arrhenia$ auriscalpium					$^{+}$				$\mathbf{1}$					25
$Inocybe\ decipiens \ldots \ldots \ldots$					$^{+}$					6				25
		$+$							\mathfrak{D}					25
$Cortinarius$ alpinus $\ldots \ldots$							$^+$						3	
							$^+$					3		
$Laccaria$ $laccata$							$^{+}$						1	
$Mycena\ griseogilva \ldots$							$^{+}$							
$Rhodophyllus$ sericeus						$^{+}$								
$Russula obscura \ldots \ldots \ldots$								$^{+}$				9		
Total number of species	3	$\overline{2}$	1		3		4							

Species occurring outside the quadrates: *Amanita vaginata, Hebeloma crustuliniforme, H. mesophaeum, Psilocybe montana, Russula aeruginea, R. alpina.*

one of the fens (A) 1,340 mg, for the willow scrub (S) 720 mg, and for the more luxuriant heath communities (SHy, BLe, and BCa) 720, 710, and 670 mg respectively. The lowest values, 5 and 10 mg, were found at the two fell-field sites Sf and Bf.

Regarding the contribution to the production of fruit bodies of the three biological groups, the *Sclerotiniaceae* accounted for 2, the litter decomposers for 10, and the mycorrhiza forming species for 88 $\frac{0}{0}$ of the total dry weight produced in the 144 quadrates over the three year period.

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Table 17. Shb 1-10, 1970-72. The macromycetes occurring in 10 quadrates in *Salix herbacea* snow-bed with some *Salix glauca,* moist and relatively early free of snow (p. 24). Vegetation analysis: *Salix herbacea:* 100/3-5; *Salix glauca:* 70/0-4; *Vaccinium uliginosum:* 30/0-4. *Equisetum arvense:* $100/1-2$; *Polygonum viviparum:* $100/1-2$; *Carex bigelowii:* 90/0-3; *Pedicularis flammea:* 80/0-1. *Dicranum majus:* 100/1-4; *Polytrichum juniperinum:* 100/1-2; *Drepanocladus uncinatus:* 90/0-3; *Bryum* sp.: 70/0-1. *Stereocaulon* sp.: 100/1-3; *Cetraria crispa:* 100/1-2.

Species occurring outside the quadrates: *Cortinarius alpinus, C. mucosus.*

Table 18. She 1-10, 1970-?2. The macromycetes occurring in 10 quadrates in *Salix herbacea* snow-bed, late free of snow (p. 24). No fruit bodies occurred in Quadrates 1 or 7. Vegetation analysis: *Salix herbacea:* 100/5-6; *Harrimanella hypnoides:* 80/0-4; *Salix glauca:* 20/0-1; *Phyllodoce coerulea:* 10/0-1; *Vaccinium uliginosum:* 10/0-1. *Polygonum viviparum:* 100/1-3; *Poa alpina:* 100/1; *Equisetum arvense:* 80/0-1; *Gnaphalium supinum:* 60/0-2; *Carex scirpoidea:* 60/0-1; *Poa arctica:* 60/0-1. *Drepanocladus uncinatus:* 90/0-4; *Brachythecium* spp.: 80/0-3; *Polytrichum alpinum:* 70/0-1. *Peltigera canina:* 70/0-1.

Species occurring outside the quadrates: *Rhodophyllus sericeus.*

DISCUSSION OF SOME SITE CHARACTERISTICS

In the following section, the variation between the sites is discussed, while the differences between the three years of investigation is stressed on p. 51-64. A number of site characteristics of supposed importance to the macromycetes is discussed in greater or lesser detail, as well as the methods by which they have been measured. It has not been possible to publish the original data in detail, but in most cases examples showing typical or extreme situations are given. Only the soil to a depth of 10 cm below the soil-litter interface and the air to a height of 10 cm above the soil surface have been considered, because the conditions here are of major importance to the mycelium and the fruit bodies.

The evidence of a concentration of the mycelium of the macromycetes in the uppermost few cm of the soil under arctic conditions is discussed on p. 66. As a supplement, the vertical distribution of the ectomycorrhizal rootlets in the soil and the depth of the soil under the fruit bodies of a number of species were investigated.

Using a soil corer, a sample was taken from each of the profiles depicted on Figs. 9 and 10, from the surface to a depth of 10 cm. The samples were dissected under a preparation microscope and the number of living ectomycorrhizal rootlets in each layer was counted. Except at DR and Sha, the ectomycorrhizal rootlets were confined to the uppermost few cm of the soil, just below the litter layer. In all cases, the number occurring below 10 cm was negligible.

The depth of the soil was measured in a number of cases where macromycetes occurred on rock ledges. Under the fruit bodies of *Cortinarius mucosus, Hebeloma crustuliniforme, H. mesophaeum, Laccaria* spp., *Leccinum rotundifoliae, Mycena aetites,* and *Rhodophyllus sericeus,* the minimum thickness of the soil layer ranged from 2 to 4 cm, the median from 3 to 13 cm.

The Soil Profile

At each site, a soil profile from the surface to a depth of 10-20 cm was described. The different layers were characterized and their thickness measured. The results are given in Figs. 9 and 10.

At all but one of the sites, the soil was covered by a litter layer of varying thickness. At the majority of the sites, a humus layer occurred, sharply delimited from the underlying mineral soil. At the dry, steeply or gently sloping sites, an upper layer of mull-like appearance gradually merged with the mineral soil.

Fig. 9. Above: soil profiles from the sites investigated. For explanation of the abbreviations see p. $14-24$. For explanation of the signs see Fig. 10 . - Below: pH measured on fresh soil samples, July 1971.

pH

In July 1971, a sample was taken from each of the soil layers in the profiles described. One volume of fresh soil was suspended in two volumes of distilled water and left overnight. The pH of the suspension was measured with a glass and a calomel electrode (Radiometer pH-meter 24). The results are given in Figs. 9 and 10.

At the majority of the sites, especially those situated in the basalt area, pH was slightly below the neutral point. At only a few of those situated in the gneiss area (BLe, BCa, and $-$ partly $-$ Sf), was the soil markedly acid.

Time of Disappearance of the Snow

Due to the differences between the sites as regards depth of the snow and exposure, there was a large variation in the time of the commencement of the snow free period. The time of disappearance of the snow from the permanent quadrates was noted at the regular inspections of the sites.

The snow disappeared from the sites in largely the same order in

Fig. 10. Above: soil profiles from the sites investigated. For explanation of the abbreviations see p. 14-24. Explanation of signs: a: litter; b: relatively undecomposed plant residues; c: mull-like soil; d: humus or peat layer; e: mineral soil. - Below: pH measured on fresh soil samples, July 1971.

all the three years. It melted earliest at DR (1970: before 1.6.; 1971: 20.5.; 1972: 2.-11.5.) and latest at the sites dominated by *Salix herbacea,* especially She (1970: after 18.7.; 1971: ea. 30.6.; 1972: 16.7.-2.8.).

Soil Water Content

Even though in the summer all the sites received equal amounts of precipitation, local differences in soil moisture conditions might be expected to occur, due to differences in slope, exposure, accumulation of snow, soil, vegetation and topography. For this reason, sampling for determination of the soil water content at the individual sites was carried out concomitantly with the inspection of the permanent quadrates. The vegetation and the litter layer were removed, and samples of the uppermost 10 cm of the soil were taken with a soil corer (the vertical moisture gradient in the uppermost 10 cm of the soil was only slight).

The soil water content was measured gravimetrically. It would have been preferable to determine the soil water potential, but the 199 3

Table 19. Median mean soil water content at the sites in Godhavn in each of the growing seasons 1970-72 (g water/100 gloss on ignition). The mean soil water content was determined on the basis of two $(*)$ or three samples taken on each sampling occasion (see p. 33). The sites have been arranged according to increasing median values.

Site	1970	1971	1972
Sha	$272*$	266	305
Sf	300	253	332
	338	300	349
	359	355	390
BCS	362	360	402
BLe	385	331	411
SE	370	381	396
	371	352	424
	$411*$	377	453
	407	405	412
$SHy \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots$	419	425	487
$Shc.$	452	422	507
BGa	499	469	543
Shb	519	473	506
$Ca.$	676*	750	804
	$727*$	770	730

necessary equipment was not available. Besides, it was judged that in no case was the soil water potential so low as to limit the growth and functioning of the mycelium. The content of stones and pebbles varied considerably from sample to sample, even for samples taken at the same site. Therefore, the water retaining capacity was considere more relevant than volume or dry weight as a basis for the calculation of the soil water content. As the mineral fraction of the soils in question was rather coarsegrained, the water retaining capacity must be dependent mainly on the organic matter content. This assumption was supported by the fact that the mean of the water retaining capacity of 35 samples from all the sites was 657 g water/100 g loss on ignition, with a standard deviation of only 26 g.

On each sampling occasion two or (in most cases) three samples were taken at each site. Each soil core (diameter 6.5 cm) was mixed thoroughly, and stones and pebbles removed. The remaining material was weighed, dried at 105°C, weighed again, ignited, and the ash weighed. The water content of the individual samples and the mean for the two or three samples taken was calculated as g/100 g loss on ignition.

In order to compare the sites, Table 19 gives the median mean soil water content for each of the three growing seasons. Fig. 11 gives two examples of the changes in the soil water content in the course of the growing season (DR and S).

Fig. 11. Soil water content. Each point represent the mean of three (in a few cases two) samples from different points within the site. Above: Site DR (southwest exposed slope dominated by *Dryas integrifolia* and *Rhododendron lapponicum).* Below: Site S *(Salix glauca* scrub). x----- x: 1970; o------ o: 1971; $\bullet \cdots \bullet$: 1972. NB! The vertical scale is different between the two graphs. 3*

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At A and Ca, the soil was constantly soaked with water and the water content was generally well above 600 $g/100$ g loss on ignition. At the rest of the sites, the soil water content varied to a greater or lesser extent in accordance with the precipitation conditions. The water content was high in the spring just after the thaw. From then on it decreased in periods of drought and increased after rain, but normally kept between 300 and 500 $g/100 g$ loss on ignition. At those sites which were influenced by run-off from larger areas (BA, BCa, Shb), the increase of the water content following a period of precipitation was often delayed. In all the three years, the sites Sha, Sf, and DR were drier than the rest, with a soil water content often below 300 $g/100 g$ loss on ignition.

In order to describe the moisture conditions in the very surface layer, samples were taken twice a day (9 a.m. and 9 p.m.), for a period of two months, of three moss mats near the Station, one consisting of *Aulacomnium turgidum* and two elf *Hylocomium splendens.* The samples were weighed, dried at 105°C, and weighed again. The water content was calculated as $\frac{0}{0}$ of the dry weight of the moss. In the *Hylocomium splendens-mats,* the water content was very dependent on the precipitation. The water content changed abruptly, from $50-200$ % on dry days to 250-500 $\frac{0}{0}$ on wet days (the lowest and highest value found being 12 and 625 $\frac{0}{0}$ respectively). In the *Aulacomnium turgidum-mat*, the changes were less abrupt; the water content varied between 230 and 721 $\frac{0}{0}$. Sampling was not carried out where the ground was covered by a loose litter layer, but the conditions here must have been similar to those in the Hylocomium splendens-mat.

Soil Temperatures

The temperature at a given depth in the soil—other factors being equal—is determined by the soil profile (which is constant for a given site) and the soil water content (which changes with time). In order to obtain information about the soil temperature at the individual sites, two rod-shaped maximum-minimum thermometers $(-30^{\circ}$ to $+50^{\circ}$ C, accuracy ± 1 °C) were placed at each site, at the soil-litter interface and at a depth of 10 cm respectively. In the spring, as soon as the soil had thawed, these thermometers were set out, in exactly the same position every year. They were removed in the autumn when fruit body production in the quadrates had ceased. The maximum and the minimum temperatures were read concomitantly with the inspection of the quadrates, i.e. approximately once a week.

The spatial variation of the soil temperature within the sites was studied at DR, BCS, S and A. At each of these sites, three to six pairs of thermometers were placed as described above, for a period of four to six weeks. On the basis of the weekly readings, the mean and the standard
		DR							SHy												
week		soil-litter interface						-10 cm					soil-litter interface				-10 cm				
	maximum			minimum		maximum				minimum		maximum		minimum		maximum		minimum			
			1970 1971 1972 1970 1971 1972															1970 1971 1972 1970 1971 1972 1971 1972 1971 1972 1971 1972 1971 1972			
	П		8.5																		
May	Ш		6.0	17.0		-3.0	-3.0														
	IV	$\overline{}$	18.0	26.5			$0.0 - 1.0$	$\overline{}$		6.0			1.0		12.5		0.0				
		$\overline{}$	11.5	16.0		-0.5	-0.5	$\overline{}$	5.0	4.0		0.0	0.0	12.0	15.0	-0.5	0.5				
	и	$\overline{}$	21.5	16.0			$1.0 - 0.5$	$\overline{}$	10.0	6.0		2.0	1.5	21.0	17.0	1.0	0.0		5.0		1.0
June	Ш	$\overline{}$	27.0	17.5	2.5	3.5	-1.0	$\overline{}$	11.0	8.0	0.5	4.0	2.0	28.5	19.5	0.5	0.0	4.0	6.0	0.5	1.0
	IV	22.5	23.0	22.5	0.0	3.0	0.0	11.0	11.0	9.0	2.0	5.0	3.0	21.0	23.0	1.5	1.0	4.5	7.0		$2.0 - 1.5$
		I 25.0	23.0	21.5	1.0	3.5	2.5	11.0	10.5	7.5	5.0	5.5	4.0	22.5	17.0	3.5	2.0	4.5	6.5	3.0	3.0
		II 28.0	30.0	23.0	3.0	3.5	2.0	13.5	13.0	9.5	7.5	6.5	3.5	26.0	19.5	3.0	1.5	6.5	7.5	4.0	2.5
July	Ш	24.0	31.0	27.5	3.5	7.5	5.5	11.0	14.5	12.5	6.0	8.5	7.0	24.5	26.5	5.5	2.0	8.0	8.5	5.5	4.5
	IV	24.0	23.5	20.5	2.0	4.5	1.5	13.0	13.5	11.0	6.5	7.5	3.5	23.5	22.5	2.5	2.0	8.0	7.5	5.0	2.0
		$1\,25.0$	24.5	23.0	4.0	4.5	4.5	12.5	12.5	12.5	7.0	7.5	5.5	23.5	18.5	2.0	3.0	8.0	8.5	6.0	3.5
		II 15.0	25.5	18.5	1.5	4.0	1.0	10.0	12.5	10.0	5.0	6.0	4.5	22.5	15.0	2.5	0.0	7.0	6.5	5.0	2.5
August	Ш	19.0	18.5	18.0	0.5	1.5	1.5	9.5	9.0	7.5	4.5	4.5	4.0	17.5	12.0	0.5	1.5	6.0	6.0	3.5	2.0
	IV	22.0	15.0	18.0	0.0	1.5	0.5	11.0	9.0	7.0	4.0	4.5	3.0	17.0	13.0	-0.5	-1.0	4.5	5.5	3.0	2.0
		$1\quad21.0$	16.0	11.5		$-1.0 - 1.0$	0.5	5.0	9.0	5.0	3.5	3.0	2.0	16.5	7.5	-1.5	4.0	4.5	4.0	2.0	1.0
September	Н	15.0	r	r	-0.5		r	8.5	\mathbf{r}	r	3.0	r	r							r	r

Table 20. Weekly maximum and minimum temperatures during the growing season, at the soil-litter interface and at a depth of 10 cm in the soil, at DR and SHy. The number of the week in the month is indicated by roman numerals. -: no measurement (thermometer not placed because the soil was still frozen). r: thermometer removed for the winter.

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deviation were calculated for the maximum and the minimum temperatures respectively. At the soil-litter interface, the standard deviation varied between 0.2 and 3.8°C. At a depth of 10 cm, the standard deviation varied between 0.3 and 1.8° C. The standard deviation was always low in relation to the mean value, a fact which reflects the homogeneity of the individual sites as regards the soil temperature.

Tables 20 and 21 give a few examples of the course of the maximum and minimum temperature over the growing season. In general, the maximum temperature at the soil-litter interface increased rapidly after the snow had disappeared, reached an absolute maximum in the second half of July or the first week of August, and decreased from about the middle of August. The minimum temperature increased more steadily, but also had a maximum in the second half of July - the beginning of August, followed by a decrease from the middle of August. The first frost occurred at very different times, from the end of July to the end of September. At the soil-litter interface, the frost free period lasted (1-)5-16 weeks. The differences between the three years at the individual sites were almost as great as the variation between the sites in a particular year.

At a depth of 10 cm, the general course of the temperature was similar to that at the soil-litter interface. However, the frost free period began somewhat later. The maximum temperature was lower and the minimum temperature higher, and temperatures below zero had not yet occurred at any of the sites, when the thermometers were removed in the middle of August - the beginning of September.

At DR, Bf, BSi, BLe and SHy, sites with a dry or relatively dry soil, the maximum temperature at the soil-litter interface was high and the temperature range wide. At A and Ca, the wet sites, the maximum temperature was lower and the temperature range relatively narrow. The temperature gradient in the soil was generally steepest during periods with high temperatures and at those sites where the maximum temperature was highest.

In 1972, the course of the soil temperature deviated somewhat from the conditions in 1970 and -71 (see p. 62).

Continuous measurements of soil temperature were taken for periods of three to five weeks at five sites (DR, BCS, S, She, and A) by means of two Lambrecht thermographs fitted with distance wires and a cylindrical temperature-sensitive body 15 cm long (type 257). The temperature sensitive body was placed in the soil in the same way as the maximum-minimum thermometers.

On the basis of the measurements, Figs. 12 and 13 were drawn. They show the percentage of time when the soil temperature was equal to or above a given value, for periods of ten days. Where the tempera40

Fig. 12. $\frac{0}{0}$ of time when the temperature at the soil-litter interface was equal to or higher than a given temperature, for periods of 10 days. Above left: Site S *(Salix glauca* scrub), 1971; above right: Site A (fen with *Aulacomnium palustre),* 1972; centre left: Site BCS (heath with *Betula nana, Cassiope tetragona,* and *Salix glauca),* 1971; centre right: Site She *(Salix herbacea* snow bed, late free of snow), 1972 ; below: Site DR (southwest-exposed slope dominated by *Dryas integrifolia* and *Rhododendron lapponicum),* 1971.

Fig. 13. $\frac{9}{6}$ of time when the temperature at a depth of 10 cm in the soil was equal to higher than a given temperature, for periods of 10 days. Above left: Site S *(Salix* or *glauca* scrub), 1971; above right: Site A (fen with *Aulacomnium palustre),* 1972; centre left: Site BCS (heath with *Betula nana, Cassiope tetragona,* and *Salix glauca),* 1971; centre right: Site She *(Salix herbacea* snowbed, late free of snow), 1972; below: Site DR (southwest-exposed slope dominated by *Dryas integrifolia* and *Rhododendron lapponicum),* 1971.

ture-especially at the soil-litter interface-increases to fairly high values, it is only for relatively short periods. For the sites and periods of time in question, the median temperature at the soil-litter interface was less than 10°C; the temperature exceeded 15°C for less than one fifth of the time. Especially at the beginning of the snowfree period, the proportion of time with high temperatures was low, e.g. at DR in the period 22.-31. May 1971.

At a depth of 10 cm, the temperature parallelled that at the soillitter interface, but exceeded 10°C only at some of the sites investigated and then only for very short periods (less than one fifth of the time).

Air Temperatures

The air temperature 10 cm above the ground was measured by means of four Lambrecht thermographs $(-10 \text{ to } +50^{\circ} \text{C}, \text{accuracy } \pm 1^{\circ} \text{C})$, for varying periods of time in 1970-72, at DR, BCS, S, A, and She. The measurements from 1971 cover the entire growing season at DR, BCS, S, and She and are therefore best suited for a comparison between the sites.

The absolute maximum temperatures measured at these four sites were 28, 30, 27.5, and 29°C respectively. At S, the absolute maximum temperature occurred on 17. June whereas at the other sites, the absolute maximum temperatures occurred on 19.-21. July. This difference is due to the development of the canopy of *Salix glauca* at S at the beginning of July.

On nights with clear skies, the minimum air temperature approached zero within one or two degrees throughout the summer, at all the four sites studied. However, it did not fall below zero from 5. June to 7. September at DR (12 weeks), from 23. June to 21. August at BCS (9 weeks), and from 4. July to 11. August at She (5 weeks). At S, air temperatures below zero occurred three times in the period from 24. June to 20. August.

Saturation Deficit in the Air

The relative humidity of the air 10 cm above the ground was measured by means of two Lambrecht hair hygrographs in 1970 and -71 at the two sites considered extreme in this respect, DR and S. The saturation deficit was calculated as $100\frac{6}{0}$ -r.h. The results from 1971 are given in Fig. 14. Throughout the summer, the saturation deficit at DR reached fairly high values in the middle of the day. At the beginning of the growing season, the maximum values were equal at S and DR, but after the development of the foliage of the willows, the values at S became lower as a result of the lower maximum temperatures. At both sites, the saturation deficit fell to zero on most nights throughout the

Fig. 14. Daily range of saturation deficit in the air 10 cm above ground, Godhavn 1971. Above: Site DR (southwest exposed slope dominated by *Dryas integrifolia* and *Rhododendron lapponicum),* 1. May-8. September. Below: Site S *(Salix glauca* scrub), 5. June-8. September.

summer. The occasional high minimum values are due to the occurrence of warm and dry foehn winds. - At DR the number of hours with a saturation deficit of less than 10 $\frac{0}{a}$ was 8.8 in July and 12.4 in August. At S the corresponding values were 11.5 and 14.4.

The discussion of the site characteristics given above shows that a number of factors of supposed importance to the macromycetes are to a greater or lesser degree intercorrelated. Slope, soil moisture content, soil temperature, and accumulation of snow influence the vegetation and the soil profile which are again mutually dependent. It is to be expected, that the macromycete flora of sites which are similar in a number of site characteristics will also be rather similar. Tables 3-18 show that this is the case.

PHENOLOGY OF THE MACROMYCETE FLORA

Figs. 15 and 16 illustrate the phenology of the macromycete flora in the years 1970-72. The figures show

- 1) Q, the percentage of 144 quadrates where any fruit bodies occurred
- 2) S, the species density $($ = the mean number of species per quadrate)
- 3) I, the individual density $($ = the mean number of fruit bodies per quadrate).

Q, S, and I have been calculated for the litter decomposers plus the mycorrhiza forming species. However, as the *Sclerotiniaceae* were abundant at the beginning of the growing season, the indices have also been calculated for all three groups together until the middle of July.

Q, S, and I have been calculated on the basis of all the fruit bodies observed at each individual inspection without regard to their age. In this way a particular fruit body may have been counted on several occasions and has thus contributed to the Q, S, and I value several times. The lifetime of a fruit body was generally two to three weeks, except in periods of drought and except for the most tiny species, such as *Mitrula gracilis, M arasmius epiphyllus,* and the *Mycena* spp. For most of the time Q, S, and I run parallel to each other; the deviations-e.g. in the beginning of July 1971 and -72-were due to the occurrence of numerous fruit bodies of *Mitrula gracilis* in a few quadrates. The maximum value of S is about 1 in all the three years; however, this is a mean and covers a variety of values, ranging from 0.1 at BCS, SE, and Sf, to 6.8 at A.

Figs. 17 and 18 show the production of fruit bodies as far as it could be estimated on the basis of the position, number and appearance of the fruit bodies in the individual quadrates at the inspections, and some experience as regards the life history of the fruit bodies of the different species.

Figs. 15-18 show the general trends in the phenology of the macromycete flora in Godhavn, and further reveal some differences between the three years which will be discussed on p. 51ff. All the three years, the following aspects could be distinguished:

1. A vernal aspect. In the spring, a vernal aspect occurred, characterized by *Sclerotiniaceae* and a few litter decomposers, mainly *Omphalina* spp. This aspect lasted from the end of May to the beginning of July, depending on the time of disappearance of the snow cover. The very first fruit bodies were found in moss cushions on southerly exposed rocks.

2. An aestival aspect. In the first week of July, the macromycete flora showed a relative maximum which was, however, restricted to the wet, mossy sites. This aspect was characterized by the *Galerina* spp., *Mitrula gracilis* and *Omphalia striatula.* This first peak was followed by a decrease in the middle of July.

3. A seasonal aspect. From the middle of July, the number of species and fruit bodies increased to an absolute maximum in early to mid August. The mycorrhiza forming species made up an increasing proportion of the macromycete flora, at first mainly small species such as *Cortinarius cinnamomeoluteus* and other *Cortinarius* spp., and *Inocybe dulcamara* (but also a few large ones such as *Leccinum rotundifoliae),* later on mainly larger forms such as *Cortinarius mucosus, C. subtorvus*, and *Russula obscura.* In the middle of August, a general decrease set in. After the beginning of September very few fruit bodies were produced, though fruit bodies left over from the maximum could still be found. The growing season in 1971 was definitively disrupted by a heavy snowfall at the beginning of September, but it might also happen-as was the case in 1972—that a fortnight of mild weather later on resulted locally in the production of a few fruit bodies, mycorrhiza forming species as well as litter decomposers.—There is no basis for a subdivision of the seasonal aspect, but it is characteristic that, providing the weather was moist, a number of ephemeral species such as *Mycena* and *Marasmius* spp. occurred in the second half of the seasonal aspect.

Thus the fungus season in Godhavn at maximum lasts four months, from the beginning of June to the end of September. The peak of the season occurs in the first half of August.

At the majority of the sites, most of the species had only a single maximum of fructification in the course of a growing season. At the wet sites, some of the litter decomposers showed two maxima, but most often the reason was that the maximum of fructification did not occur concurrently in all the quadrates. In those few cases where the fructification of a species within a single quadrate showed two more or less distinct maxima separated by a period of several weeks with reduced

Fig. 15. The phenology of the macromycete flora at Godhavn, 1970, in 144 quadrates distributed over 16 sites. Q: the percentage of the quadrates where any fruit bodies occurred. S: species density (= mean number of species per quadrate). I: individual density (= mean number of individuals per quadrate). For further explanation see text p. 44.

or no production of fruit bodies, the explanation was most probably the occurrence of more than one mycelium within the quadrate in question.

The occurrence of a species in one, two or three years in a particular quadrate may be taken as an expression of the frequency of fructification of a mycelium over a longer period. In some instances this term certainly underestimates the frequency because those cases are not counted where fruit bodies originating from a mycelium which partly overlaps the quadrate appear outside the quadrate. On the other hand, for some of the species with small fruit bodies (e.g. *Collybia cirrhata, Mitrula gracilis,* the *Galerina* spp.), the fruit bodies found within a particular quadrate may in some cases originate from several separate mycelia.

Out of 134 cases where a species belonging to the litter decomposers occurred in a particular quadrate, 90 were found in one year only, 25 were

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Fig. 16. The phenology of the macromycete flora at Godhavn, in 144 quadrates distributed over 16 sites. Above: 1971. Below: 1972. Q: the percentage of the quadrates where any fruit bodies occurred. S: species density. I: individual density. For explanation of the signs see Fig. 15.

Fig. 17. Number of macromycete fruit bodies produced between two subsequent inspections, **in** 144 quadrates distributed over 16 sites. Godhavn 1970.

found in two years, and 19 in three years. This corresponds to 67, 19, and 14 per cent of the cases respectively. The frequency of fructification was only slightly lower for the mycorrhiza forming species. Out of 161 cases, 121 were found in one year only, 34 in two years, and 6 **in** three years. This corresponds to 75, 21 and 4 per cent respectively.

As a supplement to the information in Figs. 15-18, Table 22 gives the number of finds made of some of the more easily recognizable species made outside the sites during the three year investigation period, summed up for periods of half a month. Only species which are represented by ten finds or more are included in the table. The data confirm the results from the permanent quadrates: in the spring, the first species to appear belong to the *Sclerotiniaceae,* the next are a number of relatively small litter decomposers—which continue to fruit for the rest of the growing season—and the last are the mycorrhiza forming species. There are, however, deviations from this scheme, especially among those species which have not been included in the table because they were only found on a few occasions.

Fig. 18. Number of macromycete fruit bodies produced between two subsequent inspections, in 144 quadrates distributed over 16 sites. Above: Godhavn 1971. Below: Godhavn 1972. For explanation of the signs see Fig. 17. 199

		litter decomposers		mycorrhiza forming species				
Site	1970	1971	1972	1970	1971	1972		
Sf.			0.1		0.1			
SE			0.2					
BCS					0.3			
$Bf. \ldots \ldots \ldots \ldots$	0.2	0.1	0.1	0.2	0.2			
$BSi \ldots \ldots \ldots$	0.2			0.4	0.1	0.1		
$BCa \ldots \ldots \ldots$	0.2	0.1	0.3		0.5	0.2		
$Shc. \ldots \ldots \ldots \ldots$	0.1				0.8			
$SHy \ldots \ldots \ldots \ldots$	\sim	0.1		1.1	1.3	0.1		
$Sha \ldots \ldots \ldots$	0.8			0.8	0.3	0.3		
BLe	1.5	0.5	1.4		0.3	0.2		
$DR \ldots \ldots \ldots \ldots$	0.3	0.2	0.4	1.4	0.6	0.5		
BA	1.4		1.0	0.8				
Ca.	1.4	1.6	1.6	0.6	0.6			
S.	0.6	1.4°	0.3	0.6	1.5	0.2		
$Shb \ldots \ldots \ldots \ldots$		0.5		0.3	3.0	1.0		
A.	5.0	5.8	3.0	1.8	3.2	0.6		

Table 22. Mean number of litter decomposers and mycorrhiza forming species per quadrate, calculated for each site and year. The sites have been arranged according to increasing mean number of species. $-$: no fruit bodies produced.

This applies e.g. to *Ciboria polygonum-vivipari* (belonging to the *Sclerotiniaceae)* which did not appear until the first half of August. Some of the litter decomposers, e.g. the *Mycena* spp., the *Clitocybe* spp., and *M arasmius epiphyllus* were restricted to the second half of August and the beginning of September. Among the mycorrhiza forming species there was also a certain spread as regards the time of fructification. *Leccinum rotundifoliae* appeared as early as the middle of July, but ceased fruiting relatively early. On the other hand, *Cortinarius mucosus*which also started early in the summer under appropriate weather conditions-continued fruiting into the second half of September.

It is interesting that among the mycorrhiza forming species several large and conspicuous ones were not found at all in the Godhavn area in one or two of the years. *Lactarius torminosus* and *Russula delica* were found only in 1971, and *Russula aeruginea* was not found in 1972.

It may be questioned how typical the growing seasons in 1970, -71 and -72 were and, as a consequence, how representative the observations on the phenology of the macromycetes are for the investigation area. Table 23 shows the monthly precipitation, mean maximum and mean minimum temperature for the months May-September in 1970-72, compared with the mean for the years 1962-69. As regards the temperature in the months June-August only 1971 can be considered normal.

Table 23. Precipitation (mm), mean minimum and mean maximum temperature (⁰ C) for the months May-September in Godhavn. Mean for the eight year period 1962-69 compared with the years 1970, -71 , and -72 .

1970 and especially 1972 were colder than usual. The growing season was somewhat drier than normal in 1971, whereas it was more rainy in 1970 and -72 . It is most likely that out of the three years, 1971 is the year, in which the fructification of the macromycetes is most representative for the area.

THE FRUCTIFICATION

IN RELATION TO SOME ENVIRONMENTAL FACTORS

Figs. 15-18 show that there were in the investigation area as a whole considerable differences between the fructification of the macromycetes in the three years 1970-72. The most marked differences are in the time of the appearance of the first fruit bodies, which was earlier in 1971 and -72 than in 1970; the maximum value of Q, S and I which was highest in 1971 and lowest in 1972; and the reduced production of fruit bodies, in particular of the mycorrhiza forming species, in 1972 as compared to 1970 and -71. However, the differences were not identical at all the sites.

Table 24 gives, in the individual years, the mean number of litter decomposers and mycorrhiza forming species per quadrate at the different sites as an index of the fructification. The index has not been calculated for the *Sclerotiniaceae* because this group was only poorly represented at the majority of the sites. The mean number of species per quadrate was chosen as an index because it is independent of the size or the number of fruit bodies of the species involved. Except for BLe, the mean number of species per quadrate varied in accordance with the estimate of the dry weight of the fruit bodies produced (cfr. p. 28).

As shown in Table 24, the mean number of species per quadrate was in most cases very low. Under these circumstances a difference of 0.5 between the year with the highest number of species per square meter and another year was considered significant. This difference corresponds to the occurrence of one species fewer in half the quadrates.

4*

Species	June			July		August	September		
	I	$_{II}$	I	П	I	$_{\rm II}$	Ι	П	
Monilinia rhododendri	7	3							
Sclerotinia vahliana	5	7	5	$\mathbf{1}$					
$Ciboria$ amentacea	$\overline{2}$	7			1				
Omphalina rustica	1	5	6	8	9	3			
$O.$ luteovitellina		5	10	4	6	4	1	1	
Leptoglossum lobatum		$\overline{2}$	6	9	8	4	$\overline{2}$		
Cortinarius cinnamomeoluteus		3	9	7	8	1			
$Arrhenia\ auriscal pium \ldots \ldots$		$\mathbf{1}$	6	3	8	5	$\overline{2}$		
Omphalia striatula		1	$\mathbf{1}$	4	$\mathbf{1}$	$\overline{2}$	1		
Galerina heterocystis		1	7	9	14	3			
$G.$ moelleri		1	3	4	6	$\overline{2}$	4	1	
Omphalina umbellifera			$\overline{2}$	5	5	$\overline{2}$			
$The lephora \, radiala \ldots \ldots$			$\overline{2}$	4	7	5	$\overline{2}$		
$Hebeloma$ mesophaeum			\mathbf{a}	9	13	10	7	$\overline{2}$	
$Laccaria$ $laccata$			$\mathbf{1}$	4	$\mathbf{1}$	$\mathbf{1}$	$\overline{2}$	1	
$Hebeloma$ crustuliniforme			$\mathbf{1}$	8	3	11	$\overline{2}$	$\mathbf{3}$	
Cortinarius subtorvus			$\mathbf{1}$	6	16	8	4		
$Leccinum$ rotundifoliae				10	13	9			
$Lactarius$ uvidus				7	$\overline{5}$	5			
$Inocybe\ dulcamara \ldots \ldots$				5	$\overline{5}$	4			
$Cortinarius \ alpinus \ldots \ldots$				6	5	5			
Lactarius dryadophilus				3	10	7			
$Laccaria$ altaica				3	4	3	1		
$Rhodophyllus$ sericeus				4	9	9	1	$\mathbf{1}$	
$Lactarius$ mitissimus $\ldots \ldots$				$\overline{2}$	5	4	$\overline{2}$		
A manita vaginata				1	6	3	1		
Cortinarius mucosus				6	9	9	6	5	
others $(55$ species)	5	7	10	22	52	55	22	5	
Total number of finds	20	43	73	154	229	172	60	19	
Total number of species	8	16	23	40	50	53	27	11	

Table 24. Number of finds of some macromycetes, calculated for periods of half a month. Godhavn 1970-72.

At five sites (Sf, SE, BCS, Bf and BSi) there were so few macromycetes that it was impossible to state any difference between the years. At the remainder of the sites, the fructification of either the litter decomposers or the mycorrhiza forming species, or both, was significantly lower in one or two years as compared with the year with maximum fructification. In most cases, a reduction occurred in 1972, and either in 1970 (She, S, Shb and A) or 1971 (Sha, BA and DR).

The fructification is compared with a number of environmental factors of supposed importance for the fructification of the macromycetes. Those cases are noted where a reduction of the fructification occurred concomitantly with values of a given factor which were markedly lower than the values measured in the year with maximum fructification. The evidence of a limiting effect of the different factors on fructification obtained in this way must be discussed in the light of knowledge from other sources as concerns the requirements of the macromycetes (p. 65-67)

A statistical treatment of the material was impossible due to the limited number of sites and the fact that some of the environmental variables were not measured in each growing season at all the sites. It would also have been preferable to take into account the fructification of the individual species, but this was not feasible because the majority of the species was found within the quadrates only at a few sites. Instead, each of the three biological groups *(Sclerotiniaceae,* litter decomposers, and mycorrhiza forming species) has been treated as an entity.

Time of Disappearance of the Snow

In 1970, the snow disappeared from the majority of the sites at the same date and simultaneously from all the quadrates at the individual sites. In 1971 and especially in 1972, the melting of the snow took place over a prolonged period of time, even within the sites. However, in general the snow disappeared earliest in 1972 and latest in 1970. Reduced fructification occurred concomitantly with late disappearance of the snow at A (1970) and the three snow-bed sites (Sha 1971 and -72 , Shb 1970, and She 1970 and -72), and considering the mycorrhiza forming species- BCa (1970).

The late appearance of the *Sclerotiniaceae* in 1970 as compared with -71 and -72 (Figs. 17 and 18) is due to the difference **in** time of disappearance of the snow.

Precipitation

The precipitation in the months May to September is given in Table 23. July and August must be considered the most important with relation to the fructification of the macromycetes. However, the fructification in the investigation area as a whole in the three years is neither correlated with the sum of precipitation in July nor August, nor in the two months together.

The distribution of the precipitation on the days of the months is shown in Fig. 19. In the middle of the summer there is a tendency for the precipitation to occur on one or a few consecutive days, followed by a period of drought lasting one to several weeks. In 1970 there was one period of drought lasting two weeks at the end of June and one lasting three weeks in July. In 1971 there was one period of five weeks in June-July, and one of two weeks in the second half of July. Comparing Figs. 17 and 18 with Fig. 19 it appears that the periods of drought

Fig. 19. Daily precipitation (mm) in the period May-September, measured at the Geophysical Observatory in Godhavn. Above 1970. In the middle: 1971. Below: 1972.

at the beginning of August 1970 and in the middle of July 1971 were followed by a decrease in the production of fruit bodies of litter decomposers, but this decrease was mainly due to the decrease of a single species, *Mitrula gracilis,* at Site A. Thus, the periods of drought did not result in a general reduction of the fructification in the rest of the growing season. In 1972 there were three drought periods: one of two

weeks at the end of June, one of almost three weeks in July, and one of two weeks at the beginning of August. On the basis of experience from the two previous years it is considered that the general reduction of the fructification in 1972 should not be attributed to any of these drought periods, in particular because fructification was also reduced at A and Ca, the two wettest sites.

Soil Water Content

It was observed that when the soil water content at a site was less than 300 $g/100 g$ loss on ignition (cp. p. 33-36), no fruit bodies were produced. This points to the soil water content as a factor limiting fructification. However, the value 300 g water/100 g loss on ignition may be regarded the minimum value for the fructification of the least exacting species. It must be assumed that some species require a higher soil water content for fructification, especially those which are confined to sites where the soil moisture content is generally high. Therefore the absolute soil water content has not been considered, but at each individual site, the fructification has been compared with the variation of the soil water content over the three growing seasons. Reduced fructification occurred concomitantly with a low soil water content in the case of the mycorrhiza forming species at DR (1971), the litter decomposers at BA (1971) and BLe (1971), and both groups of macromycetes at Sha (1971 and -72).

Solar Radiation

The solar irradiance (wavelenghts $0.3-2.5 \mu m$) on a horizontal surface at ground level was measured by means of a Kipp & Zonen solarimeter. The measurements cover largely the period from when the quadrates became free of snow until the first fall of snow in autumn which persisted on the ground for some days.

The daily solar irradiance is given in Figs. 20 and 21. The figures reveal considerable differences between the years, especially as regards June and July. The number of days in June (in 1970 only from 9. June), July and August with an irradiance higher than 600 cal/cm2 was in 1970, -71 and -72 13, 4 and 0 respectively, and the number of days with an irradiance higher than 500 cal/cm² 28, 21 and 8. On the other hand, the number of days with an irradiance less than 100 cal/cm² was 3, 5 and 12 respectively. An important feature seems to be the extremely low radiation values at the end of July-beginning of August 1972 (Fig. 21).

The importance of the solar irradiance in relation to the phenology of the macromycetes is due to its influence on the soil temperature. In Godhavn, the relationship between the solar irradiance and the soil

Fig. 20. Daily solar irradiance (wavelengths $0.3-2.5 \mu m$) measured at the Arctic Station, 9. June-13. September 1970.

temperature (as expressed by the temperature sum) was studied. The temperature sum is an integrated expression of the temperature conditions which is defined here as

$$
\Sigma_n (T-T_t), \, \text{when} \, \, T > T_t
$$

 $n = 24$ hours. T is the hourly temperature values, and T_t is a threshold temperature which here is 0° C. The temperature sum is given as degreehours. The daily temperature sum may be visualized as the area which on a thermograph sheet is circumscribed by the temperature curve, the vertical lines indicating O and 24 hours, and the horizontal line indicating the threshold temperature (here 0° C).

Figs. 22 and 23 show the relation between the daily solar irradiance and the daily temperature sum in the soil at DR, BCS, S, A and She (for description of the temperature measurements see p. 39). At the soil-litter interface, a positive correlation of greater or lesser significance can be stated between the daily solar irradiance and the daily temperature sum, for days with a minimum temperature above 0°C. At a depth of 10 cm, the correlation is less obvious. At S the daily temperature sum is more closely correlated with the time since the beginning of the frost free period.

Fig. 21. Daily solar irradiance (wavelengths $0.3-2.5 \mu m$) measured at the Arctic Station. Above: 29. May-9. September 1971. Below: 7. May-30. September 1972.

The conclusion must be that the marked differences between the growing season in 1970, -71 and -72 as regards the daily solar irradiance values must, at least at some of the sites, have resulted in correspondingly marked differences in the soil temperature. These differences are reflec-199 $\overline{5}$

Fig. 22. The relation between daily solar irradiance and daily temperature sum at the soil-litter interface. Filled-in symbols indicate days with minimum temperature *(continued p. 59)*

Fig. 23. The relation between daily solar irradiance and daily temperature sum at a depth of 10 cm in the soil. Filled-in symbols indicate days with minimum temperature $\langle 0^{\circ}$ C. Above left: Site S *(Salix glauca* scrub), 1971; above right: Site A *(fen*) with *Aulacomnium palustre),* 1972; centre left: Site BCS (heath with *Betula nana, Cassiope tetragona,* and *Salix glauca),* 1971; centre right: Site She *(Salix herbacea* snow-bed, late free of snow), 1972; below: Site DR (southwest-exposed slope dominated by *Dryas integrifolia* and *Rhododendron lapponicum),* 1971.

< 0°C. Above left: Site S *(Salix glauca* scrub), 1971; above right: Site A (fen with *A ulacomnium palustre),* 1972; centre left: Site BCS (heath with *Betula nana, Cassiope tetragona,* and *Salix glauca),* 1971; centre right: Site She *(Salix herbacea* snow-bed, late free of snow), 1972; below: Site DR (southwest-exposed slope dominated by *Dryas integrifolia* and *Rhododendron lapponicum),* 1971.

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ted e.g. by the weekly maximum and minimum temperatures which are discussed in the following section.

In order to see whether there was a correlation between the sum of solar radiation received over the whole growing season and the fructification, the sum of solar irradiance was calculated for the period from the disappearance of the snow to 1. September, for each year and each individual site. Even though the snow in general disappeared earliest in 1972 and latest in 1970, the sum of solar radiation received in the period mentioned was at the majority of the sites approximately equal in the three years. Reduced fructification occurred concomitantly with a low sum of the solar irradiance only as regards the mycorrhiza forming species at She (1970 and -72) and both groups of macromycetes at S (1972) and Sha (1971 and -72).

Soil Maximum and Minimum Temperatures

From a biological point of view, maximum and minimum temperatures are not very appropriate parameters except when they are close to the tolerance limits of an organism. However, weekly maximum and minimum temperatures were the only temperature parameters available for at least one, and in most cases three growing seasons, from all the sites. Besides it must be expected, that a number of other temperature parameters are to a higher or lesser degree correlated with the maximum and the minimum temperature.

An attempt was made to determine the temperature range within which fructification of the macromycetes occurred. At each site where maximum and minimum temperatures were available for a particular year, the time was established when the first and the last fruit bodies appeared, as well as the corresponding weekly maximum and minimum temperature. Table 25 gives the minimum, the median, and the maximum value of these maximum and m·nimum temperatures. In a number of cases, the maximum and the minimum temperature had in a period prior to the appearance of the first fruit bodies been equal to or even higher than at the time of fructification. This may indicate that a period with temperatures above a certain level is required for at least some species to fruit, but the cause may also be e.g. unfavourable moisture conditions. The minimum and median values quoted in Table 25 are certainly rather representative, whereas the maximum values are to a higher degree determined by the temperature conditions in the particular investigation period.

The time of appearance of the first fruit bodies of *Sclerotiniaceae,* litter decomposers and mycorrhiza forming species ranged from the last week of May to the second week of August, from the second week of June to the second week of September, and from the last week of June

to the third week of August respectively. The time of appearance of the last fruit bodies of litter decomposers and mycorrhiza forming species ranged from the last week of July to the second and the third week of September respectively. With this background it is noteworthy that there is a rather high degree of similarity between the three groups as concerns the maximum and minimum temperatures under consideration.

Fruiting took place both at the beginning and at the end of the growing season, even if the minimum temperature at the soil-litter interface fell below zero. The lowest maximum temperatures stated here at the time of appearance of the first fruit bodies ranged from 10.0 to 12.5°C, the median maximum temperatures from 15.0 to 18.0°C. For the *Sclerotiniaceae,* the conditions at the time of appearance of the last fruit bodies have not been considered. The lowest as well as the median maximum and minimum temperatures at the time of appearance of the last fruit bodies of litter decomposers and mycorrhiza forming species were only slightly lower than the corresponding values stated for the appearance of the first fruit bodies.

At a depth of 10 cm, both the maximum and the minimum temperature at the time of appearance of the first fruit bodies of *Sclerotiniaceae* was in some cases zero or below. This is in accordance with the fact that the sclerotia are situated at the soil-litter interface or just below the surface of the litter layer. - For the litter decomposers and the mycorrhiza forming species, the lowest maximum temperatures at the time of appearance of the first or the last fruit bodies ranged from 4.0 to 5.0°C, the median maximum temperatures from 7.0 to 9.5°C. The lowest minimum temperatures ranged from 0 to 1.5°C, the median minimum temperatures from 3.5 to 4.5°C.

It must be assumed that the range of maximum and minimum temperatures permitting fruit body formation varies between the species and that the more exacting species occur preferably at the warmest sites. Therefore, the difference in fructification between the years has, at the individual sites, been compared with the differences in range and course of the maximum and minimum temperatures, the absolute values have not been considered.

At a number of sites there was in the last week of July 1972 a fall of the minimum temperature at a depth of 10 cm in the soil. The decrease was only 1.0-4.5°C relative to the minimum temperature measured in the previous week, but may nevertheless have been of importance, particularly because the minimum temperature at this depth in the soil ought to be at its peak at this time of the year (cfr. Tables 20-21). Concomitantly, there was in 1972 a reduction of the fructification of the mycorrhiza forming species at DR, BA, SHy and She, of the litter decomposers at Sha, and of both groups of macromycetes at A. Most probably a similar agreement could have been stated for the sites S, Ca and Shb if information about soil temperature had been available not only for 1972, but also for 1970 and $-71.$ - In the same period there was a fall of up to 1.5°C of the maximum temperature at a depth of 10 cm, and a decrease of the maximum and minimum temperature at the soil-litter interface of 1.0-7.5 and up to 3.0°C respectively. However, as compared with the absolute values and the normal conditions, the decrease is considered less important in the case of these parameters.

At the soil-litter interface, the frost free period began in general latest in 1970. Reduced fructification occurred concomitantly with a short frost free period at least as regards the mycorrhiza forming species at BCa (1970), SHy (1972), and She (1970 and -72), and $-$ as regards both groups of macromycetes-A (1972).

The Development of ihe Foliage of the Mycorrhiza Associates

The development of the foliage of *Betula nana, Salix glauca, S. herbacea* and *S. arctophila* was studied. The method was not very accurate, but sufficient for the purpose. At each inspection, an estimate was made for the individual quadrates,

a) (in the spring) of the percentage of the canopy of each species which had developed

b) (in the autumn) of the percentage of the canopy of each species which was still green.

For each site, the mean of the estimates from the individual quadrates was calculated. On the basis of these mean values, the time in the spring when $75 \frac{0}{0}$ of the foliage had developed was calculated, as well as the duration of the period from this time and until the time in the autumn when $25 \frac{0}{0}$ of the canopy had changed colour. These calculations were made for each site, for each of the three years.

In relation to the time of disappearance of the snow, there was a general retardation of the development of the foliage in -72 as compared with the two previous years. This retardation must be due to the low radiation values encountered in -72 . The period from the disappearance of the snow and until 75 *°lo* of the foliage had developed lasted for *Betula nana* 5 to 9 weeks, in 1970 and -71 3 to 6 weeks; for *Salix glauca* 4 to 9 weeks as compared with 2 to 6 weeks, and for *Salix herbacea* 1 to 6 weeks as compared with 2 to 5 weeks. As a result, $75 \frac{0}{0}$ of the foliage had developed earliest in 1971 and approximately at the same time in the two years -70 and -72. However, the difference in most cases did not exceed a single week. - Only at Shc, the fructification varied in accordance with the time of the development of $75 \frac{0}{0}$ of the foliage. This event took place on 8. and 18. August in 1970 and -72 respectively, and on 15. July in 1971.

The period from the time in the spring when $75 \frac{0}{0}$ of the foliage had developed until in the autumn 25 *°lo* of the canopy had changed colour lasted 6 to 10 weeks for *Salix glauca,* 6 to 9 weeks for *Betula nana,* 8 to 9 weeks for *Salix arctophila,* and 4 to 10 weeks for *Salix herbacea.* As regards *Betula nana* and *Salix herbacea* there was a tendency for the period to be longest in 1971 and shortest in 1972. For *Salix glauca,* the period was slightly shorter in 1970 than in -71 and -72 . However, in most cases the difference did not exceed one week. Only in the snow-bed communities (Sha, Shb, and She), did a reduction occur of the fructification of the mycorrhiza forming macromycetes together with a marked reduction of the period when the deciduous mycorrhiza associates were developed and green.

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The fructification of the macromycetes at the sites in the Godhavn area may be positively correlated with a number of factors, among which the soil water content and the soil temperature (and the solar irradiance) seem to be the most important. A positive correlation with the duration of the frost free period and the development of the canopy of the deciduous mycorrhiza associates may also occur. The greatest number of cases of agreement stated between reduced fructification and low values of a particular factor was in 1972 between fructification and the minimum soil temperature (and the daily values of solar irradiance); in 1971 between fructification and soil water content; and in 1970 between fructification and the time of disappearance of the snow, mainly in the snowbed communities.

DISCUSSION

In this section, the results of the investigation in Godhavn are discussed and compared with the results of other investigations from the Arctic and a few representative investigations from the temperate forest zone, mainly Denmark and southern Sweden. The justification for making this comparison is that both the Godhavn area as a whole and the areas in the temperate zone referred to are characterized by the occurrence of shrubs or trees able to form ectotrophic mycorrhiza.

Godhavn is situated just south of the borderline between the low and the high Arctic and is characterized by the occurrence of willow scrub and a mean temperature in July above 5° C. The climate is fairly, but not extremely humid in relation to the total range of precipitation within the Arctic. Like the rest of the ice-free coastal fringe of Greenland, the Godhavn area is mountainous. Conditions comparable with those prevailing in the large bogs and meadow tundras in North America and Eurasia are only encountered locally, e.g. the sites A and Ca.

One of the most characteristic and important features of the Arctic is the brevity of the growing season. The duration of the frost free period in the soil (or possibly the duration of the period with continuous frost (MOSER, 1958)) may influence the composition of the macromycete flora. In Godhavn, the ground is snow-covered for about eight months, and at the soil-litter interface, the frost free period under normal conditions ranges from two to four months. In the temperate forest zone, the duration of the frost free period at the soil-litter interface in beech and spruce forest may be six to seven months (NIHLGARD, 1969; unpublished data from the Danish IBP-project, section PT), in open bog vegetation six months (LANGE, 1948a). - One of the effects of the brevity of the growing season in the Arctic is the limited period when the foliage of the deciduous mycorrhizal associates is developed and functioning, in Godhavn about two months (p. 63). M0LLER (1965) has tabulated the mean date for full leafing and for fifty per cent leaf fall for a number of deciduous tree species in Denmark. For species with ectotrophic mycorrhiza, the period between these two events ranges from $4^{1/2}$ to $5^{1/2}$ months.

Another feature characteristic of the Arctic is the potentially high values of solar irradiance in the middle of the year, i.e. the beginning of the growing period. The potential solar irradiance at the latitude of Godhavn is ea. 1,000, 900 and 650 cal/cm2/day in June, July, and August respectively (cp. GATES, 1962). However, the atmosphere and local conditions may reduce the solar radiation considerably before it reaches the ground (Figs. 20 and 21). Thus the steep mountains just north of Godhavn hide the midnight sun. On overcast days, the solar irradiance is of course low, but this may also be the case on bright days, because-in Godhavn as in other coastal areas in the Arctic-mist may often roll in from the sea in the morning and withdraw again only after noon. The daily solar irradiance in Godhavn during the growing season is about twice the values measured e.g. in Denmark during the fungus season (August ca. 375, September ca. 230, October ca. 130 cal/cm²day, unpublished data from Højbakkegård, Denmark). However, the effect on soil temperature of equal amounts of radiation is different in the open arctic vegetation from in a temperate forest, where only a low proportion of the radiation penetrates the canopy and reaches the forest floor $(3-4)$ ⁰/₀ under beech and spruce (NrnLGARD, 1969)).

During the growing season, the temperature range at the soil-litter interface and in the uppermost few centimeters of soil is not very different in the Arctic from in a temperate forest. In southern Sweden, NrnLGARD (1969) found maximum temperatures at the soil-litter interface under beech and spruce from 18 to 20°C and a highest minimum temperature of 10 to 12°C. In Denmark, the values 21 and 12.5 to 14.5°C respectively have been measured in a beech forest (unpublished data from the Danish IBP-project, Section PT). LANGE (1948a) found a maximum temperature of 24°C and highest minimum temperature of 7°C in the moss layer in a more open vegetation. Comparable and even higher maximum temperatures were measured in Godhavn (see Tables 20 and 21), whereas the highest minimum temperatures were only slightly lower than those reported from the temperate forest zone. However, there are several important differences between the temperature regime in and below the open arctic vegetation and in a forest in the temperate zone:

The first point is that even though fairly high maximum temperatures occurred at some of the sites in Godhavn, these temperatures prevailed only for short periods of time (p. 42). In general the soil temperature was low as compared with the optimum temperature for the

growth of the mycelium of the macromycetes. For a number of species from the temperate forest zone, BoHus (1957) found an optimum of approx. 25°C; FRIES (1949) found an optimum of 20 or 25°C for the majority of eighteen *Mycena* spp. DEBAUD (1973) states that the optimum temperature for mycelial growth was close to 18°C for a number of alpine *Clitocybe* spp. A temperature of 30° C was lethal, whereas 4° C suppressed growth only temporarily. FLANAGAN & SCARBOROUGH (1974) state that the sterile mycelia which made up a large part of the soil microflora at the U.S. Tundra Biome sites and which, due to their ability to decompose cellulose and lignin, and the occurrence of clamp connections were considered basidiomycetes, in no case showed any particular adaptations, e.g. psychrophilism. - An attempt was made to delimit the temperature range within which fruiting occurred in the Godhavn area (p. 60). Fruit bodies were formed even when at the soillitter interface the minimum temperature fell below zero and the maximum temperature did not exceed 7.5 to 12.5°C. At a depth of 10 cm, the corresponding minimum and maximum temperatures were (for the litter decomposers and the mycorrhiza forming species) 0 to 1.5°C, and 4.0 to 5.0°C respectively. However, the values quoted must refer to the least exacting species.

A second point is that in the Arctic, the vertical temperature gradient in the soil is very steep - consequently the biological activity is limited to the uppermost few centimeters of the soil. This applies also to the macromycetes. Downing & WIDDEN (1974) state that the maximum concentration of mycelia (of all types of fungi) in arctic soils occurs only a few cm below the surface. With mycorrhiza forming species, MILLER & LAURSEN (1974) found conspicuously high numbers of clamped hyphae in the top 1-2 cm in plant communities with a high proportion of ectomycorrhizal rootlets (they point out, however, that e.g. *Russula* and *Lactarius* do not form clamps and that not all clamp-forming basidiomycetes form ectotrophic mycorrhiza, e.g. the genera *Coprinus, Galerina* and *Psilocybe).* - An investigation in Godhavn of the vertical distribution of the ectomycorrhizal rootlets in the soil and of the depth of the soil under fruit bodies of a number of macromycete species emphasizes also the relative importance of the uppermost few centimeters of the soil $(p. 31)$.

A third point is that while in a temperate forest, the horizontal and the day to day variation of the temperature at the forest floor and in the soil is relatively small, this is not the case in the Arctic. In Godhavn it was demonstrated that at least at the soil-litter interface there was a positive correlation between the daily solar irradiance (wavelengths 0.3-2.5 μ m) and the soil temperature, as expressed by the daily temperature sum (p. 56). HANSEN (1973) states that the maximum and minimum temperatures at the soil surface are strongly correlated with exposition and vegetation. In Godhavn the dry, more or less steeply southwards sloping sites had high temperature maxima and a broad daily and weekly temperature range, whereas the level, wet sites had lower maximum temperatures and a more narrow temperature amplitude (p. 39).

The monthly precipitation in Godhavn in the growing season was $50-60$ mm. As in the case of the solar radiation, the effect of equal amounts of precipitation is different between the low, open arctic vegetation and a temperate forest. In a close forest, the interception in the canopy during the growing season amounts to $30-45$ % of the total precipitation, depending on the tree species (WILKINS & HARRIS, 1946). On the other hand, the evaporation from the soil surface and the field layer must be higher in the Arctic, due to the impact of the wind and the higher saturation deficit of the air. The mean number of hours per day, with a saturation deficit less than 10 $\frac{0}{0}$, is given on p. 44 for the two sites in the Godhavn area considered extreme in this respect, DR and S. In the temperate forest zone, the mean number of hours per day in the fungus season with a saturation deficit less than 10 $\frac{0}{0}$ is often higher than the values found in Godhavn, in e.g. a Danish beech forest 17.7 hours in the period August-September and 22.0 hours in October (unpublished data from the Danish IBP-project, section PT).

As a result, when there is no precipitation, the moss and the litter layer dries out very rapidly at those sites in the Godhavn area where there is not a constant seepage of water from below (p. 36). This makes the moss and the litter layer an unsuitable substrate for the macromycetes and may be one of the causes of the small representation of the litter decomposers (p. 28). The soil is less rapidly desiccated and the vertical moisture gradient in the uppermost 10 cm of the soil is only slight. It is estimated that during the investigation period, the water content of the soil did not fall to values too low for the growth of the vegetative mycelia at any of the sites in Godhavn (cp. GRIFFIN, 1972), but that it was locally, for certain periods of time, too low for the production and maintenance of macromycete fruit bodies.

In view of the marked differences between the Arctic and the temperate forest zone as regards a number of environmental factors of importance to the macromycetes, it is not surprising that there also exists a number of qualitative and quantitative differences as regards the macromycete flora.

One of the more obvious differences is the general reduction of the macromycete flora as one goes north from temperate into arctic areas, locally as well as regionally. The diversity of the macromycete flora at a given site may be expressed by the mean number of species found per unit area over a period of some years. A comparison between the Godhavn area and Maglemose in Denmark (LANGE, 1948a) shows that the number of species found per square meter over a three year period was lower at the sites in Godhavn (0.1-10.6, median 2.3) than in the plant communities in Maglemose $(4.2-17.3, \text{ median } 10.3)$. - LANGE (1957) reports the number of species per square meter, observed on a single occasion, for various plant communities at lvigtut, Godthab and Sdr. Strømfjord on the west coast of Greenland. These values $(0.6-6.2)$ from lower latitudes still within the Arctic are not necessarily maximum values, but they correspond to the maximum values in Godhavn (0.1-6.8). - The low constancy percentages found in Godhavn (p. 28) indicate that not only is the number of species low, but the mycelia of the individual species occur also rather sporadically.

In the Arctic, the number of species of mosses and particularly of flowering plants is low and there is a general reduction in quantity of the net primary production as compared with the temperate forest zone. This implies a reduction of the niche diversity for the litter decomposers. The complete absence of wood-decomposing macromycetes from the tundra mentioned by VASSILKOV (1967) is a result of this. The small representation of litter decomposers as compared with mycorrhiza forming species in Godhavn (p. 28) may also partially be explained by the reduction in diversity and quantity of the substrate available. The relative paucity in litter decomposing macromycetes seems to be a general feature of the macromycete flora of the Arctic.

The frequency of fructification of the litter decomposers and the mycorrhiza forming species in the three year investigation period in Godhavn is discussed on p. 46. For comparison, LANGL (1948a) in Maglemose in Denmark found for seven fleshy species, that out of 173 cases where a species was observed in a particular quadrate, the species was found in one year in 42 $\frac{0}{0}$ of the cases, in two years in 41 $\frac{0}{0}$ of the cases, and in three years in 17 $\frac{0}{0}$ of the cases. For thirteen ephemerous species, the corresponding values-based on a total of 405 cases-were $25, 29$ and 46 $\frac{0}{0}$. The mycorrhiza forming species in the present investigation are equivalent to LANGE's fleshy species and the litter decomposers correspond to his ephemerous species. In the Godhavn area as a whole, the mycelia of the litter decomposers and the mycorrhiza forming species fruited with almost equal frequency (p. 48), whereas LANGE found that in Maglemose the ephemerous species were more constant than the fleshy species (l.c. p. 125). This may be a general difference between the Arctic and the temperate forest zone. - The mycelia of both litter decomposers and mycorrhiza forming species in Godhavn had only one peak of fructification in the course of a growing season (p. 45), as opposed to many macromycetes in the temperate forest zone.

An estimate of the dry weight of fruit bodies produced per unit area per year has been given on p. 28. For comparison, KALLIO (1972) in Finland found the dry weight of fruit bodies produced in a mountain heath with low birches to be 0.652 kg/ha/year, in a pine forest 4.023 kg/ha/year, and in a birch forest 10.970 kg/ha/year (corresponding to 65, 400 and 1,100 mg/m2/year). RICHARDSON (1970) found for a Scottish pine forest a fruit body production corresponding to 2,650-4,590 mg/m²/ year, BoHus & BABOS (1960) in Hungary for various types of deciduous forest 70-13,200 mg/m2/year, and HERING (1966) in northern England for oak and mixed broadleaved forests on various soil types from 30 to 950 mg/m^2 /year. Thus, at the majority of the sites in Godhavn, the dry weight of fruit bodies produced per unit area per year was lower than in forests in the temperate zone, but locally fruit body production amounted to values equal to or even higher than those found for temperate forests.

In the Arctic, the phenology of the macromycete flora is influenced by the brevity of the growing season. VASSILKOV (1967) mentions that in the tundra it is not possible to distinguish between different aspects of the macromycete flora. However, in Godhavn a vernal, an aestival, and a seasonal aspect could be discerned $(p. 45)$. - LANGE (1957), in a chapter on the periodicity of the macromycete flora in West Greenland, states that the peak of the fungus season in Ivigtut $(61^{\circ}15' \text{ N})$ occurred in the first half of September and in Godthåb $(64^{\circ} N)$ at the very beginning of September. In Sdr. Strømfjord (67° N), the maximum seemed to occur as early as around 1. August, the subsequent decline being due to the very dry summer and autumn in this area. The present investigation confirms the reported trend for the peak of the fungus season to occur earlier the further north one goes, in Godhavn in the first half of August.

Numerous investigations from the temperate forest zone have demonstrated a positive correlation between precipitation and the fructification of the macromycetes. LANGE (1948a) showed that the macromycete flora attained its full development fourteen days to three weeks after a heavy (autumnal) downpour. Such a delay could not be demonstrated in the Godhavn area (cp. Figs 15 and 16 with Fig. 19), but the fructification of both litter decomposers and mycorrhiza forming species may locally be reduced in dry growing seasons (p. 55).

Evidence has not so far been given that temperature influence the fructification of the macromycetes in the temperate forest zone, except in the autumn when low temperatures bring the production of fruit bodies to an end. In Godhavn, a reduction of the fructification occurred in a few cases when the growing season was very short, mainly in the snow-bed communities (p. 53). However, it appears that in general the conditions prevailing during the growing season are more important than merely its duration. The fact that the soil temperatures are low as compared with the temperature requirements of the macromycetes and that

a reduction of the fructification in 1972 occurred at quite a number of sites concomitantly with a decrease of the minimum soil temperature in the last week of July, points to the soil temperature as a minimum factor. It is considered that the general temperature level in the soil, as expressed by e.g. the temperature sum, is more important than the occasional occurrence of low minimum temperatures. However, as demonstrated for the temperature sum, a number of temperature parameters are to a greater or lesser degree determined by and correlated with the solar irradiance which in this way becomes the ultimate factor determining the fructification of the macromycetes in the individual years.

CONCLUSION

The macromycetes may serve as an example to show the narrow margin available for the organisms in the Arctic for the fulfilment of the yearly life cycle.

As a matter of fact, the macromycetes in the Arctic live as between Scylla and Charybdis. If the weather in the growing season is overcast and rainy, the solar irradiance is reduced and the soil temperature lowered. Thereby the growth and development of the macromycete mycelia are delayed so much that there is insufficient time left for fructification before the definitive decrease of the soil temperature in the autumn. This sequence of events may explain the occurrence in the Arctic of years when the fructification of the macromycetes is reduced, under circumstances where the moisture conditions cannot have been limiting.

On the other hand, except at the wet or moist sites, the clear sky which is a necessary condition for the occurrence of maximum irradiance - together with the openness of the arctic vegetation to the impact of the wind, and the generally rather high saturation deficit of the air $$ results in a rapid desiccation of the moss and litter layer. Consequently, the fructification is suppressed; this happens more often for the litter decomposers than for the mycorrhiza forming species. At some sites, the dryness may make the litter layer totally unsuitable as a substrate for litter decomposing macromycetes. Unlike in temperate areas there is no moist autumnal period where the soil temperature is still relatively high and the conditions thus favourable to fructification.

The diversity and abundance of the macromycetes, particularly the litter decomposers, are considerably reduced in the Arctic as compared with the temperate forest zone. This must be due partly to the severe physical environment, partly—as regards the litter decomposers to the fact that only limited amounts of substrate, of a low diversity, are annually released by the primary producers.

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Postscript (added in proof)

After the present manuscript was finished, M. EYNARD has published a thesis: Contribution a l'etude ecologique des Agaricales des groupements a *Salix herbacea* (Lyon 1977). His investigation includes field observations (in Pare National de la Vanoise, in the Alps) on the phenology and occurrence of the species, and laboratory experiments on the temperature and pH-requirements of some of the species found in the field. EY NARD states that the composition of the fungus flora and the duration of the fruiting period of the individual species in the *Salix herbaceae* snow-beds depend on the duration of the snow free period. On the basis of experiments with 19 *Agaricales* species, EYNARD inter alia found that twelve species in culture had their optimum of growth at 18°C, two at 20, three at 22, and one at 26°C. Depending on the species, the growth rate at 8°C ranged from 93 to 25%, and was at 4° C up to 40% of the maximum growth rate. The minimum temperature for growth ranged from \div 2°C to zero. For the majority of the cold susceptible species, the lethal temperature was between \div 6 and \div 12°C, but seven species survived \div 12°C for 40 days. After having been brought back to 18°C, the mycelia resumed growth almost immediately. The maximum temperature for growth ranged from 28 to 31° C. Comparing these results with the soil temperature conditions in the field during the growing season, EYNARD concludes that the species are to a higher or lesser degree adapted to the temperature conditions at the sites where they occur.—There is a fairly high degree of similarity between some of the sites studied by EYNARD, and the three sites dominated by *Salix herbacea* investigated in Godhavn, regarding the vegetation, the temperature conditions, and the fungus flora. Most probably the results of EYNARD's investigations of the physiology of alpine Agarics can be applied to arctic Agarics as well, whereas a comparison of the ecology and phenology of the macromycetes in the *Salix herbacea* snow-beds must take into account the differences in solar radiation and precipitation conditions between arctic areas and alpine areas in the temperate zone.