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Growth, Yield and Nutrition in Carpets of a Forest Moss (*Hylocomium splendens*)

Tillväxt, produktion och näringsekologi i mattor av en skogsmossa

by

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Preface

During the years 1947 and 1948 the author studied the nutritional physiology and ecology of a so-called nitrate plant, *Chamaenerion (Epilobium) angustifolium*, working at the Botanical Laboratory in the University of Lund. This plant had been reported to prefer nitrate as the source of nitrogen in solution culture (MARTHALER 1937, cf. OLSEN 1921), but was now found to grow well with ammonium salts as sole source of nitrogen, provided the pH was kept within suitable limits (TAMM, in prep.). This result led the author to believe that the distribution of *Chamaenerion* was governed less by the occurrence of nitrate in the soil than by the intensity of competition from other plants. It is true that *Chamaenerion* often contains nitrate in the leaves, particularly in places where it occurs abundantly (HESSELMAN 1917), and the presence of nitrate in leaves undoubtedly indicates an occurrence of nitrate in the soil. However, according to ROMELL (1934, 1935) nitrate occurs in forest soil chiefly where competition for nitrogen is low. It is thus clear that the problem of the distribution of *Chamaenerion* and other "nitrate plants" cannot be solved merely by a study of the relation between plant occurrence and soil nitrification. An observed correlation might imply a direct causal relation, but might also be brought about by the dependence of both the plants and the soil nitrification on the intensity of competition. An experimental approach may also be difficult, because we cannot exclude the possibility that under certain circumstances nitrate nitrogen is superior, even if laboratory experiments show that the plant can use ammonia nitrogen.

The interest of the author was therefore focussed on the problem of how competition might be studied. There is no difficulty in finding effects of competition either in nature (see for example TAMM 1948) or in experiments. But these effects do not tell us much about why some plants spread at the expense of others. Even in such a simple case as that concerning "nitrate plants", where it is often possible to consider light and water supply as relatively constant, there are several possibilities to be taken into account: different species may have (1) different optima and/or tolerances regarding ion concentration and balance in the environment, and (2) different abilities to extract nutrients where they are scarce; (3) they may need different amounts of a certain nutrient for healthy growth, and (4) they may change the substrate, for example by the release of organic or inorganic substances which affect their neighbours or the soil microorganisms. All these possibilities are realized in different cases, and ought to be studied in more detail by physiological experiments as well as in nature.

There is however a further property of plants which has received little attention in connection with competition phenomena. Plants may have very different types of nutrient economy. In one plant much of its nutrient content may be given back to the soil in the autumn with the litter or otherwise, in another a large part may be recovered from leaves and dying shoots and used for the next year's growth. Woody plants may also deposit varying amounts of nutrients in heartwood and bark, temporarily removing them from the cycle. In 1948 the author started a preliminary investigation of the nutrient economy of various plant species in different habitats (supported by a grant from Lunds botaniska förening). It was however felt that before we could interpret the results of such comparisons, we ought to have a more detailed knowledge of the nutritional economy and ecology of a single plant species, or, better still, a single plant community. For that reason the present investigation of the *Hylocomium splendens* community was begun in the autumn of 1948. It is hoped that this work may form a starting point for future studies of nutrition and competition within plant communities of greater importance than the forest moss carpets.

Here I wish to express my sincere gratitude to all those who have helped me during this work. The investigation was begun at the Botanical Laboratory in the University of Lund, and thanks are due to the head of the Laboratory, Professor H. BURSTRÖM, for all his interest and helpful criticism. Later I have been able to continue and extend the investigation in the Department of Botany and Soils, Forest Research Institute, Experimentalfältet. For this I am much indebted to the head of the department, Professor C. MALMSTRÖM. I also wish to thank the head of the Institute, Professor M. NÄSLUND, for his permission to publish this paper in the Reports of the Forest Research Institute.

Most of the chemical analyses presented in this paper have been carried out by Miss B. ALVERIN, who has also helped me to modify and improve some of the methods used. A part of the remaining analyses has been made by Mrs. I. DOVNER. Mrs. K. KNUTSON has given invaluable help and advice regarding chemical methods. The flame-photometric methods used have been worked out and checked by my wife, Mrs. G. EHRLIN-TAMM, in cooperation with Mrs. KNUTSON. Miss ALVERIN and my wife have also kindly assisted in the statistical calculations.

In 1950 I collected moss samples in Norway, supported by a grant from "Fonden för skogsvetenskaplig forskning". It is a great pleasure to acknowledge the kindness and help received from all the institutions visited there, and from many members of staff. In particular I wish to thank Professors K. FÆGRI, O. HAGEM and E. MORK, Mr. A. DANIELSEN and Miss A. OMVIK, and Fylkesskogmester K. MØRKVED.

Meteorological data have been obtained through the courtesy of the Norwegian Meteorological Institute, Oslo, and the Swedish Meteorological and Hydrological Institute, Stockholm.

Mrs. E. NYHOLM has kindly determined most of the moss species listed in Tables XXVII and XXVIII.

Most of the diagrams have been drawn by Miss K. SVENSSON.

Some of the problems connected with this investigation have been discussed with Dr. H. EGNÉR (atmospheric supply of nutrients), Dr. B. MATÉRN (statistical methods), and Dr. D. v. WETTSTEIN (germination and protonema growth of *Hylocomium splendens*). I am much indebted to them, as well as to all others not mentioned here who have taken an interest in my work and given me advice and help.

The English has been corrected by Dr. E. GORHAM, University College London, who has made a number of valuable suggestions regarding both language and content.

The manuscript has also been read by Professors C. MALMSTRÖM, L.-G. ROMELL and M. G. STÅLFELT, who have all suggested improvements. For these, as well as for earlier discussions of problems connected with the ecology of *Hylocomium splendens*, I am most grateful. Professor MALMSTRÖM first suggested that I should investigate the factors governing the distribution of *Chamaenerion angustifolium*.

Finally I should like to thank my parents, who have made it possible for me to devote myself to the study of plant ecology and physiology and who in all ways have tried to facilitate my studies and investigations. My wife has not only assisted me in important parts of the work but also given me never failing support and encouragement.

CARL OLOF TAMM

TABLE OF CONTENTS

Introduction

The present investigation deals with growth, nutrition and structure, in different habitats, of a plant community characterized by the dominance of *Hylocomium splendens* Br. Eur. (= *H. proliferum* (L.) Lindb.). The community as a whole is studied, as well as its individual constituents; and explanations are sought for the behaviour both of the individual plants and of the community composed of them.

The incentive for the investigation has been our surprisingly vague knowledge of one of the fundamentals of plant sociology: to what extent is plant life under the direct influence of physico-chemical factors of the environment, and to what extent is it determined by biotic factors as competition or the physiological status of the plants (which depends on earlier development as well as on genetic constitution).

This lack in ecological science is particularly serious when the distribution and behaviour of plant communities is studied instead of that of single species. Plant communities are believed to be less subject to random variation in distribution than are single species, and thus more suitable for investigations of the correlation with any external factor. This is certainly true in many cases, but it is usually less easy to analyse the cause of correlation between the occurrence of a community and a certain factor than to analyse a correlation between the occurrence of a species and the same factor. One difficulty—but not the worst one—is that plant communities are less well defined than are plant species. More important is the fact that the influence of external factors is modified by the community itself, which to a certain extent creates its own environment. The substrate is changed by plant activity and the supply of light, water and different nutrients may be restricted by competition.

This complexity of the habitat, where physical and chemical factors interact with biotic factors, accounts for the fact that experiments in nature may give very different results from laboratory experiments where the same primary factor is changed. In the latter case we can usually be reasonably certain that the visible effect is caused more or less directly by the investigated factor or factors, if the experiment is correctly designed. In ecological experiments, especially in natural plant communities, the indirect effects may dominate and even obscure the effect postulated from the results of laboratory investigations.

In ecology we must evidently study the interaction between plants at the same time as we study the importance of external factors for the plants.

To solve problems regarding the importance of external factors for plants, the most reliable method is the experiment. This is particularly true in the case of autecological problems, i.e., problems concerning plant species in relation to environment, where parallel experiments in the laboratory and in nature seem to be the obvious approach (see for example BLACKMANN & RUTTER 1946—1949).

Where synecological problems are concerned, i.e., those dealing with plant communities in relation to environment, the experiment is also the best method in a number of cases, e.g., when we want to determine the relative importance of different external factors such as the supply of light or different nutrient salts. Also the effect of competition may well be studied experimentally, e.g., by thinning or trenching.

These different treatments are all alike insofar as they change the community considerably if applied in a place where the factor in question is sub-optimal (or indicative of a small supply of some other factor, as would be the case with severe competition). However, while we may conclude after a successful experiment that a given factor was more or less sub-optimal for certain plants in the original community, it is often difficult to evaluate its mode of action. For example, where either occurrence or growth are affected, the question may be a simple one concerning the absolute supply of a given factor. But it may also be a complex question of factor interaction, and competition for this and other factors. There is always a strong variation in the growth of individual plants in the community; are these growth variations caused by differences in the supply of nutrients, water or light, by differences in competition from neighbours or other biotic factors, by strictly internal factors (genetic constitution), or by an interaction between two or more of these complexes of factors?

With the last question we have arrived at the problem of the heterogeneity of the plant community. Individual plants may have a different ability to modify the environment of their neighbours, depending on their size, life-form, growth potential, etc. The heterogeneity in the plant community thus makes the habitat heterogeneous with respect to the supply of light, water, nutrients, and possibly other factors, even if the subsoil is homogeneous, which of course is not always the case. A heterogeneity of the habitat due to competition must necessarily affect some (or all) of the factors limiting plant growth. If a growth factor is supplied in optimal quantity we cannot have competition for this factor until the supply has been depleted enough to bring about a deficiency for at least some of the plants.

If we thus study the heterogeneity of a plant community, we have a good chance to elucidate our primary problem, the interaction between unmodified external influences and modifying biotic factors in forming a habitat. The following questions are of special interest: 1) In what respect is the community heterogeneous? We have here to pay attention to the variation in properties such as life-form, species, degree of cover, individual size and growth-rate, rate of sexual and vegetative propagation, or in short variation in the structure of the community (in a wide sense). The chemical composition of the plants may also vary individually and is therefore of interest to us. 2) Which environmental factors affect these properties, particularly the growth of the community and its constituents, and do these factors act uniformly over an area, or do they favour or disfavour some plants in comparison with others? 3) Can the heterogeneity of the community be fully explained by a heterogeneity in the environment, or is there a residual heterogeneity due to biotic influences within the community itself? If so, can one discover how plant interaction modifies the external factors?

An investigation of plant communities in general with respect to these three questions is, we may hope, not impossible, but involves an enormous amount of work. Conditions are more favourable if we choose a very simple community, composed of only one layer and one main constituent. Even if it is not permissible to generalize directly from such a "type community" to other communities, it will certainly be easier to decide in which respects other communities resemble our type community or differ from it, once the type community is known in detail.

The moss carpets common in coniferous woods would appear to be extremely well adapted to our purpose, especially the carpets composed mainly of *Hylocomium splendens*. The absence of roots and the mode of growth of this species make it possible to determine its total dry matter production, otherwise a difficult problem. Moreover, this community is one-layered (a synusium) in a very strict sense, because all the living organs of the plant—nutrient absorbing as well as photosynthesizing—form only one layer. It is also known that the nutrient supply to these moss carpets presents interesting problems (STÅLFELT 1937 a, ROMELL 1939). We may also hope that an investigation of this small and simple community may shed some light on the problems of the more complex community of which the moss layer is one of the constituents—the forest. There is always an interaction between the different layers in a complex plant community, and a detailed study of the ecology of one of the layers will probably tell us something about these interactions and therefore about the ecology of the other layers.

Chapter I. Terminology and Methods

Terminology

The taxonomic nomenclature follows HYLANDER (1941) for vascular plants and MAGNUSSON (1937) for lichens. The bryological nomenclature is the same as that used by KRUSENSTJERNA (1945), based upon JENSEN (1939).

The chief subject of the investigation has been a plant community characterized by dominance of *Hylocomium splendens*. The distinction of plant communities on the basis of dominance is not entirely satisfactory (cf. BRAUN-BLANQUET 1951), but in the present case little or nothing can be gained by a more elaborate sociological terminology. It might thus be possible to subdivide our *Hylocomium splendens* community according to its minor constituents, e.g., with or without *Rhytidiadelphus loreus*, which occurs in most Norwegian samples. But also within the region where this moss is common we can find pure *Hylocomium splendens* carpets, virtually devoid of *Rhytidiadelphus loreus* or other species which might indicate one or other of the climatic differences which indubitably exist between western Norway and eastern Sweden.

The *Hylocomium splendens* community is a one-layered community of low rank (a society, DU RIETZ 1936), which as a rule is a component of a phytocoenose with more layers. Most of the sample plots are situated in forests, the canopy of which has been described. The field vegetation has also been briefly described where it has occurred. In order not to complicate the problems too much, the sampling has when possible been made on patches either without or with very scattered field vegetation. As the moss vegetation changes from patch to patch, description of the field vegetation within plots of standard size has been considered of little interest.

A few morphological concepts, needed in the following chapters, may be explained here in connection with a brief description of *Hylocomium splendens*. An individual of this moss consists of a sympodial chain of annual shoots (Fig. 1). These shoots or "fronds" will be called "segments". The youngest segment is — during the larger part of the year — only a small bud, while its parental segment is expanded and green (usually bright green, sometimes yellowish green). The next older segment is more brownish green, and the next brown; however, the colour of all segments varies a great deal. The

Fig. 1. *Hylocomium splendens.* Unbranched and branched sympodia.

oldest segments are dead; often they lack leaves and side-branches of the second and third order. They gradually become incorporated into the humus layer.

The different segments can be dated after the autumn when they develop from bud to frond (cf. Figs. 3 and 4). When samples collected in different years are compared, we need distinctions which indicate the age of the segments. We may then call the bud "segment 1" (age 0 to 1 year); its parental segment which is between one and two years old then becomes "segment 2", etc.

The sympodia of *Hylocomium splendens* may be straight or branched (cf. Fig. 1). For the sake of brevity, individuals with branched sympodia are referred to as "branched individuals", and the rest as "unbranched" ones. Of course the segments in both cases have leaf-carrying side-branches of different orders.

Sampling methods

In sampling, the entire moss carpet from one or more patches in a habitat has been collected. If a sample representative of a larger habitat was desired, small pieces of moss carpet were taken over the whole habitat. In many cases, however, information was desired about the moss growth per unit area, and as this figure is never constant over a large area, each sample consisted of the moss carpet from a small plot (usually 6.25 dm^2) cut out by means of a frame.

The samples were then air-dried and divided according to species. The *Hylocomium* fraction was then divided in segments of different age; and in certain samples "branched" and "unbranched" individuals were treated separately. In the samples for yield determination, other moss species were separated into "this years shoots" and the rest. This separation was comparatively easy in the case of *Ptilium crista castrensis, Thuidium tamariscinum* and also *Pleurozium Schreberi,* where the annual shoots could often be recognized by bending of the stem. It was more difficult in *Dicranum, Rhytidiadelphus loreus* and *triquetrus, Plagiothecium undulatum* and other species, where ½, in some species ¹/₃, of the green part of the moss was used (cf. ROMELL 1939). Those specimens of the above-mentioned species which lacked characteristic limits between the annual shoots were treated in the same way. The age of liverworts and lichens could not be determined. On the whole the age determinations of other species than *Hylocomium splendens* are less reliable; fortunately these species usually only make up minor parts of the samples.

The air-dry samples were usually ground in a Wiley micro-mill (sieve of 40 meshes per inch), with the exception of samples intended for iron analysis which were not ground. The dry weight was determined after 48 hours in a vacuum oven at 55° C. This method of drying does not remove as much water as drying at 105° C (difference about one per cent of the sample weight), but can be repeated at will without altering the sample. In a few cases where great accuracy was not necessary, drying was carried out at 105° C, for example with rainwater residues.

Comparisons between different segments from the same sample can be made equally well on air-dry as on vacuum-dry basis, since the water content of air-dry segments does not vary much with their age.

Chemical analysis

As the chemical methods had to be modified during the course of the investigation to suit the amounts of sample available, which were often very small, the following descriptions do not always cover the first determinations. This is especially true of the determinations of potassium and calcium. The flame photometer came into use during the course of this investigation, so that the earliest potassium and calcium figures were obtained by other methods. In fact the flame photometric method has been a prerequisite for the determination of cations in rainwater and moss extracts, which would not otherwise have been possible on the present scale. Moreover, this method has been much superior in reproducibility, compared with colorimetric potassium determination according to NYDAHL (cf. KNUTSON 1949) and titrimetric calcium oxalate determination, when these methods were used on a micro-scale.

As the method by which the determination has been made is not always stated in the Tables and Figures, it may be pointed out that with one minor exception (see below on calcium determination) no systematic difference appears in the present material between results obtained with different methods.

Nitrogen has been determined by KJELDAHL's method, used on a micro-scale. To 40—70 mg of sample were added 1.5 ml of sulphuric acid and ca 0.5 g of catalyst ($K_2SO_4 + CuSO_4 + HgSO_4$), the digest being heated for three hours after solution of the sample. The ammonia was distilled off in the apparatus of PARNAS & WAGNER and collected in 0.01 N hydrochloric acid; then back-titrated with 0.02 N sodium hydroxide. The indicator was a mixture of methyl red and methylene blue. A sharp change from red to colourless to green was obtained if the solutions were aerated with CO_2-free air before titration, which is more convenient than boiling.

The average difference between duplicate determinations on moss samples has been 1.9 per cent of the value found, or expressed in absolute amounts 0.013 mg N. This difference corresponds to a standard deviation of 0.012 mg N (0.013 : 1.13, cf. e. g. HALD 1948, Table VIII.).

Most of the rainwater ammonia determinations have been made by a similar method, using amberlite IRC 100 to concentrate the ammonia (EGNÉR, ERIKSSON & EMANUELSSON, 1949); in a few cases micro diffusion analysis has been used (CONWAY 1950). All values reported are averages of two or more duplicates.

Analysis of ash components in *Hylocomium* has as a rule been carried out after digestion with nitric and perchloric acid. Usually 0.5 to 1 g of the sample was boiled in a KJELDAHL flask with 25 ml nitric acid and 10 ml perchloric acid. After digestion the sample solution was diluted with water, filtered warm to remove silica, and made up to 100 ml in a measuring flask. Aliquots of this solution were then used for the determination of the different elements.

Phosphorus. An aliquot is pipetted into a small glass bowl and evaporated with 3 ml nitric acid and 1 ml 1 : 1 sulphuric acid, to insure that the phosphates are in the ortho-form. Dilute hydrochloric acid is added to remove peroxides possibly formed during the oxidation of the organic matter with perchloric acid. (Such peroxides may interfere seriously with the determination of phosphorus, at least by stannous chloride methods.)

After evaporation the sample containing sulphuric acid and some perchloric acid is made up to volume and mixed. An aliquot of this solution is neutralized in a 100 ml measuring flask, using sodium carbonate solution from a burette (indicator: α-dinitrophenol). Sample solutions and solutions containing known amounts of phosphorus are then diluted with water to ca. 50 ml and treated according to SCHEEL (1935): addition of 5 ml sulphite-metol solution (metol = p-aminomethyl phenol sulphate), 10 ml molybdate-sulphuric acid mixture, and 20 ml acetate buffer. After each addition the flasks are vigorously shaken; the space of time between the two last additions should be exactly ten minutes. The solutions are then made up to volume and mixed. Extinction is measured at 7,000 ÅU.

The average difference between duplicate determinations on moss samples has been 2.3 per cent of the value found, corresponding to a standard deviation of 2.0 per cent. Some of the earlier moss analyses were made both by this method and by ZINZADZE's method (using stannous chloride, see KNUTSON 1949); the results from both methods agreed well, but ZINZADZE's method gave somewhat less reproducible values. As the latter method is considerably more sensitive than SCHEEL's method, it has been the one used for the determination of phosphorus in rainwater and in individual moss segments. For some reason or other, the results of duplicate determinations on rainwater samples have differed considerably, so that the data in Tables XX and XXI only give the order of magnitude of phosphorus in rainwater beneath trees.

Cations. For the determination of potassium, calcium, sodium, iron and aluminium the presence of large amounts of perchloric acid is objectionable. Therefore aliquots of the sample solution have been evaporated on a hot plate and then in an oven at 200° C for one hour; this treatment removes most of the perchloric acid. The samples are then treated with dilute hydrochloric acid on a steam bath and after a second evaporation dissolved in 0.02 N hydrochloric acid. Part of this solution is diluted to a concentration suitable for flame photometric determination of K, Ca and Na (ca. 5—15 p. p. m. of K and Ca), and filtered.

Potassium. The solution to be analysed is brought into a "gasol"-air flame (gasol is a mixture of butane with some propane) by means of an atomizer constructed according to RAUTERBERG & KNIPPENBERG (ref. see EHRLIN-TAMM 1950). The red light from the potassium line 7665/7699 ÅU is focussed on a red sensitive phototube (Pressler 125T) after passing a Jena metal interference filter No. 768a. The voltage of the gas-filled phototube has been 90—120 V. The current is measured on a Multiflex galvanometer (MG 4) with a sensitivity of 5×10^{-10} A/mm. Sample solutions and standard solutions are always measured symmetrically, as described by EHRLIN-TAMM (1950). While ash solutions are diluted to a convenient degree, most rainwater samples are run directly after filtration and acidification.

The average difference between duplicate determinations on moss samples has been 3.0 per cent of the value found, corresponding to a standard error of 2.7 per cent.

A few of the first potassium determinations were made by a colorimetric chloroplatinate method (see p. 13). Most of these determinations have later been checked flame photometrically and found to agree within the analytical error (which was larger in the colorimetric procedure).

Calcium. Calcium has been determined in an apparatus similar to that for potassium, except for the flame (acetylene-air) and the photocell (a photomultiplier RCA 931 A). One or two Jena metal interference filters 616a are used. The voltage of the multiplier cell has been $9 \times 85 + 50$ V. The current has been measured with a Multiflex galvanometer MG 3.

The reproducibility of the calcium determinations has been almost the same as that of the potassium determinations on the same solutions (3.1 per cent difference between duplicates as compared with 3.0). The method thus appears satisfactory, especially as most elements occurring in plant ash do not disturb the analysis of calcium and potassium. Most common cations and anions have been tested in the concentrations met with in plant ash extracts and rainwater. The potassium values are only affected by acidity and, in acetylene flame, by sodium. Calcium values may be depressed by phosphoric acid in butane flame, but not in acetylene. Very large sodium concentrations increase calcium readings. Silica in small amounts, such as those remaining in solution after digestion and filtering, does not interfere. A serious source of error in the calcium analysis is, however, the presence of aluminium, which depresses calcium readings (HULT 1946). In the cases where the aluminium content of the moss is known (Table XIX), this depression can only affect the calcium figures very little (one or two units in the last decimal place).

A slight discrepancy has been found in a few of the Norwegian samples between calcium determined flame photometrically and by oxalate precipitation; it cannot, however, be explained by the aluminium effect, as there are differences in both directions. As the amounts of sample were very limited, the determinations could not be repeated, but the flame photometric values have been used. Since the oxalate method sometimes gave large differences between duplicate determinations (these were repeated where enough sample was left), it seems more probable that the oxalate values are in error than the flame photometric ones.

The oxalate precipitation was carried out at pH 4 in 15 ml centrifuge tubes, which were allowed to stand over night and were then centrifuged. The precipitate was washed with water, centrifuged three times, and then titrated hot with 0.01 N permanganate. In some series the precipitate was dissolved in hydrochloric acid without washing and then measured flame photometrically. The latter method was used during a period before enough was known about disturbing influences on the flame photometer readings. No systematic difference between values obtained by these different methods, or by gravimetric determination of calcium oxalate, has been observed. It should be stressed that while different methods have been used in different series of analyses, the same method has always been used for the different fractions of the same sample.

Sodium. As sodium does not belong to the indispensable elements, the figures are of less interest than those of potassium and calcium. Sodium is, however, often abundant in rainwater and ground water and therefore some determinations have been made. The flame photometer used for calcium has been altered for sodium determination by replacing the metal interference filter 616a with a similar filter No. 590a. Very small amounts of sodium can then be detected. Unfortunately for the accuracy of the analyses, the sodium content of *Hylocomium splendens* is extremely low. Moreover there is a large risk of sodium contamination during preparation as every segment must be handled directly and sodium occurs almost everywhere in the laboratory. Thus the data on moss only give the order of magnitude of the sodium content. The presence of potassium tends to increase sodium readings slightly in acetylene flame. This error can be largely avoided by the use of a butane flame, at the expense of some of the sensitivity. In the present case this error has been considered as of no great importance in comparison with the other sources of error.

Aluminium, iron and manganese have been determined by conventional colorimetric methods, using aluminon, ortho-phenanthroline and periodate as reagents. The methods are essentially those described by HEDIN (1947; for aluminium) and SANDELL (1950; iron p. 378, manganese p. 432). Aluminium values are corrected for the disturbance due to iron. The determinations are too few to admit a reliable estimate of reproducibility, but some information in this respect can be found in Table XIX, where the results of duplicate determinations are given. The absence of manganese in rainwater from an open field (Table XXI) has been checked by the peroxidisulphate method, as NYDAHL (1949) states that the periodate method may give too low values at very low manganese levels.

In a few samples silica has been determined gravimetrically after dry ashing in platinum dishes (KOLTHOFF & SANDELL 1937). The silica has then been volatilized with hydrofluoric acid. The contents of potassium, calcium and sodium in the residue have then been determined in the flame photometer.

Chapter II. Sample Localities

The occurrence and growth of *Hylocomium splendens* have been studied in a number of places in different parts of Sweden and Norway, but samples for more thorough investigation of growth and chemical composition have been collected only in the following places:

Roslagen (= eastern part of Uppland), middle Sweden, lat. ca. 60°, long. E. from Greenw. ca. 19°; forests and meadows.

Rönninge, eastern Södermanland, middle Sweden, lat. N. 59° 9′, long. E. 17° 45′; spruce forest.

Ås, eastern Norway, lat. N. 59° 40′, long. E. 10° 46′; spruce forest.

Os, western Norway, lat. N. 60° 13′, long. E. 5° 30′; spruce forest.

Rådalen, western Norway, lat. N. 60° 17′, long. E. 5° 21′; spruce and pine forest.

Fjell, western Norway, lat. N. 60° 19′, long. E. 5° 7′; *Calluna* heath and pine forest close to the Atlantic ocean.

Åsane, western Norway, lat. N. 60° 27′, long. E. 5° 21′; ombrogenous mire.

Kulbäcksliden, north Sweden, lat. N. 64° 12′, long. E. 19° 34′; spruce forest.

Imsdalen, Tröndelag, middle Norway, lat. N. 64° 10′, long. E. 12° 20′; spruce forest on poor sand.

Bredesmoen, Tröndelag, middle Norway, lat. N. 64° 12′, long. E. 12° 15′; spruce forest on fertile moraine.

As may be inferred from this list, the investigated areas form two series, one at approximately lat. N. 60° and one at approximately lat. N. 64°. Both series contain plots from eastern Sweden (comparatively dry climate) and from eastern Norway (comparatively humid climate). In the first series we also have samples from extremely humid western Norway. Climatic data for stations within these different areas can be found in Table XXVI and Figs. 44—45, p. 134 ff.

Most of the localities listed above will be briefly described in connection with the results obtained on samples collected there. Some of the Roslagen samples have, however, been used for different purposes, and will therefore often be referred to. The habitats where they have been collected will for that reason be described here, together with one of the Norwegian habitats (Os); the samples from the latter locality will often be compared with the Roslagen samples.

Most of the Roslagen samples have been collected in the forest belonging to the farm Grenholmen, parish of Roslags-Bro, lat. N. 59°52′, long. E. 18°55′. The distance to the open sea (Ålands hav, part of the Baltic) is only about 7 kilometres, and the nearest bay of the Baltic — with almost fresh water — is only a few hundred metres away from the sample plots.

The subsoil in the sampled forest area is moraine, originally containing considerable amounts of lime and clay. During the postglacial upheaval of the country, which was covered by the sea after the glaciation, the fine particles were washed out of the top soil in more exposed localities. On rocky hills very little soil remains, except in fissures; in other places there is often an abundance of stones at the surface. In more sheltered areas the washed-out finer and coarser particles were deposited; so that mosaics are common, consisting of clayey areas, areas of nearly undisturbed moraine, areas of washed-out moraine and areas with stones and gravel covering a more or less deep layer of clay.

During the period since the uplift above sea level, weathering and leaching have removed the calcium carbonate in the top soil down to at least 0.6 m in the forest, which lies 10 m or more above sea level. Where it is possible to recognize a soil profile, the soil-forming processes have resulted in a brown earth, or in types intermediate between brown earth and podzol, occasionally with a very thin bleached layer. The shallowness of the soil, the stoniness and the irregular topography often make profile recognition difficult, especially in the neighbourhood of the rocky hills.

The humus type is usually a mull, but in places with shallow soil a more or less typical mor (raw humus) often occurs. This has been the case in most sample plots. In such places the forest is comparatively slow-growing, consisting mostly of spruce and pine. On the hills the trees usually root in fissures. Where the soil is deeper, tree growth is better, with spruce as the dominant tree and with a rich field vegetation.

Three different localities numbered (Grenholmen) I, II, and III have been sampled in this forest. Site I (Fig. 2) is a comparatively flat area at the upper end of a slope. It comprises a small opening in the forest, surrounded by spruce, pine and, at some distance, birch. Scattered shrubs occur: *Corylus avellana, Lonicera xylosteum, Ribes alpinum,* together with a few small trees (spruce, birch and *Sorbus aucuparia*). The field layer contains dwarf shrubs (*Vaccinium myrtillus* and *V. vitis idaea*) characteristic of mor layers, but herbs and grasses are codominant, for example *Anemone hepatica, Deschampsia flexuosa, Fragaria vesca, Majanthemum bifolium, Milium effusum, Oxalis acetosella.*

A moss layer occurs throughout the forest, but is best developed where the field layer is not very dense. In Site I this is particularly so on the many stones and tree stumps, which are covered by *Hylocomium splendens,* either pure or mixed with *Pleurozium Schreberi* or *Ptilium crista castrensis.* Pure communities of these species also occur, as well as of *Dicranum undulatum* and *Hypnum cupressiforme.* When growing directly on the ground the moss community often contains *Rhytidiadelphus triquetrus.*

The light supply in Site I varies from fairly good in the middle of the opening to low in the margins beneath drooping spruce branches. Tree growth is good around Site I, but most trees do not attain a height of 20 m.

Site II is situated less than 100 m from Site I, on and around a small rocky hill (see map Fig. 10 and the photograph Fig. 9). At the foot of the hill, conditions are rather similar to Site I, although tree growth is not so good and the vegetation is more dominated by the typical mor plants (the *Vaccinia* and *Deschampsia flexuosa*). Most of the sample plots in Site II lie on shallow soil or directly on the bedrock, where the field layer vegetation is scarce or absent. The trees on the hill are slow-growing — mainly spruce rooting in fissures. In this place as in many similar ones, mosses occur chiefly in the neighbourhood of the trees. This is especially true of *Hylocomium splendens. Pleurozium Schreberi* seems to be somewhat less closely "associated" with the trees In the open areas lichens (*Cladonia rangiferina* and *sylvatica*) predominate; *Polytrichum juniperinum* also thrives in such places (cf. KRUSENSTJERNA 1945 p. 113 ff.).

Site III is situated half a kilometre from Sites I and II in an open stand of old pine and spruce. The samples were taken where only a moss plus a humus layer covers the bedrock. Field layer vegetation is lacking, but the moss carpet is well developed.

Fig. 2. Site I, Grenholmen, Roslags-Bro parish, Uppland. 19. X. 1951.

Of the Norwegian samples those collected in "Os prestgårdsskog" (Os parsonage forest) were most thoroughly studied. This forest is situated ca. 20 km south of Bergen on fertile clayey and morainic soils. Most of the forest was planted about 40 years ago with spruce, which does not occur spontaneously in this region. Large areas have also been planted with other conifers in connection with reforestation experiments carried out by Vestlandets forstliga försöksstasjon. Also other research work has been carried out in this forest, e. g. forest meteorological observations (cf. GODSKE 1948). Spruce usually grows well when planted on deep soil in western Norway, although there is an initial phase of growth inhibition lasting from a few to many years. The *Hylocomium* samples were collected in a highly productive spruce stand. One sample was taken in a very dense stand, where light intensity was low and the ground was covered by dark green *Hylocomium* without a field layer. The other samples were taken 20—30 m away, where the stand formed the western limit of a clear felling, made in the spruce forest several years earlier because of insect injuries. These sample plots had a good light supply, at the same time they were inside the spruce crown projections. Field vegetation was also lacking or scarce here, and the *Hylocomium* carpet extremely well-developed. Only a few metres, or even decimetres, outside the spruce canopy a rich and variable field vegetation was growing; there the moss community was less vigorous and less homogeneous.

Sites similar to those just described are common over large parts of Sweden and Norway. This is also the case with several of the other localities listed above. A few samples, however, represent unusual — though not abnormal —

occurrences of the *Hylocomium* community. It has been thought that the behaviour of the community under conditions extreme in one respect or other might throw light on behaviour under more normal conditions, and certain types of unusual habitats have therefore been sought, e.g. sites where sea salt supply can be expected to be at its maximum (Fjell), where the whole vegetation depends on nutrient supply as rain and dust from above (bog mires), or where *Hylocomium* forms a community independent of a tree or shrub canopy (Noor in Roslagen).

Chapter III. Seasonal Growth Curve of *Hylocomium splendens*

A prerequisite for comparisons between the moss growth within different plots is a satisfactory knowledge of how and when the moss grows. It is known that many mosses have two growth periods in the year, one in the spring and one in the autumn (see HAGERUP 1935). It seems probable that these periods are induced by external influences; moss kept moist may continue its growth during summer, as has been shown for *Homalothecium sericeum* by ROMOSE (1940). During winter low temperature and darkness check the growth of most other plants, and may well be responsible for the growth-pause of the mosses. Where *Hylocomium splendens* is concerned, we have physiological support for the view that both the summer and the winter rest period are caused by external influences. It should be added that there are hardly any absolute rest periods in *Hylocomium,* but merely periods of slower growth. STÅLFELT (1937 b) has found that photosynthetic activity in *Hylocomium splendens* and some other moss species is low during periods of intermittent drying, which may explain the summer rest period. On the other hand the moist moss maintains a posititive balance of photosynthesis over respiration, even at very low light intensities, provided the temperature is low (= winter conditions). The net gain of photosynthesis, however, is of course low, so we may still speak of a growth-pause.

STÅLFELT'S results only apply to the increase in dry matter due to photosynthesis; the same is true of ROMOSE'S data, while HAGERUP studied morphological growth. These phenomena are of course not identical, but it is unlikely that large errors will result from the use of increase in dry weight as an expression of the quantitative growth. As translocation is slow in the moss plant, there is probably not much storage of substances used later for the growth of other organs, as may be the case in higher plants. The difference between organic matter and dry weight is small in *Hylocomium* (low ash content). The qualitative aspect of growth, including differentiation of new

Table 1. Relative weights of *Hylocomium* segments in different years, expressed as per cent of weight of segment 3. Samples collected in Site I in the beginning of August and containing, respectively, 264, 300, 325 and 155 "unbranched" individuals.

Fraction of sample	Segment	Sample from			
		7. VIII. 48.	5. VIII. 49.	7. VIII. 50.	2. VIII. 51.
"Unbranched" individuals only	51	—	—	—	17
	50	—	—	34	100
	49	—	20	111	*100*
	48	16	79	*100*	82
	47	77	*100*	111	81
	46	*100*	96	101	—
	45	106	89	—	—
"Unbranched" and "branched" individuals	51	—	—	—	18
	50	—	—	37	103
	49	—	22	115	*100*
	48	15	84	*100*	80
	47	80	*100*	110	78
	46	*100*	94	95	—
	45	107	85	—	—

organs, is of equal physiological interest, but is very difficult to study quantitatively in nature. We shall therefore concentrate on the dry matter increase, which may be measured in different ways, and put the morphological changes in second place. In the following discussion the term growth will be used in a rather wide sense for a dry matter increase with or without observed morphological changes; if only morphological growth is meant it will be especially stated.

For the investigation of the seasonal course of growth under natural conditions several collections of *Hylocomium* have been made at Site I (Grenholmen) during different seasons from August 1948 to August 1952. (Samples could be collected only when the ground was free from snow cover; a collection planned for December 1950 could not be made for that reason.) The different samples have been collected in the same way, including both shaded and unshaded moss, and moss growing on stones as well as moss from the ground, but the sampling has not been "randomized" in the statistical sense. From each sample all "unbranched" *Hylocomium* individuals with five or more (four in the first two samples) segments were taken out. Specimens with fewer segments or with broken-off branches were not used for the growth measurements. Specimens with five or more segments but with branched sympodia formed separate subsamples.

The average weight of the segments of different age was determined in the subsample of unbranched sympodia (Fig. 3). It may, however, be suspected that the "unbranched" specimens are not representative of the whole samples but are more slow-growing than the average. For this reason the different

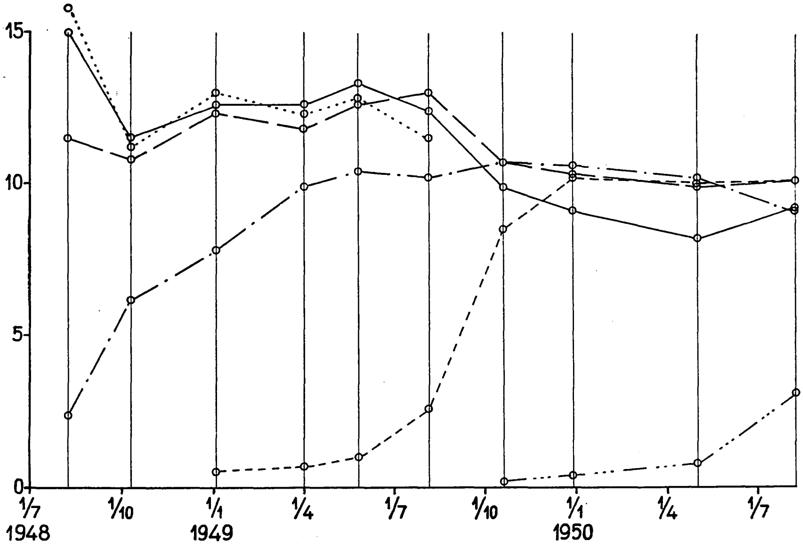


Fig. 3 a. Air-dry weight of different segments of *Hylocomium splendens* from Site I at different seasons from August 1948 to August 1950. "Unbranched" specimens. For symbols, see Fig. 3 b (right-hand page).

segments of "branched" individuals have also been weighed. The average weight of the segment has less significance in this case, as the number of segments increases from year to year (cf. Table II). Therefore the weights of the segments of the different samples have been expressed in per cent of the weight of a certain full-grown segment (segment 3) in Table I.

From this table we may conclude that the "unbranched" specimens have a slightly slower growth-rate than the average, viz. "branched"+"unbranched". This implies of course that the "branched" individuals grow faster than the "unbranched" ones, as is shown more in detail in Table II. The error in growth-rate if we use "unbranched" specimens only instead of "unbranched" + "branched" appears to be 3 to 5 per cent annually, to judge from Table I. This error does not seem very serious if we only wish to determine the general trend of the growth curve. We thus may use Fig. 3 to obtain a picture of *Hylocomium* growth, in spite of the fact that it is based upon "unbranched" individuals only.

Before we discuss Fig. 3 we may, however, try to work out a growth curve in a slightly different way, using data similar to those in Table I. By expressing the different segments in a sample as per cent of a certain "base" segment we may eliminate one of the sources of error in Fig. 3, viz. the varying size of the average moss individual in different samples. On the other hand we may introduce new errors. If the segment assumed to be 100 per cent is subject to

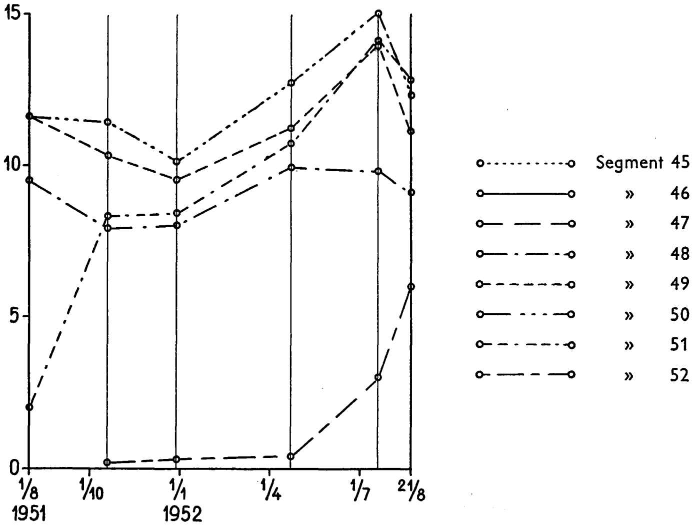


Fig. 3 b. Air-dry weight of segments, as in Fig. 3 a, from August 1951 to August 1952.

either growth or decomposition, errors in the figures for the other segments will follow, and a random variation in the weight of the base segment will cause a more or less systematic error in the figures for the other segments.

Nonetheless Fig. 4, which shows the size of each segment relative to one of the fullgrown segments, closely resembles Fig. 3. Much of the irregular variation in Fig. 3 has disappeared in Fig. 4, and it seems likely that these graphs, Fig. 4 in particular, give a true picture of *Hylocomium* growth.

It should be added that beside the groups of "branched" and "unbranched" individuals there is also a fairly large group of specimens broken during sampling and preparation, or earlier. There is, however, no sign pointing to a very different growth-rate within this last group. On the contrary, in some cases where the defective specimens have been examined more closely, no clear difference from the group "branched" + "unbranched" specimens has been found (one example can be found in Table XVIII).

From a study of Figs. 3 and 4, and from morphological observations, we now arrive at the following picture of the growth of a *Hylocomium* segment. It starts as a small bud, usually visible in early autumn, as soon as its parental segment has grown out. It grows slowly during autumn, winter, spring and early summer. At the end of the spring it makes up some ten per cent of its parental segment's weight. In summer (usually in July or August) a period of rapid growth starts, which fades out in late autumn. During this period

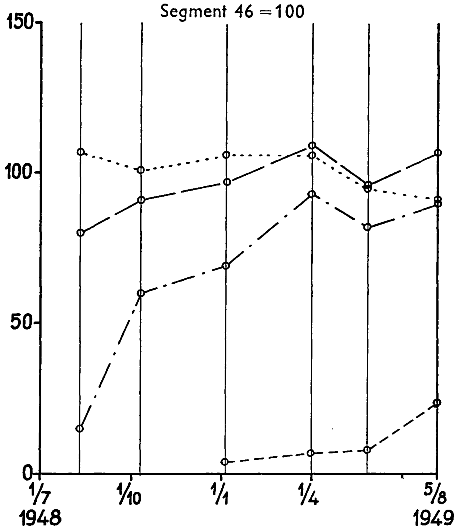


Fig. 4 a. Weight of different segments of *Hylocomium splendens* from Site I at different seasons, expressed in per cent of segment 46. August 1948 to August 1949. "Branched" and "unbranched" specimens.

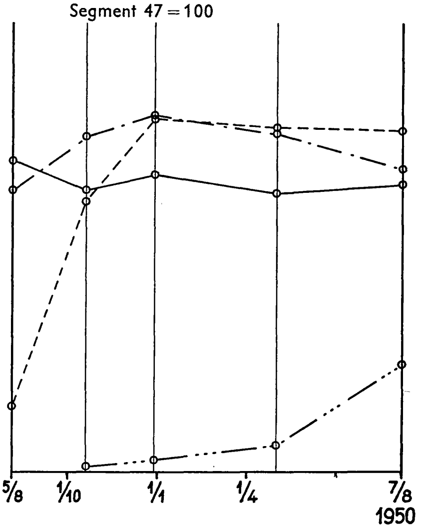


Fig. 4 b. Weight of segments as in Fig. 4 a, in per cent of segment 47. August 1949 to August 1950. "Branched" and "unbranched" specimens.

For symbols, see Fig. 3 b (p. 23).

the segment attains its full size, or nearly so. Side-branches of the first order grow out in late summer, followed by those of second and third order. Changes during winter, spring and early summer are relatively small, except that fertile individuals develop antheridia and oogonia. During July to September there is probably a new growth period, as shown for segment 47 in Fig. 4 a, for segment 48 in 4 b and for segment 51 in 4 c. The growth during this period is much less marked than the growth of the same segment a year before, but as a slight elongation of the branches seems to occur, there is probably a real weight increase. It is not known whether there is a thickening of the cell walls, as it is very difficult to measure the wall thickness of the narrow and strongly refractive *Hylocomium* cells. An alternative explanation of the "second growth period" by particularly intense decomposition of the "base" segment would imply a decomposition of this segment at a rate similar to or faster than that of still older segments. These, however, appear to be much more decomposed.

The sporogonia start to grow out during this period (the autumn when the segment becomes two years old), continue growth during the winter and ripen in spring. The weight of the average segment changes but little during winter and spring. The fertile segments may behave differently, but make up only a

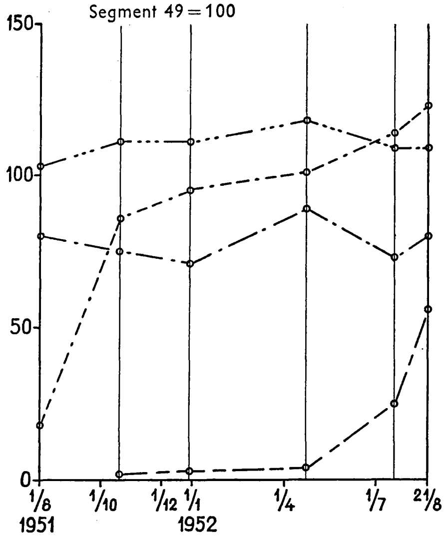


Fig. 4 c. Weight of segments as in Fig. 4 a, in per cent of segment 49. August 1951 to August 1952. "Branched" and "unbranched" specimens. For symbols, see Fig. 3 b (p. 23).

small percentage of the total in most habitats. Up until they are two years old most segments maintain their green colour, though less brightly than earlier. After the third spring, however, the segments have apparently performed their functions and the cells gradually die, while the colour changes to brown. It must be pointed out that the life-time and vigour of the cells varies enormously within the same individual, between different individuals in the same habitat, and between different habitats. The great variation in colour is especially easy to observe.

This description of growth applies in the first place to average *Hylocomium* individuals from Site I, Grenholmen, but also with more or less accuracy to individuals from several other types of habitats, particularly to normally dry forests where the moss community grows upon a typical mor humus layer. In moist habitats the beginning of the growth period in summer is often earlier than in dry ones (cf. STÅLFELT 1937 a p. 181). Within the same habitat the starting time may change from year to year (cf. August 1948 with August 1952 in Fig. 4). In shaded places *Hylocomium* segments persist green, and apparently alive, longer than in more exposed ones. In some places decomposition appears to start earlier than in others; this has been the case with several samples from very humid western Norway. On the other hand, break-

Table II. A comparison of average weight in branched and unbranched *Hylocomium* sympodia. Sample 493, collected in Site I, Grenholmen, 5. VIII. 1949.

Group of individuals	Number of segments		Average weights of segments, mg (Within brackets relative figures: sum of segments in per cent of segment "47")				
	"45"	"49"	"45"	"46"	"47"	"48"	"49"
Unbranched	300	300	11.5 (89)	12.4 (96)	13.0 (100)	10.2 (79)	2.6 (20)
Branched once, in 1946	13	26	22.2 (66)	$\frac{26.2}{2}$ (78)	$\frac{33.6}{2}$ (100)	$\frac{22.9}{2}$ (68)	$\frac{6.6}{2}$ (20)
Branched once, in 1947	20	40	22.3 (83)	20.8 (78)	$\frac{26.8}{2}$ (100)	$\frac{20.3}{2}$ (76)	$\frac{5.5}{2}$ (21)
Branched once, in 1948	40	80	17.5 (109)	18.7 (116)	16.2 (100)	$\frac{18.9}{2}$ (117)	$\frac{4.5}{2}$ (28)
Branched once, in 1949	18	36	12.8 (63)	16.2 (80)	20.3 (100)	12.0 (59)	$\frac{4.9}{2}$ (24)
Branched twice or more times	25	77	20.4 (69)	18.7 (91)	15.4 (100)	11.8 (112)	3.1 (32)
All branched	116	259	18.7 (80)	17.6 (91)	15.8 (100)	10.7 (92)	2.7 (26)
Branched + Unbranched	416	559	13.6 (85)	14.1 (94)	14.0 (100)	10.4 (84)	2.7 (22)

down is apparently slow in moss communities in more northern regions, where the old segments may maintain their colour and weight for a very long time (cf. Table IX).

Individual irregularities in growth also occur. The new segment may bud from the apex of the parental segment, giving rise to a monopodium instead of a sympodium. This abnormality is very common in certain localities, but generally rare. Where it occurs more frequently, it is difficult to determine the age of certain segments. Another irregularity is the formation of new sympodia from old side-branches and stem parts. The new segments are usually weak and slender. The phenomenon is probably caused by the death of parts of the stem while some of the old tissues are still alive. The death or deterioration of the middle part of the stem apparently removes the apical dominance exerted by the top—perhaps by stopping hormone transport—thus causing formation or growth of a new bud.

The main purpose of the growth investigation has been to find out a suitable time and method to determine the growth per unit area of the *Hylocomium* community. Evidently photosynthesis and dry matter increase in *Hylocomium* is not restricted to one segment at a time, but can occur in the two or even three youngest segments simultaneously. In samples collected in spring or early summer the third youngest segment (= segment 3) can usually be considered as full-grown (Fig. 4). The sum of all segments 3 from a certain area thus represents one year's growth within the area, although the segment in question has grown during more than two years. To determine one year's growth in this way may possibly equalize differences between different years. Nevertheless large growth differences between different years have been found, se Tables I and IX. It can even happen that these growth variations are so large that segment 2 in summer samples is considerably heavier than its parental segment, though segment 2 has probably not yet attained full size. In such cases a growth determination based upon segment 3 yields values which are too low (compared with the current growth), but it is difficult to say how much too low, as segment 2 may still grow. Detailed comparisons can therefore only be made between samples collected the same year and preferably at the same season. On the other hand we can then compare either segment 2 or segment 3. In places where decomposition starts very early, it may be better to compare segment 2. Slightly different methods have been used for comparisons of moss yields in different cases, and have been stated in each case.

In practice it is not easy to determine the weight of segment 3 directly, because some individuals are always broken during preparation and it is difficult to determine the age of loose segments except for segment 1 (bud) and segment 2. Therefore in the yield investigations the total amounts of the two youngest segments per unit area have been determined. If desired the amounts of segment 3 may then be calculated from the ratio between segment 3 and segments 1 + 2, determined from all undamaged individuals (cf. in this connection Table IX).

Chapter IV. Individual Variation in Size and Growth of *Hylocomium splendens*

It is a truism to state that plants, even of the same species and age, growing side by side, may differ considerably in size and growth-rate. These differences must, however, have some causes, which have been studied in the case of the *Hylocomium* community. Before discussing the causes of the size and growth variation we must find out how large the variation is and what rules it follows. This chapter is therefore devoted to a description of individual variation in size and growth. Other properties are also subject to individual variation, e.g., chemical composition, as will be shown later.

Statistical concepts

Variation can usually be visualized in a diagram as well as expressed by statistical parameters. Both methods will be used here to describe the variation within the *Hylocomium* community. Statistical methods are very useful when we have to work with complex relationships, like partial correlations, and make it possible to evaluate the importance of different sources of variation. On the other hand one-sided use of statistics may gives us a schematic picture of nature. The calculation and use of simple statistical characteristics often presupposes a more or less normal distribution of the data, which may or may not exist. When the nature of the variation studied is completely unknown it may be advantageous to use both the graphical and the statistical method.

Definitions of the statistical terms used here can be found in any modern statistical textbook (e. g. BONNIER & TEDIN 1940). To describe a variation about a mean value we use the mean square and its square root, the standard deviation. The mean square is obtained by dividing the "sum of squares" (of deviations from the mean value) by the number of degrees of freedom, which directly depends on the number of values.

If we want to decide whether a difference found between two or more means is "significant" in the statistical sense, we take the ratio between the mean squares for "between groups" and "within groups" (the larger as numerator). We then consult a table (e. g. in BONNIER & TEDIN 1940) to determine the values for such "variance ratios" for different levels of significance at random variation. If our value is higher than that attained once in 1,000 cases, we may call it highly significant (often marked with three asterisks). If it is lower, but still above the value attained ten times in 1,000 cases, we call it significant (two asterisks). Between 10 and 50 times in 1,000 cases we can only call it suggestive (one asterisk).

If we find a high significance for a variance ratio between/within groups, it is unlikely that the difference in mean value (or components of variation, cf. Table III) between groups would be caused by purely random variation. We can then ascribe the difference to some external cause, but the statistical analysis does not tell us anything about the nature of this cause.

When we are dealing with two interrelated properties the most convenient estimate of the correlation is the correlation coefficient, which measures the sum of the deviations of the single values from the straight regression line computed from the whole body of figures. The correlation coefficient, r, is expressed in relative units and is always between $+1$ and -1. Positive values indicate positive correlation, negative values negative correlation. Values near zero, either positive or negative, indicate little or no correlation, values near $+1$ and -1 very strong correlation. With increasing number of data, the correlation coefficient becomes more accurately estimated (in the same way as a mean or a standard deviation), and the value required for statistical significance becomes lower.

In many cases three or more properties are interrelated, and we may want to know the correlation between two of these properties. The direct correlation coefficient between the properties *a* and *b*, r_{ab}, is then unsatisfactory, as it may be influenced by the dependence of both properties on a third property *c*. The influence of *c* has then to be eliminated by calculating the partial correlation coefficient between *a* and *b*, $r_{ab.c}$.

Reliability of average figures for Hylocomium growth

Before we discuss the problem of how size and growth varies within the *Hylocomium splendens* community we must consider another question of a statistical nature: how reliable are the data and curves presented in Chapter III?

These data are based upon averages calculated from great numbers of individuals. The "error" due to random variation within the sample can be estimated by dividing the sample in smaller parts, the different segments of which are weighed separately. If necessary the segments can be weighed individually. The standard deviation or "error" of mean values such as those plotted in Figs. 3 and 4 can then be estimated. In the relative units used in Fig. 4 and Table I the standard errors of the given figures vary between 1 and 5 in the investigated cases (samples from 7. VIII. 1948 and 5. X. 1948). The value of these standard errors is, however, doubtful, because there are other possible errors which are not included in the standard errors. Factors possibly causing variation are differences in proportion of exposed and shaded *Hylocomium*, and of *Hylocomium* from ground and from stones and tussocks, respectively. A rough idea of the importance of these errors can be obtained from the sample collection from 5. I. 1949, when eight small samples were collected in Site I, instead of one large sample as on other occasions. One of these eight samples was an average sample, collected as usual, but the other seven were taken from different habitats within Site I.

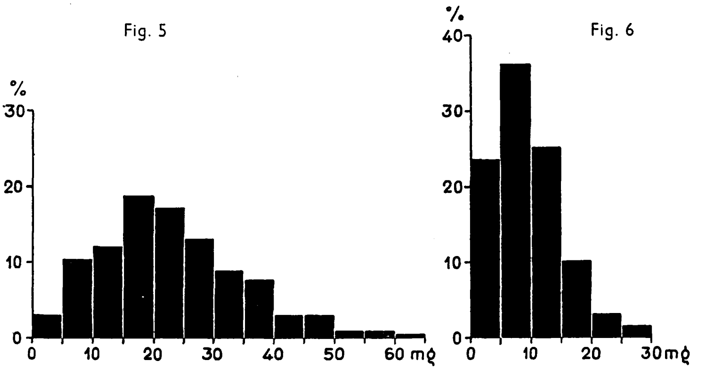
The average weights of the different segments of the 232 "unbranched" individuals in these eight samples have been (segment 46 = 100 per cent):

Segment	45	46	47	48	49
	105±5	(100)	96±6	61±6	4±1

(Note. The figures for 5. I. 1949 plotted in Fig. 4 are not identical with these figures: Fig. 4 deals with the sums of "branched" and "unbranched" individuals.)

The "errors" obtained for the eight samples from 5. I. 1949 should probably be considered as maximum estimates of the random variation for the data used in the seasonal growth curve. The reason is that the samples in this case were chosen for their dissimilarity (representing the different conditions realized within Site I), while otherwise an attempt has been made to obtain as similar samples as possible,

In this connection it should be emphasized that only a small part of this random variation can be called "error" in a strict sense. The instrumental error introduced by the weighing only makes up one per cent or less of the weight of an average segment. There is also an error due to the fact that the segments may not always be separated in the right places; sometimes a small piece adheres to the parent segment. But also this error seldom exceeds one or two per cent of the segment weight. For the means of eight samples we found the above standard deviations, between 5 and 10 per cent of the figures for full-grown segments. The standard deviations of each sample mean then average 20 per cent, and the standard devia-



Figs. 5 and 6. Distribution of weight classes of segment 2 of *Hylocomium splendens* in samples from Os prestgårdsskog, collected 15. VI. 1950. Fig. 5. Sample 672, moderately exposed. Fig. 6. Sample 677, shaded.

tions of the individual moss plants must be still higher. Evidently the biological variation inherent in the *Hylocomium* community is much greater than the errors in the measurements.

Unfortunately we must also pay attention to more or less systematic errors due to possible changes in the segment used as a base for the calculations. While these errors can hardly invalidate our conclusions as discussed on p. 23, they prevent more accurate growth determinations by the method used. Sampling from a large number of randomly assigned places on each occasion can diminish the error in absolute figures, thus improving the curve in Fig. 3. This very large increase in labour would, however, only correspond to a small increase in accuracy. If a more detailed curve for the seasonal growth of *Hylocomium splendens* is desired, some method involving direct growth measurements is preferable.

Distribution in size-classes

We may now consider the main problem of this chapter: the individual variation in size and growth. At first we shall study the distribution in size-classes of the *Hylocomium* segments from small sample plots.

Figs. 5 and 6 present the distribution in weight classes of segment 2 (segment 49) from two samples collected in June, 1950, in Os near Bergen, western Norway. Similar diagrams have also been drawn for several other samples, especially from Sites I and II (Grenholmen), but these samples have not contained as many individuals as the samples from Os. Apart from this these other diagrams agree with Figs. 5 and 6. Fig. 5 is based upon all segments 2 of *Hylocomium splendens* from sample 672 (207 in number), which have been weighed individually. Sample 672 is the entire moss carpet from a plot 25 × 25 cm beneath a spruce, but with a good light supply (at the margin of a clear felling). Fig. 6 represents the 127 segments 2 from sample 677, which is a similar moss carpet, collected beneath a dense canopy of spruce.

We see at first in the diagrams that the average weight of a segment is much higher in sample 672 (exposed) than in sample 677 (shaded); the same is true of the maximum weight. The most striking feature in Fig. 5 is, however, the low frequency of small segments. The same would be the case in Fig. 6, had not the low average weight (in comparison with the class width) concealed the fact. This will be shown more clearly in Fig. 8.

In communities of perennial plants a high degree of replacement of individuals by seeds (or spores) is indicated by the presence of a large number of small individuals, of different age but including seedlings (cf. LINKOLA 1935, PERTTULA 1941). Where the small size-classes are under-represented, the renewal of the plants by seedlings must be slow, if occurring at all (TAMM 1948). Consequently such an underrepresentation of young and small plants is a characteristic feature of many closed plant communities, where propagation by seedlings is possible only when some disturbing influence decreases competition.

The under-representation of moss individuals with small segments, which recurs in *Hylocomium* samples from very different habitats (see Figs. 14 to 18), should probably be interpreted in the same way as the corresponding phenomenon in higher plant communities: propagation by spores is rare in the established community. A high frequency of germinating spores or protonemata is no proof that propagation occurs, as seedlings are also common in many communities where they never attain maturity. Indeed, no cases where young *Hylocomium* plants grow out from protonemata have been observed in the communities studied.

Variation in growth-rate. Renewal of the moss individuals

Before we can accept definitely the conclusion that propagation by spores is rare in the *Hylocomium splendens* community, we need to know more about the growth rate of the individuals of different size. Another pertinent question is the origin of the small individuals, if there are no "seedlings".

The growth-rates of the *Hylocomium* individuals in samples 672 and 677 are depicted in Figs. 7 and 8, where the weight of segment 2 (49) is plotted against the weight of its parental segment (48). All individuals with the segments in question are weighed except those damaged during preparation. The following conclusions can be drawn from the diagrams: 1) Segment 49 is much larger than segment 48, an observation also valid for other samples, cf. Table IX. 2) There is a very large growth variation, slightly greater in the exposed sample (Fig. 7) than in the shaded one (Fig. 8). 3) There is no clear difference in growth-rate between small and big individuals, i.e., the regression line follows fairly well a straight line from the origin. 4) The dots representing sympodia branching from 1948 to 1949 lie well within the range

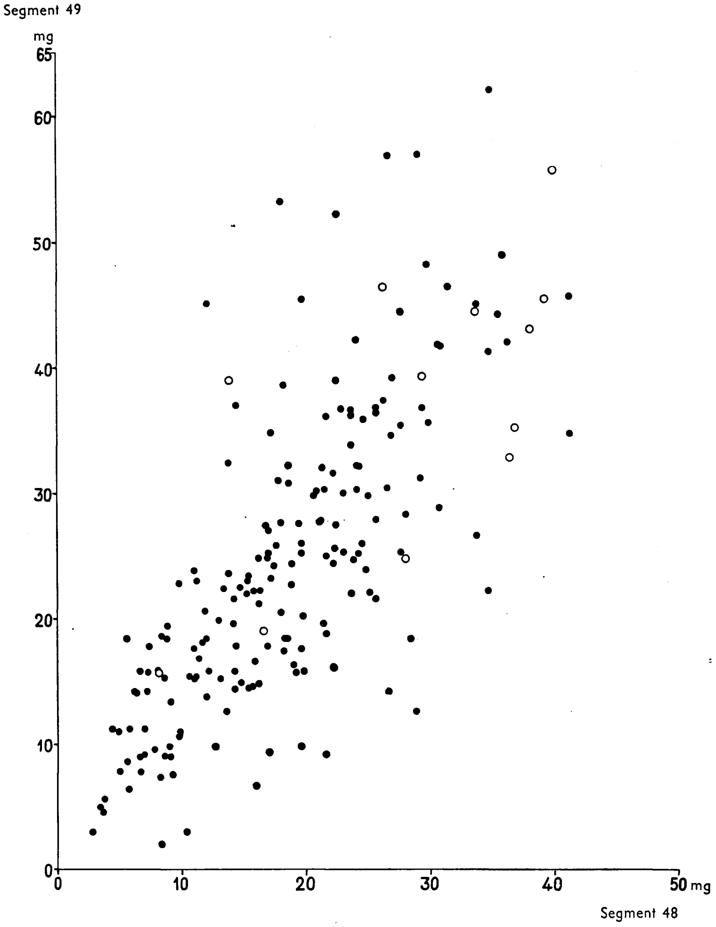


Fig. 7. Weight of segment 49 of *Hylocomium splendens* plotted versus the weight of segment 48. Sample 672, moderately exposed.

● "Unbranched" individuals ○ "Branching" individuals

of variation of the unbranched ones. When large samples have been studied, we have as a rule found higher average weights and faster growth of "branching" individuals (cf. Table II), but the individual growth variation is apparently big enough to prevent this difference from showing up when merely a few individuals are compared.

According to 3) individuals of all size-classes have approximately the same average growth rate, and the growth of the small individuals is not sufficiently rapid to suggest a continuous renewal of the moss individuals by "seedlings". The occurrence of a few "branching" but rather small segments in Figs. 7

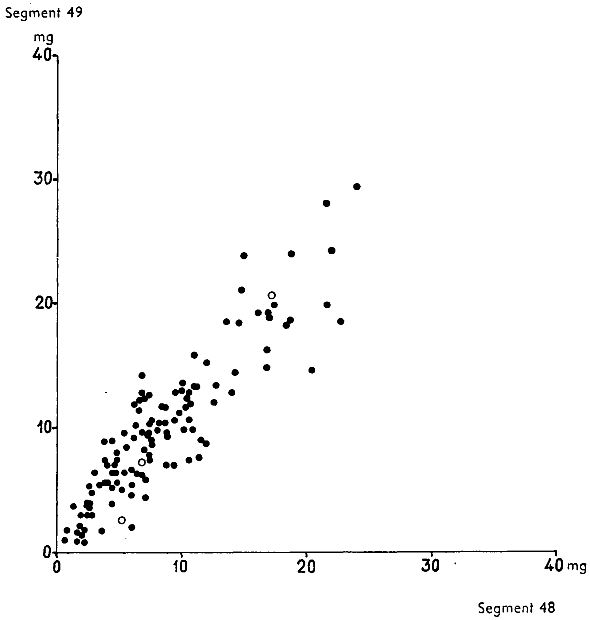


Fig. 8. Weight of segment 49 of *Hylocomium splendens* plotted versus the weight of segment 48. Sample 677, shaded.
● "Unbranched" individuals ○ "Branching" individuals

and 8 may give us a clue to the origin of the very small individuals. (Small individuals are of course those with small segments; unbranched sympodial chains containing both very small and large segments are exceptions, in spite of the great growth variation.) The daughter segments of such small "branching" segments, or at least one of each pair, are usually very weak and slender. Such slender segments may also, as mentioned on p. 26, grow out from old segments, isolated from their daughter segments by the death of stem parts. It is very difficult to decide whether all very small individuals have this origin or not, as they are extremely fragile and often break off during preparation; but it is clear that a large percentage of the small individuals have started as such side-sympodia. Of those small individuals which cannot be traced to a parent segment of more normal size, a large number have maintained approximately the same size for several years, as long as they can be followed back. It has not been possible to decide whether the remaining group of defective small individuals contain some "seedlings" or not.

A renewal by vegetative propagation, branching, is continuously going on in the moss community. Though most sympodia seem to be long-lived, injuries always occur, e.g. by animal excrement or trampling, and the places of killed or damaged specimens will soon be occupied by neighbours. The branching is also a means of preserving a suitable segment size of *Hylocomium splendens* (see Table II), especially as fast-growing specimens tend to branch more often than the average, as witnessed by the slightly faster growth of the "branched" individuals as compared with the "unbranched" ones (Tab. I).

In spite of the rarity of propagation by spores in the *Hylocomium* community, we must of course anticipate such propagation when *Hylocomium* colonizes new sites, e.g. in a young forest growing up on a burnt area.

More points of interest in connection with the growth variation

The large variation about the regression line in Figs. 7 and 8 is in principle the same as the "error" spoken of in connection with the reliability of the growth curve. For a correct understanding of ecological problems it is, however, absolutely necessary to consider variations of this kind not only as obstacles causing "errors" but also as a source of information. The deviations from the regression lines in Figs. 7 and 8 are of interest because they express the influence on moss growth of the variation in all factors other than the weight of the parent segment. Among these other factors, some may be internal, for example the vitality of the parent segment, or the size or vitality of the grandparent segment. Other factors are external, such as the supply of light, moisture, different kinds of nutrients, influences of animals and—last but not least—influence of other plants, exerted by competition for the factors mentioned or by litterfall, shading, etc.

Before we discuss the causal relationships we should find out as much as possible about the nature of the variation in Fig. 7 and similar diagrams. There are at least two questions which can be studied by statistical methods: 1) Does the variation depend on the distance between the individuals, so that neighbours are more alike in growth-rate than specimens picked out at random from a sample plot? 2) Does the size of a segment depend not only on its parent segment's size but also on the size of its grandparent segment, so that a small parental segment may be compensated for by a large grandparent segment and vice versa. A negative correlation between a segment and its grandparent segment is also possible; its meaning will be discussed later.

To study question 1) all individuals from sample 672 which branched before 1948 were used. There were 19 such pairs of sympodia, unusually many for a sample from a plot 25×25 cm. The average of the ratios between the weights of segment 49 and segment 48 was 1.35 for the 38 sympodia. Table III presents the result of a further statistical analysis. The variance ratio formed from the mean squares for the variation between and within pairs is only 2.16, which is not statistically significant, but coincides approximately with the value for 5 per cent probability (ca. 2.2) and may thus perhaps be called suggestive. The statistical

Table III. Variation in ratio of segment 2 to segment 3, within and between pairs of connected sympodia. Sample 672, collected 15. VI. 1950 at Os near Bergen, and constituting the entire moss carpet from a 25×25 cm plot beneath a spruce, light exposure fairly good.

Source of variation	Degrees of freedom	Sum of squares	Mean square	Standard deviation
Total variation	37	10.7034	0.2893	±0.54
Between pairs.....	18	7.1880	0.3993	—
Within pairs.......	19	3.5163	0.1851	± 0.43
Variance ratio $\frac{0.3993}{0.1851}$ = 2.157 Probability slightly above 0.05				

analysis thus fails to show any clear difference in variation between neighbouring plants as compared with that between randomly chosen plants within the same small plot. This result is probably due to the limited number of cases; very likely a larger sample would have given a significant variance ratio, as the existence of such local differences is very probable.

From another point of view, however, Table III can give valuable information, viz. an idea about the variation within the pairs as compared with that between randomly chosen plants. In the last column of Table III we find the over-all standard deviation among the 38 individuals, 0.54, and the standard deviation within pairs, 0.43. Even if these figures are not so accurately determined as if the sample had been larger, it is evident that a considerable part of the variation remains when we compare *individuals of the same clone growing a few centimetres apart*. This result must be kept in mind when we consider the causes of variation.

Perhaps it may be of interest that Table III deals with a less usual type of group difference: components of variation, not fixed relations among means, are responsible for the difference in mean squares between and within groups (cf. EISENHART 1947).

Question 2), the correlation between a segment and its grandparent segment, can best be studied by calculating the partial correlation coefficient between these two segments after elimination of the influence of the segment between. Such calculations have been carried out for four different samples, listed in Table IV together with the results of the calculations.

If we first look at the direct correlation coefficients in Table IV, we find "highly significant" values in all cases, though the coefficients are higher for correlation between two directly connected segments than between segments 2 and 4. The bud (segment 1) shows less correlation with its parent segment than this segment with segments 3 and 4. One of the possible explanations might be that some buds had started their growth period when the sample in question was collected, while others had not.

The highest correlation coefficients have been obtained in samples from shaded plots, +0.85*** between segments 3 and 4 in sample 492, and +0.87*** between segments 2 and 3 in sample 677. The correlation coefficients between segments 3 and 4 have been lower than those between segments 2 and 3 in the Norwegian samples (Nos. 672 and 677). In this connection we may remember that decom

Table IV. Correlation coefficients between weights of different segments from the same *Hylocomium splendens* individuals.

No. of sample	Date of sampling	Locality Exposure	No. of specimens	Correlation coefficients between segments						
				1 and 2	2 and 3		3 and 4		2 and 4	
				direct r_{12}	direct r_{23}	partial $r_{23\cdot 4}$	direct r_{34}	partial $r_{34\cdot 2}$	direct r_{24}	partial $r_{24\cdot 3}$
185	7.VIII.48	Site I. Grenholmen. Moderately exposed.	100	+0.42***	+0.74***	+0.51***	+0.79***	+0.62***	+0.63***	+0.11
492	14.VIII.49	Rönninge. Very dark spruce forest	57	not det.	+0.77***	+0.68***	+0.85***	+0.79***	+0.56***	—0.30*
672	15.VI.50	Os. Moderately exposed spruce forest	130	not det.	+0.73***	+0.51***	+0.69***	+0.42***	+0.65***	+0.28**
677	15.VI.50	Os. Very dark spruce forest	69	not det.	+0.87***	+0.75***	+0.70***	+0.32**	+0.68***	+0.19

position started very early in this samples, so that segment 4 appeared to be considerably affected. This process may of course lower the correlation coefficients, if different segments are decomposed at a different rate.

In Table IV the partial correlation coefficients are also given. They are all lower than the direct coefficients. As far as the correlation between two directly connected segments is concerned, all partial coefficients but one are still "highly significant". The exception is $r_{34\cdot 2}$ in sample 677, which is "significant" only.

In the last column of Table IV we find the partial correlation coefficients between a segment and its grandparent segment, after elimination of the segment between. Of the four values three are positive and the fourth negative. Only one of the values, +0.28** in sample 672, is "significant". The negative value — 0.30* is "suggestive". There is thus not much evidence for the dependence of a segment on its grandparent segment, in addition to that resulting from the physiological connection between two directly joined segments. Even if a partial correlation may exist in some cases, values such as +0.28 and — 0.30 do not imply more than a very loose relation.

The most likely cause of the correlations between different segment — partial as well as direct correlations — is of course direct physiological action of one segment on the other. A strong positive partial correlation would for example be expected between segments 2 and 4, if substances were translocated from dying segments to the youngest segment. Another effect of the parental segment is that it supports the younger ones. A strong negative partial correlation between granddaughter and grandparent segment might be difficult to understand, but it is possible that a more loose negative correlation may be brought about by a kind of "position effect". A general tendency of a moss plant which once had reached a favourable position, to maintain this position for at least some years, and a corresponding persistent effect of unfavourable positions, would be expected to give rise to such a negative partial correlation. It is not quite clear whether this case can be realized in a plant community in equilibrium.

While it would be dangerous to explain an existing strong correlation in this rather speculative way, the absence of a partial correlation between granddaughter and grandparent segment in two or three cases out of four, and the possible existence of a weak positive correlation in the fourth case, suggests that the factors described above do not have great importance. It is of course possible but not very likely that both factors—physiological action from segment 3 to segment 1, and persistence of a favourable position of the individual—are important but balance each other even under the very different conditions in the four sample plots in question.

Conclusions

The results of our studies on the individual growth variation within the *Hylocomium splendens* community can be summarized as follows:

The size of a *Hylocomium* segment depends to a certain extent on the size of its parent segment, but it is subject to a strong and irregular variation. The causes of this variation are almost certainly to be found outside the moss plant, as strong variation occurs even between moss individuals belonging to the same clone. Besides, it is difficult to imagine genotypes with dispositions for weak and strong growth under the prevailing conditions growing side by side for a long time in a community where propagation is mainly vegetative. The heterogeneity in moss growth thus leads us to believe that one or more environmental factors (including biotic factors) change from place to place and from year to year in an irregular way within the *Hylocomium splendens* community.

Another major point of interest in the structure of the *Hylocomium* community is the low frequency of small individuals, which shows us that the rate of renewal, except by branching, must be very small.

It would be interesting to compare the structure of the moss community with that of other plant communities, particularly with respect to the growth variations. The quantitative growth of herb and grass specimens during a series of years is difficult to measure. We know, however, that the same individual may occupy a similar position in the community for many years (TAMM 1948).

It is easier to measure tree growth than the growth of herbs and grasses. Records of diameter growth during two subsequent years for pine, birch and spruce give pictures similar to Figs. 7 and 8, with a large variation around a regression line. Diameter growth is, however, not the same as total production, and some of the scatter may be due to imperfect correlation between diameter growth and total production. A similar view may be taken in the case of top shoot length of beech, where Holmsgaard (1950) has found only a loose correlation between the lengths of two subsequent shoots.

At present we have to confine ourselves to the moss community, but the value of measurements of growth variation ought to be stressed more often in plant ecology. The competitive activity of a plant is a function of its growth potential, and variations in the growth of the members of a plant community thus indicate variations in the intensity of competition.

Chapter V. Variation in Production and Structure of the *Hylocomium splendens* Community under Different External Conditions

Moss yield versus light and tree canopy

The photosynthesis of *Hylocomium splendens* and some other forest mosses has been studied by Stålfelt (1937 b). Working with samples from a pine forest with a moderate light supply to the ground he arrived at the conclusion that within such habitats light occurred in excess of the demands of the mosses (l. c. p. 47). While this conclusion seems well supported by the experimental data, little is known about the range of conditions where it holds in nature.

In order to study the relation of the moss production to light intensity, a series of samples was collected in May and July, 1949, from Site II, Grenholmen (see Figs. 9 and 10).

The light intensity is here a function of the tree canopy, with the darkest plots beneath spruce with drooping branches and the lightest plots at some distance from the trees. As the light supply to the ground is composed partly of diffuse light and partly of irregularly distributed direct sunshine, all light measurements in forest except long-term integrations are approximate only. In the present measurements only the diffuse light on the sample plots has been recorded; the measurements were carried out on a day with overcast sky (11. IX. 1949). A barrier-layer photocell (view angle almost 180°) was placed with the opening upwards just above the moss carpet (or field layer, where such occurred). The photocell was made horizontal with a water-level. The light on a reference point in the middle of the small opening on the map Fig. 10 was measured at short intervals, and the light on the sample plots was expressed in per cent of the light on the reference point. Only relative figures can be obtained by this method, but they make it possible to arrange the plots according to increasing light supply. Regarding the reliability of this arrangement, it may be mentioned that two other series of light measurements have been made on the same plots, using a simple photographic exposure meter; these measurements placed the plots in virtually the same order, although the per cent light values differed somewhat. The percentages of light given in the Tables and Figures must

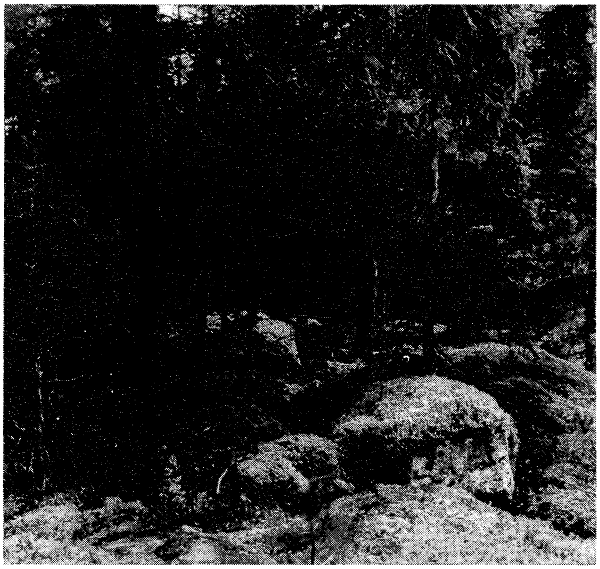


Fig. 9. Site II, Grenholmen, Roslags-Bro parish, Uppland. 30. IV. 1950.

not be considered as percentages of the light on an open field, or above the tree crowns, where the light certainly is stronger than at our reference point.

From the sample plots the entire moss carpets within a frame 25 × 25 cm were out out and divided according to species. Segments 1 and 2 of *Hylocomium* were collected together and analysed chemically. In part of the samples the ratio of these segments to segment 3 was determined on all undamaged individuals (see Table X). As the sum of segments 1 and 2 happened to be roughly equivalent to segment 3 in weight, the former sum was considered appropriate for growth comparisons within the series. Some of the samples were taken two months later than the main series, but growth was slow during this period (26. V.—25. VII. 1949), so both series are fairly comparable (cf. Fig. 11).

The other moss species contained in the samples are listed in Table XXVII. Annual shoots corresponding to those of *Hylocomium* could often be distinguished in *Pleurozium Schreberi* and *Ptilium crista castrensis* (cf. p. 13). Where this was not possible about half of the green parts of these species was taken to represent one year's growth (cf. ROMELL 1939). In the case of *Brachythecium* species and liverworts approximately one third was taken, as parts which appeared to be rather old also had a green colour. This uncertainty in the growth determinations of course introduces an error in the yield figures, but as a rule mosses other than *Hylocomium* have only made up smaller fractions of the samples (see Table V), which makes the error less important. A more serious obstacle has been the occurrence of lichens (*Cladonia rangiferina* and *sylvatica*) in some of the samples. No determination of the age of the lichen shoots has been possible, and the three samples in Table V containing appreciable amounts of lichens have therefore had to be excluded from the yield diagrams. It should, however, be pointed out that

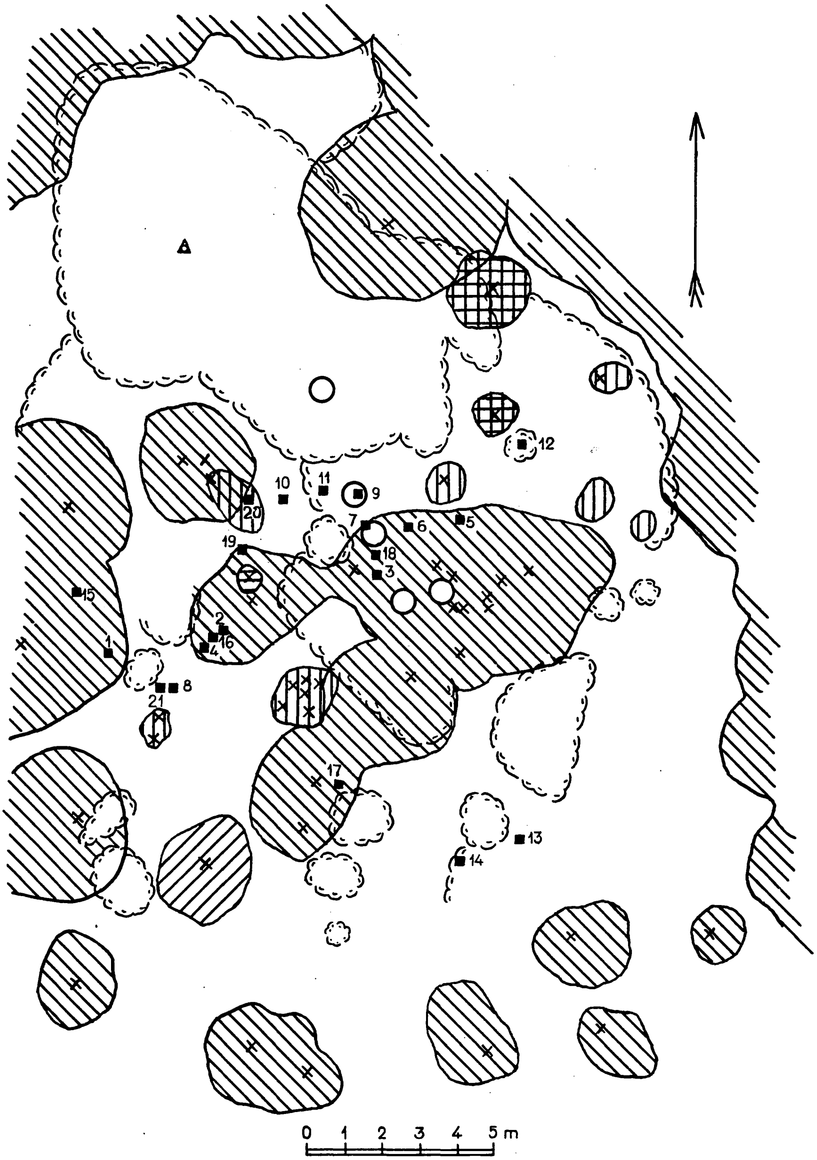


Fig. 10. Map of Site II, Grenholmen, with the location of the sample plots and the funnels for collection of rainwater.
For symbols, see right-hand page.

these three samples show a rather low production in the ground layer, even if all the lichens are considered as one year's growth, which must be a large exaggeration since lichens grow very slowly. One explanation could be that plots where lichens thrive are less suitable for *Hylocomium*, either because of some external factor, because of a poisoning effect of the lichen acids (cf. Burkholder et al. 1944, 1945), or even because of a parasitism by the lichens (cf. McWhorter 1921).

The figures for total moss production in the sample plots are given in Table V together with the amounts of the major constituent species. To obtain a clear picture of the relation between moss growth and light we may look at Fig. 11 a, for the relation between moss growth and tree canopy at Fig. 11 b. We see here that plots beneath tree crowns show an increasing moss production with increasing light supply, while this is not the case in the open, where the light intensity exceeds 50 per cent. On the other hand, plots in the open produce less moss with increasing distance to tree crown projections. The maximum moss production seems to obtain beneath the border of the tree crown projections or just outside them, always supposing that there is no interference from a shrub or field layer. Dwarf shrubs with a high degree of cover occur only on three plots, viz. Nos. 8, 13 and 14, and even there the *Vaccinium myrtillus* and *V. vitis idaea* cover is not dense.

As is was considered desirable to confirm the results obtained from the samples in Table V, regarding both the correlations found in Fig. 11 and the chemical data discussed in Chapter VI, a new series of samples was collected from the same locality half a year afterwards, 28. XII, 1949. It might be suspected that winter samples would not give exactly the same relationships, but unfortunately these samples had to be taken from smaller areas (1.13 dm^2), because most of the larger patches with uniform *Hylocomium splendens* carpets had been sampled already in the first investigation. On account of the small size of the plots, the yield data from the winter samples (listed in Table VI, botanical composition in Table XXVII) are not very reliable. However, most

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Explanations to Fig. 10.

▨ Pine with crown projection *(Pinus silvestris)*

▧ Spruce » » » *(Picea abies)*

⊠ Birch » » » *(Betula verrucosa)*

⊟ Juniper shrub with crown projection *(Juniperus communis)*

⊞ Rowan (mostly shrubs) with crown projection *(Sorbus aucuparia)*

■ Sample plot

○ Rainwater funnel

▷ Standard point for light measurements

◌ Rock or stone

Table V. Production per unit area by the ground layer within different plots in Site II, including the contributions from different species. Samples from 26. V. 1949 (Nos. 1—14) and from 25. VII. 1949 (Nos. 15—21). Dry weight determined in vacuum at 55°C. Yield estimated from sample plots 6.25 dm². Location of plots, see map Fig. 10. For species occurring in amounts lower than 10 mg/dm², see Table XXVII, p. 137.

No. of sample	Relation to tree canopy	Light (% of that in opening)	Moss growth, dry weight in mg per dm²				Lichens* (Total amount, mg per dm².)
			Hylocomium splendens Segm. 48 + 49	*Pleurozium Schreberi* (Annual shoots)	Other species (Annual shoot when distinguishable, otherwise ½ to ⅓ of green parts)	Total moss growth	
1	Inside	12.5	282	88	*Dicranum* sp.** 10	380	0
2	"	20	330	112	*Aulacomnium palustre* 14......	456	0
3	"	25	283	149	—	432	0
4	"	35	530	109	*Aulacomnium palustre* 29......	658	0
5	"	45	426	355	—	781	0
6	"	50	204	318	—	522	106
7	Beneath border......	60	386	122	*Dicranum* sp.** 16 *Ptilium crista castrensis* 56...	580	328
8	1 m outside	55	1 034	22	—	1 056	0
9	1 " "	70	829	86	*Aulacomnium palustre* 42 *Dicranum* sp.** 18	975	0
10	1 " "	70	242	330	*Dicranum* sp.** 19 liverworts 13	604	211
11	1.5 m "	80	752	82	*Dicranum* sp.** 91	925	0
12	2 " "	70	371	147	*Dicranum* sp.** 14	532	0
13	2 " "	70	469	136	—	605	0
14	2.5 " "	65	474	24	—	498	0
15	Inside	20	550	56	*Dicranum* sp.** 13	619	0
16	"	25	513	115	*Aulacomnium palustre* 11......	639	0
17	"	30	425	80	*Dicranum* sp.** 14	519	0
18	"	35	440	314	—	754	0
19	Beneath border......	45	485	162	*Aulacomnium palustre* 27......	674	0
20	Beneath border......	55	812	101	—	913	0
21	1 m outside	55	883	55	*Dicranum* sp.** 18	956	0

* *Cladonia rangiferina* and *sylvatica*.

** As a rule *Dicranum scoparium*, in some cases also *D. undulatum*.

plots show a moss growth during the autumn which is of the same order of magnitude as that for the adjacent summer sample. The maximum yield sample, No. 562, is found 1 m outside a spruce crown projection, close to the highly productive plots Nos. 8 and 21. Exceptions from the relationship found in Fig. 11 a are samples 570 and, less decidedly, the adjacent summer sample 15. It may be worth noting that plots 15 and 570 are the only two

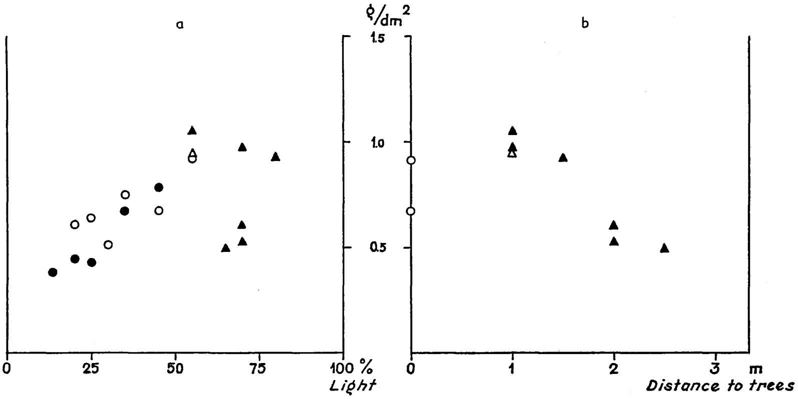


Fig. 11. Annual growth of dry moss within the sample plots in Site II in relation to (a) light and (b) distance to the nearest tree crown projection. Data from Table V.

	26. V. 1949.	25. VII. 1949.
Sample inside tree crown projection	●	○
» outside » » »	▲	△

Table VI. Production per unit area by the ground layer within different plots in Site II, as previously in Tab. V. Samples from 28. XII. 1949. Estimated from sample plots 1.13 dm^2. Vacuum drying 55° C. For species occurring in amounts lower than 10 mg/dm^2, see Table XXVII, p. 137.

No. of sample	"Reference number" (in Table V)	Relation to tree canopy	Light (% of that in opening)	Moss growth, dry weight in mg per dm^2			
				Hylocomium splendens Segm. 49	*Pleurozium Schreberi* (Annual shoots)	Other species (Annual shoots when distinguishable, otherwise $^1/_2$ to $^1/_3$ of green parts)	Total moss growth
565	1	Inside......	12.5	231	40	—	271
564	2	"	20	167	76	—	243
570	15	"	20	472	78	—	550
559	3	"	25	156	97	—	253
573	17	"	30	246	97	*Ptilium crista castrensis* 10......	353
563	4 & 16	"	30	320	133	—	453
572	18	"	35	275	195	—	470
557	5	"	45	286	148	*Ptilium crista castrensis* 93......	527
571	19	Beneath border......	45	306	49	*Aulacomnium palustre* 56......	411
556	7	Beneath border......	60	288	131	*Dicranum scoparium* 11......	430
567	20 & 10	0.5 m outside	60	549	45	—	594
562	8	1 " "	55	726	12	—	738
555	9	1 " "	70	227	23	*Dicranum scoparium* 29......	279
561	11	1.5 " "	80	395	206	—	601
558	12	2 " "	70	450	69	*Dicranum undulatum* + *D. scoparium* 79......	598
569	13	2 " "	70	427	158	—	585
568	14	2.5 " "	65	306	45	—	351

plots which receive rainwater dropping from the ends of branches of *two* fairly large spruces. The importance of such a supply will be discussed later.

The winter sample series thus adds little to the information we have already got from Figs. 11 a and b, where the sample size made the data less subject to sampling errors.

Moreover, we can never expect very strict relationships between yield and external factors in investigations of this type. The light measurements are rather primitive and, as has been pointed out earlier, not representative for the whole growing period. A rough estimate of the sun exposure of the plots has been made in order to correct the measurements of the diffuse light, but no clear correlation with the yield appeared. Plots 15 and 170 are, however, among the plots which are exposed to direct sunshine during a short part of the day. Also the concept "distance to tree crown projections" may imply very different conditions according to the height, shape and species of the tree in question. Some of the plots, as mentioned, also contain some field vegetation, mainly *Vaccinium myrtillus* and *V. vitis idaea*, but also scattered *Deschampsia flexuosa*, which to some extent may act as a substitute for a tree canopy, whatever the effect of the canopy on the moss carpet may be.

We can obtain further information about the light/yield relationships from the samples collected in western Norway (Table VII). All the samples in Table VII were taken beneath tree crowns. The tree species forming the canopy may be of some importance for the moss yield, as will be discussed later. If we for that reason only compare samples collected beneath spruce we find again a decreasing moss production with decreasing light, as in Fig. 11 a. Sample 672 shows the highest yield of all moss carpets studied. It was collected from a well-developed and uniform moss carpet growing under conditions which must be extremely favourable for *Hylocomium splendens*. Its annual production (dry weight, estimated from the weight of segment 2) is 1.3 g/dm^2 (or t/ha), possibly somewhat more if the growth of segment 2 was not completed. Estimated from segment 3 (48) the production is lower, 1.1 g/dm^2, which is only little more than the maximum figure found in Site II (plot 8), where the yield also was estimated from segment 48. The lowest production was found in samples 634 and 677 beneath a dense spruce canopy. Sample 634 was collected just outside a distinct border, inside which no or few mosses occurred. Outside the border there was a continuous but thin carpet mainly of *Hylocomium*; inside the ground was covered with spruce needles.

The samples in Table VII were taken from different localities, but the forest type (planted spruce) and tree growth did not differ much between Rådalen and Os. Sample 640 was taken in pine forest of a poorer type at Grimseid, not far from Rådalen.

The results presented in Fig. 11 and in Tables V, VI and VII are quantitative

Table VII. Moss production per unit area within sample plots in western Norway. Samples collected in June 1950, at and near Rådalen (Nos. 631, 632, 633, 634, 640) and Os prestgårdsskog (Nos. 672, 677, 679). Estimated from sample plots 6.25 dm^2. Vacuum drying 55° C. For botanical composition, see Table XXVIII, p. 140. Segment 48 calculated (see p. 27)

No. of sample	Date of sampling	Light supply	Tree canopy	Amount of dry moss in mg/dm^2				Annual production of moss in mg/dm^2 estimated from		
				Hylocomium splendens			Other species "Annual shoots"			
				Segm. 50	Segm. 49	Segm. 48 (calc.)		6 + 8	7 + 8	5 + 6 + 8
1	2	3	4	5	6	7	8	9	10	11
631	9.VI.	Very good..	Pine	73	350	259	80	430	339	503
632	,,	,, ,, ..	,,	108	538	410	13	551	423	659
633	,,	Moderately low......	Spruce	69	481	323	131	612	454	681
634	,,	Very low...	,,	35	248	159	72	320	231	355
640	10.VI.	Fairly good.	Pine	82	515	—	24	539	—	621
672	15.VI.	Good......	Spruce	120	828	643	470	1298	1113	1418
679	,,	Fairly good.	,,	75	530	—	98	628	—	703
677	,,	Very low...	,,	35	242	212	69	311	281	346

expressions of phenomena which can often be observed in nature, but are difficult to treat in an objective way, as there are usually many disturbing factors.

A light/yield relationship is often obvious where mosses are growing beneath spruce. The mosses grow abundantly beneath the outer parts of the crowns and decrease in density and vigour towards the centre of the crown, where *Hylocomium splendens* is often replaced by scattered individuals of other species (e.g. *Thuidium tamariscinum* and *Plagiothecium* species). In the darkest places the ground is covered only by spruce needles. There is thus no doubt about the reality and wide applicability of the yield/light correlation; yet before we can infer a direct causation we should discuss factors other than light (see Chapter IX).

The correlation of *Hylocomium* yield to distance from trees is not quite as easy to observe in nature, because pure *Hylocomium* carpets are seldom found at a great distance from trees, except beneath a shrub or field layer, which may affect *Hylocomium* in the same way as do the trees. In habitats of the same type as Site II, with spruce growing in fissures of otherwise bare rock, a picture similar to Fig. 9 can often be observed: the mosses prefer the neighbourhood of the trees, and avoid large open areas. Only on steep slopes, particularly if facing north, do they seem to be independent of other vegetation. Apparently they require protection against intense and prolonged sunshine; this applies particularly to *Hylocomium splendens* and *Ptilium crista castrensis*, while for example *Pleurozium Schreberi* shows the same preferences but is somewhat more tolerant of sunshine. This intolerance is best exhibited in clear fellings, where *Hylocomium* and *Ptilium* are soon killed, at least in most parts of Sweden (cf. KUJALA 1926).

Although protection against sunshine is an important factor for moss growth, it is probably impossible to explain the yield/distance-to-tree relationship solely as an effect of sheltering. Some of the sample plots beneath or near the border of the tree crown projections are more exposed than some of the less productive plots away from trees. Moreover one gets the impression that *Hylocomium splendens* can stand a certain amount of sunshine if it has grown up in an exposed habitat (cf. p. 103).

An alternative explanation of the yield/distance-to-tree relationship might be that the trees give off something necessary or favourable to the mosses, a hypothesis which we shall discuss in Chapter VII.

Moss yield versus humidity

In Tables V, VI and VII data are given for moss samples from plots with different light supply. We may, however, also use these data for a comparison of moss yield in regions with different humidity, at least as a preliminary to more detailed investigations. Such would be required if we found any clear correlation yield/humidity, as there might be several factors, climatic and otherwise, differing between different regions.

To compare *Hylocomium* growth in different climates it is probably best to choose the maximum yields of *Hylocomium* communities from forest of as similar type as possible. The reason for choosing the maximum yield is that there may be several local factors depressing growth, but an increase of growth over that determined by major climatic factors is less probable in most natural habitats. To represent a dry climate we may choose the maximum figure for Site II (Grenholmen, Roslagen), plot 8, which has yielded little more than 1 t/ha (dry weight), measured in May, 1949. The annual precipitation is here in average ca. 550 mm. A corresponding figure for a very wet climate (precipitation ca. 2,000 mm/year) is that for sample 672 (Table VII), which yielded about 1.3 t/ha if estimated from segment 49, but less if estimated from segment 48, as in plot 8, Site II.

It may be objected that these values are far too few to admit a comparison. They are, however, chosen from among the best developed moss carpets within each region. Sample 672 in particular was taken in a fine moss carpet. *Hylocomium* communities appearing to be more luxuriant have only been observed on steep slopes, where water trickled down along the rock.

The difference in yield between the wet and dry regions is according to this comparison small and statistically insignificant. It should be remembered

Table VIII. Moss production per unit area within sample plots in Västerbotten, North Sweden (Nos. 516 to 519) and in Nordtröndelag, Norway (Nos. 775 and 778). All plots from spruce forest with a moderately good light supply to the ground; plot size 6.25 dm^2. Values marked c are calculated (see p. 27). Vacuum drying 55° C. For botanical composition, see Table XXVIII, p. 140.

No. of sample	Date of sampling	Condition of forest	Amount of dry moss in mg/dm^2					Annual production of moss in mg/dm^2 estimated from		
			Hylocomium splendens				Other species "Annual shoots"			
			Segm. 50	Segm. 49	Segm. 48	Segm. 47		5 + 8	6 + 8	7 + 8
1	2	3	4	5	6	7	8	9	10	11
516	15.VII.1949	Old and slow-growing	—	80	341	366 c	494	—	835	860
517	”		—	50	248	280 c	326	—	574	606
518	”		—	83	287	266 c	541	—	828	807
519	”		—	67	276	216 c	512	—	788	728
Average			—	—	—	—	—	—	756	750
775	26.VIII.1950	Slow-growing	181	613	640 c	—	152	765	792	—
778	”	High productive......	87	261	318 c	—	147	408	465	—

that segment 49 was larger than segment 48 and 47 in Sweden as well as in Norway (Table IX). In any case the difference in yield does not correspond in magnitude to the difference in precipitation (3 or 4 :1) or humidity.

We may also compare samples collected in Västerbotten, North Sweden and in Tröndelag, Norway at the same latitude (Table VIII). These samples may be considered as fairly typical for places with an open spruce canopy and a well-developed moss cover. Kulbäcksliden with ca. 500 mm/year in precipitation and Imsdalen with almost double this figure fail to show any clear difference in moss yield.

Further information about the effect of humidity can also be obtained from comparisons of moss growth in years with different precipitation. Unfortunately every moss segment grows during more than one year, which implies a certain equalization of growth differences due to the climate. Half the weight of a segment is, however, formed during one late summer and autumn. If there is a direct correlation between moss growth and humidity, one would expect small segments from years when this season has been dry, and large segments from years with a moist summer and autumn.

In Figs. 44 and 45 (p. 134) we see that the summer 1947 has been dry in all sampled areas; at Ås and Väddö the early autumn has also been dry. The year before as well as the three following years have been more normal, though at Ås July, August and September 1949 show rain deficits. If we now compare the relative moss growth during these years (Table IX) we find the following: 1) No consistent difference in size between segments 46 and 47 can be observed, except that segment 46 is broken down to some extent in samples from 1950. 2) Also segments 47 and 48 do not differ in any consistent way. 3) Samples from more northern localities (516—519, 775 and 778) show a comparatively even growth during different years. 4) In all "southern" samples but one segment 49 is larger than segment 48, usually much larger. The only exception is sample 896 from open pasture in Roslagen, a very unusual habitat. The small size and varying morphology of the moss specimens in this sample made the distinction of the segments somewhat uncertain.

To summarize: the exceptionally dry summer and autumn of 1947 did not retard the growth of segment 47. The strong growth of segment 49 cannot be explained by high precipitation during the summer and autumn of 1949. Of course it is possible to speculate about climatic interference with growth processes other than weight increase, e.g. bud development, which might bring about a delay in response to the climate, but what we are most interested in here is the direct effect of climate on moss growth.

It must be admitted that the humidity cannot be estimated from precipitation data only. The temperature is important and so is the kind of precipitation—heavy showers, drizzling rain and snow may affect the mosses in different ways. The duration of the dry periods is probably also of importance. Temperature data are given in the Table XXVI, p. 136, but it is even more difficult to correlate the temperature values with moss growth than in the case of precipitation, as the relative differences in temperature between different years are less than the differences in precipitation. The really important thing is probably the time when the moss carpet is wet enough to photosynthesize, but this time can not be estimated from standard meteorological publications. It is, however, probably safe to assume that the duration of these wet periods is correlated to the amount of precipitation, and that it is much longer in western Norway than in eastern Sweden.

It would also be difficult to make the water factor responsible for the strong individual growth variation of *Hylocomium*, at least outside the canopy. The supply of water may well vary in different spots beneath a tree, depending on where the drops gather on the branches. But in the moss carpet the moisture will soon equalize, if the rain shower is not too short. In openings and in the margin of the canopy the moss carpet will usually be moist at the time when drops start to fall from the branches. Excess water has comparatively small physiological effects (cf. STÅLFELT 1937 b, Fig. 1).

These considerations lead us to the conclusion that the water factor does not limit moss growth, at least not in more humid climates. On the other hand we must admit that the growth periods of *Hylocomium splendens* in eastern Sweden are to a large extent controlled by humidity: a dry summer

Table IX. Relative weights of *Hylocomium* segments in samples from different habitats. Weights expressed as per cent of weight of segment 3. Samples 516—519, 775 and 778 from northern localities (lat. N. ca. 64°); all others from southern localities (lat. N. ca. 60°).

Sample No.	Locality	Date of sampling	Nos. of segm. 3 counted	Weight of segment						
				45	46	47	48	49	50	51
516—519	Spruce forest, Kulbäcksliden......	15.VII.49.	ca. 250	100	106	100	101	25	—	—
493	Site I. Grenholmen	5.VIII.49.	472	85	94	100	84	22	—	—
492	Spruce forest, Rönninge..........	14.VIII.49.	ca. 100	—	98	100	89	20	—	—
625—628	Spruce forest, Ås..	5.VI.50.	137	—	79	100	100	193	23	—
631—634	Mixed conifer forest, Rådalen........	9.VI.50.	64	—	76	77	100	136	25	—
656	Calluna-heath, Fjell	14.VI.50.	141	—	70	81	100	127	19	—
666	Mixed forest, Fjell	14.VI.50.	71	—	112	114	100	104	19	—
672	Spruce forest, Os .	15.VI.50.	93	—	62	70	100	128	20	—
677	Spruce forest, Os .	15.VI.50.	39	—	92	99	100	118	18	—
708	Site I............	7.VIII.50.	435	—	95	110	100	115	37	—
775	Spruce forest, Imsdalen..........	26.VIII.50.	160	—	77	88	100	97	28	—
778	Spruce forest, Bredesmoen.......	26.VIII.50.	120	—	84	101	100	98	31	—
895	Site III..........	16.VII.51.	ca. 600	—	—	98	85	100	94	12
896	Open pasture, Noor	2.VIII.51.	115	—	—	131	148	100	123	26
898	Site I............	2.VIII.51.	239	—	—	78	80	100	103	18

or a dry habitat retards the start of the growth period, compare in Fig. 4 growth during the wet summer of 1952 with that during the more normal summer of 1949. A reasonable explanation of this apparent contradiction might be that growth is controlled by a limited supply of some other factor, which is earlier exhausted when growth starts earlier. Where eastern Sweden is concerned, we must also consider the possibility that water has a certain direct importance for growth, at least in some habitats. Beneath dense spruce crowns in particular very little water may percolate to the ground (cf. Table XX). Decreasing water supply may thus contribute to the yield/light relationship in Fig. 11 a. That water deficiency should be responsible for the low moss yield on plot 634 and 677 (Table VII) is, however, extremely unlikely, as the precipitation there is very high. Moreover, the lower precipitation beneath a canopy may to some extent be compensated by a lower evaporation.

The question of whether the mosses depend on something contained in the rainwater is still open. Most of the arguments against the importance of the precipitation do not apply to the possible salt content of the rainwater, as will be discussed later.

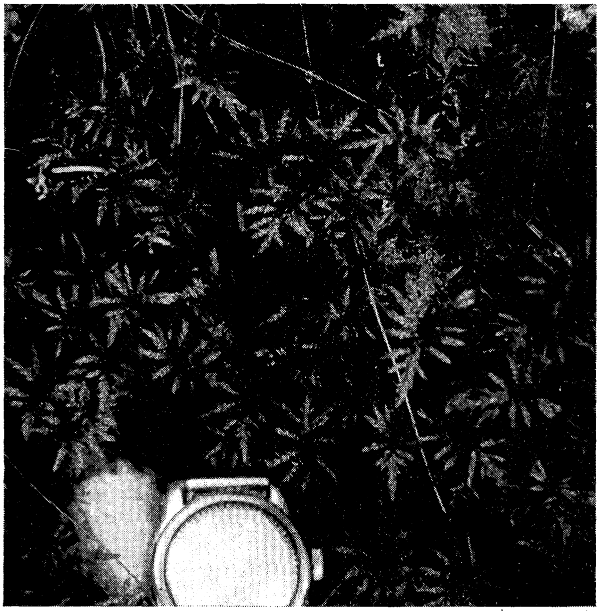


Fig. 12. *Hylocomium splendens* on a very dark plot, close to No. 1 in Site II (see map Fig. 10). Ca. 2/3 natural size. 12. IX. 1949.

Variation in morphology and community structure under different conditions

So far we have only studied the dry matter production of *Hylocomium splendens* and its dependence upon some ecological factors. But other properties of the moss and the moss community may also be affected by these factors. *Hylocomium splendens* is known to be a species of variable appearance. We may therefore expect morphological differences when samples from different habitats are compared. Such differences have in fact been observed. We have already mentioned variations in the segment size and colour of different samples. If we study samples from extreme or unusual habitats we may also find aberrations in branching and growth mode. *Hylocomium* on sloping stones sometimes grows pressed against the stone; in such localities it often happens that the young bud is formed in the apex of the parental segment, thus forming a monopodium. The same aberration, which makes it difficult to distinguish the segments, has also been observed on *Calluna* heaths and in deciduous forests. In exposed habitats injuries to buds and segments are sometimes visible, often combined with a high frequency of "branched" individuals.

It must, however, be emphasized that these morphological aberrations are scarce or absent in most forest habitats. On the contrary, it is striking how uniform *Hylocomium splendens* is on plots with rather different external

Fig. 13. *Hylocomium splendens* on a moderately exposed plot, close to No. 7 in Site II (see map Fig. 10). Ca. 2/3 natural size. 12. IX. 1949.

conditions. Fig. 12 (very low light supply) and Fig. 13 (good light supply) illustrate this point. These photographs were taken in eastern Sweden, but could equally well represent *Hylocomium* from western Norway.

As said before, the main difference between *Hylocomium* collected from different forest plots lies in the colour, which is deeper green in darker habitats. *Hylocomium* from very dark places is also more slender than elsewhere, and a difference in cell wall development can be anticipated from the experiments of DAVY DE VIRVILLE (1927—1928), who found a more or less pronounced etiolation at low light intensities. Such a difference would tally well with the chemical data presented in the next chapter.

Considering the striking morphological changes produced in the experiments of DAVY DE VIRVILLE (l.c.) for several moss species, we must remember that the light range studied here has been much narrower than in his experiments.

The colour differences between *Hylocomium* from dark and exposed plots are of course only average differences, as very dark green and yellow green segments may occur close to each other, at least in plots with intermediate light supply.

Even if there is no marked and consistent difference in the morphology of

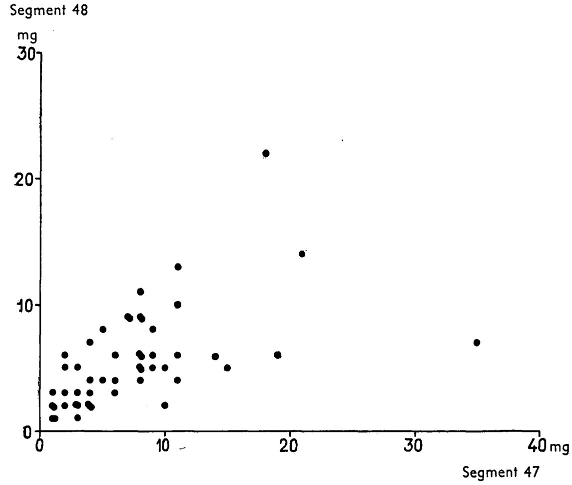


Fig. 14. Sample 1, Site II.
Deeply shaded.

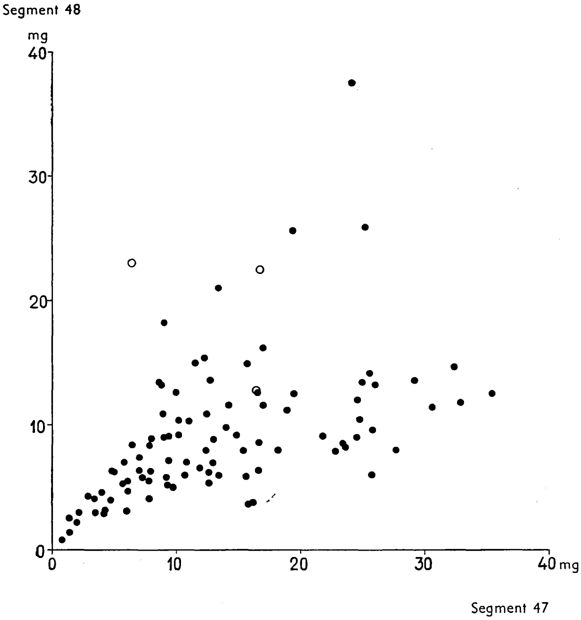


Fig. 15. Sample 3, Site II.
Moderately shaded.

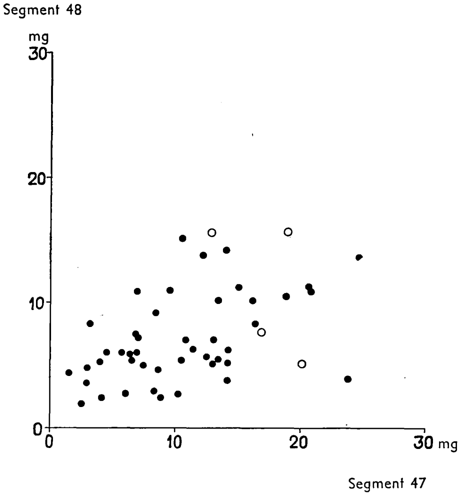


Fig. 16. Sample 7, Site II.
Moderately exposed.

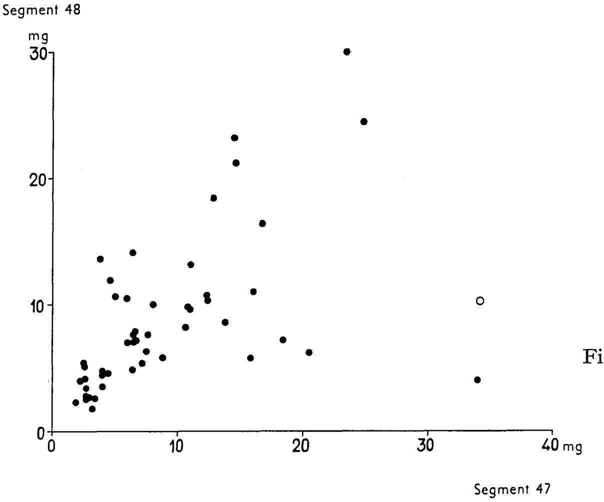


Fig. 17. Sample 8, Site II. Moderately exposed.

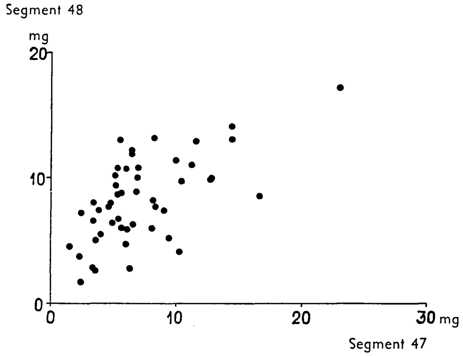


Fig. 18. Sample 11, Site II. Moderately exposed.

Figs. 14 to 18. Weight of segment 48 of *Hylocomium splendens* plotted versus the weight of segment 47. Samples collected 26. V. 1949, see map Fig. 10..

● "Unbranched" specimens
○ "Branching" »

Hylocomium from different forest plots, there might well be structural differences in the community. Properties of interest in this connection are for example the frequencies of very small individuals and the dependence of a segment on its parent segment. Both these properties can be studied in Figs. 14 to 18, where the weight of segment 2 is plotted against the weight of segment 3 for all individuals not damaged during preparation, in some of the samples from Site II, Grenholmen. Table X also shows the average size of these segments, and the correlation coefficients which are the mathematical expressions of the correlations illustrated in Figs. 14 to 18. In addition some other figures are shown, which might vary with varying morphology.

Table X. Average weight of *Hylocomium* segments within sample plots with different light supply (Site II, samples from May 1949). Weights expressed in mgs and as per cent of weight of segment 47. Weights of stems and side-branches, respectively, and correlation coefficients between segments 48 and 47 are also given.

Plot No.	Light (% of that in opening)	No. of specimens	Average weight of individual segments					Weight of 10 stems, mg (segment 47)	Weight of side-branches of 10 stems, mg (segment 47)	% side-branches (of segment 47)	Correlation coefficient $r_{47\cdot48}$
			Segment 49		Segment 48		Segment 47 mg				
			mg	% of 47	mg	% of 47					
1	12.5	50	0.6	8	5.5 ±0.6	74	7.4 ±0.9	34.4 27.1	72.2 50.1	68 65	0.54
3	25	97	0.9 ±0.1	7	9.1 ±0.6	70	13.1 ±0.9	54.0 60.9	120.5 118.4	69 66	0.44
5	45	75	0.9	8	7.9	71	11.2	28.4 39.2	46.4 76.5	62 66	—
8	55	50	1.2	13	8.8 ±0.9	92	9.6 ±1.1	47.6 35.6	76.7 50.4	62 59	0.49
7	60	49	0.8	7	7.2 ±0.5	67	10.8 ±0.8	26.3 42.3	59.1 72.9	69 63	0.46
13	70	65	0.7	10	5.6	79	7.1	36.2 30.3	61.0 66.0	63 69	—
10	70	90	0.9	11	7.6	92	8.3	35.6 36.2	58.1 63.9	62 64	—
11	80	50	1.4	19	8.2 ±0.6	114	7.2 ±0.5	25.4 23.4	61.2 43.3	71 65	0.60

Very small *Hylocomium* individuals (1 mg and less) are rare in all the diagrams Figs. 14 to 18. This corroborates the conclusion about the dominance of vegetative propagation in the *Hylocomium* community (p. 31) which was based upon Figs. 5 and 6. Reproduction by spores is probably only successful in open or unstable communities.

The dependence of a segment on its parent segment (as regarding weight) was somewhat greater in the dark plots 492 and 677 than in the exposed plots 493 and 672, Table IV. Such a trend cannot be found in Table X, where the correlation coefficients are fairly similar in all plots. The corresponding diagrams Figs. 14—18 suggest that the variation is of the same type in all these plots, and that a straight regression line is as good an approximation as any other. The variation is greater here than in Table IV (the correlation coefficients are lower), which may imply that some factor causing variation is less important in the plots of Table IV. Such a factor may be the occurrence of scattered birch leaves on the ground in the autumn (cf. p. 105).

The other functions in Table X, the ratios between different segments, and the percentages of "branches", do not differ much, or vary in an irregular way.

The internal structure of the *Hylocomium splendens* community thus appears to be rather uniform under the different conditions in the conifer forests sampled, at least with respect to the more essential features.

Gimingham & Robertson (1950) have come to the conclusion that humidity exerts a strong influence on moss community structure, determined as percentages of species with certain growth-forms. They also suggested that light was of influence in this respect. However, their investigation is not comparable with the present one, since they studied many different communities. Yet we may confirm their results in part: there is a certain range of light and humidity where communities of *Hylocomium splendens* and species with similar growth-forms are common. Near the limits of this range, moss yield decreases and communities composed by other growth-forms become more frequent. The role of the humidity for the moss community structure does not appear quite clear to the present author's mind. The view taken on p. 94 with regard to the ecological importance of surface enlarging organs of forest mosses may offer another explanation of why certain growth-forms are more common in forests and other habitats with high air humidity.

Chapter VI. Nutrient Content of *Hylocomium splendens* and its Nutrient Uptake

Information about the nutrient uptake of *Hylocomium splendens* can be obtained from a combination of growth data with figures for the nutrient contents of different segments. The contents of nitrogen, phosphorus, potassium and calcium have been determined segment for segment in most of the samples mentioned in the preceding chapters. In some cases the contents of other elements have also been studied.

Table XI presents the nutrient contents of *Hylocomium splendens* from Site I, Grenholmen, in four samples collected at yearly intervals. The corresponding relative weights of the segments have been presented in Table I. We find in all four cases decreasing percentages of N, P and K with the age of a segment, while Ca increases steadily. The bud is richest in most nutrients (calculated on a per cent basis); even the Ca concentration of the bud as a rule exceeds that of its parent segment. The difference in composition between a segment and its parental segment decreases somewhat with age, especially in the case of nitrogen, which becomes nearly constant in old segments.

There are differences between the four different samples in Table XI, if we compare segments of the same age. When these differences concern young segments only, we may suspect that the nutrient content is different in different years. But there are also differences between old and dead segments from different samples, which suggest local differences within the habitat, which are not entirely equalized in the sampling. We shall soon discuss such

Table XI. Nutrient contents, as per cent dry weight, in different segments of *Hylocomium*, collected in Site I in different years.

Segment	Element	Date of sampling			
		7.VIII.48.	5.VIII.49.	7.VIII.50.	2.VIII.51.
1	N	1.26	1.35	1.19	1.42
	P	0.35	0.33	0.24	0.33
	K	0.98	1.06	1.13	1.01
	Ca	0.22	0.32	0.38	0.40
2	N	1.01	1.03	0.97	1.05
	P	0.20	0.20	0.16	0.20
	K	0.58	0.56	0.58	0.51
	Ca	0.24	0.24	0.28	0.23
3	N	0.85	0.93	0.93	0.86
	P	0.14	0.16	0.10	0.13
	K	0.46	0.52	0.42	0.46
	Ca	0.28	0.28	0.33	0.29
4	N	0.74	0.99	0.87	0.84
	P	0.11	0.13	0.11	0.11
	K	0.38	0.46	0.46	0.42
	Ca	0.36	0.40	0.42	0.37
5	N	0.74	0.91	0.86	0.81
	P	0.10	0.12	0.09	0.11
	K	0.38	0.41	0.40	0.44
	Ca	0.48	0.51	0.59	0.47
Sample No.		185	493	708	898

local differences in more detail. In this connection we may consider the variation in composition between the samples in Table XI as an estimate of the "error", when samples from different seasons are compared.

The percentages of nutrients in the "growth curve samples" are presented in Table XII. The changes in composition of a segment during a year are, according to Table XII, as a rule not greater than the "error", estimated from Table XI. Exceptions are the N, P and K contents of the bud and of segment 2, which slowly decrease during the year. The above-mentioned differences between segments of different age from the same sample show that these changes continue also within older segments, though the variation between samples is too great in Table XII to make is possible to follow this development. The composition of full-grown *Hylocomium* segments thus appears to be fairly similar all the year round; minor differences between different seasons cannot be determined from data of the type presented in Table XII.

Table XII. Per cent dry weight of nitrogen, phosphorus, potassium and calcium in different segments of *Hylocomium*, collected in Site I at different seasons.

Segment	Element	Date of sampling					
		7.VIII.48.	5.X.48.	5.I.49.	1.IV49.	25.V.49.	5.VIII.49.
49	N	—	—	—	1.69	1.65	1.35
	P	—	—	—	0.39	0.37	0.33
	K	—	—	—	—	0.84	1.06
	Ca	—	—	—	—	—	0.32
48	N	1.26	1.12	1.20	1.17	1.07	1.03
	P	0.35	0.25	0.26	0.23	0.21	0.20
	K	0.98	0.90	0.78	0.55	0.49	0.56
	Ca	0.22	0.21	0.30	—	0.24	0.24
47	N	1.01	0.89	1.06	1.02	0.92	0.93
	P	0.20	0.16	0.18	0.16	0.16	0.16
	K	0.58	0.62	0.64	0.61	0.52	0.52
	Ca	0.24	0.21	0.34	—	0.30	0.28
46	N	0.85	0.84	0.95	0.87	0.94	0.99
	P	0.14	0.12	0.14	0.13	0.14	0.13
	K	0.46	0.46	0.52	0.56	0.43	0.46
	Ca	0.28	0.30	—	—	0.36	0.40
45	N	0.74	0.76	0.86	0.81	0.83	0.91
	P	0.11	0.09	0.12	0.10	0.10	0.12
	K	0.38	0.41	0.44	0.42	0.44	0.41
	Ca	0.36	0.38	—	—	0.40	0.51
44	N	0.74	0.72	0.80	0.81	0.84	0.88
	P	0.10	0.08	—	0.09	0.09	0.11
	K	0.38	0.31	0.40	—	—	0.36
	Ca	0.48	0.49	0.56	—	0.54	0.54
43	N	0.72	0.77	—	—	0.88	0.89
	P	0.10	0.08	—	—	0.09	0.10
	K	0.34	0.39	—	—	—	0.33
	Ca	0.45	0.41	0.63	—	0.57	0.61
Sample No.		185	308	319	324	330	493

Nutrient uptake

To get information about the nutrient uptake we need the absolute amounts of nutrients contained in different segments. In Figs. 19 to 26 such values have been calculated from the average weights of the segments (cf. Fig. 3) and from the nutrient contents recorded in Tables XI and XII. The weights of segments are those for "unbranched" individuals, which according to p. 22 grow a little slower than the average. (Note. The values for 5. 1. 1949 in Fig. 21 and Table XII refer to sample 319 only, while the corresponding values in Figs. 3 and 4 are calculated from the whole series of samples 314—321.)

Fig. 19

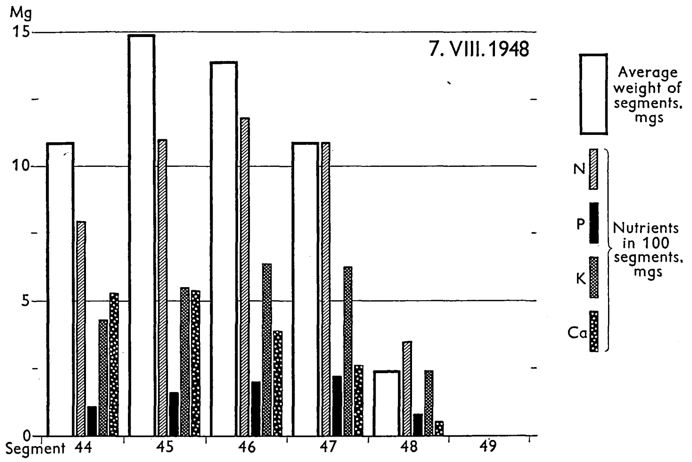


Fig. 20

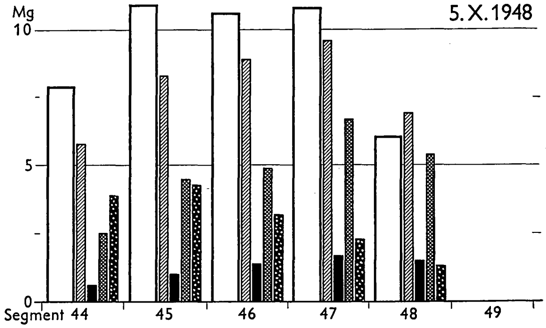


Fig. 21

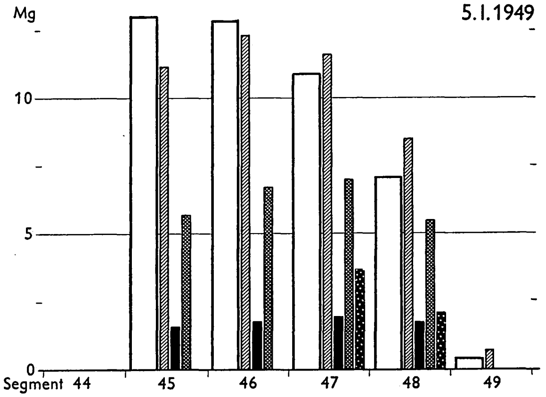


Fig. 22

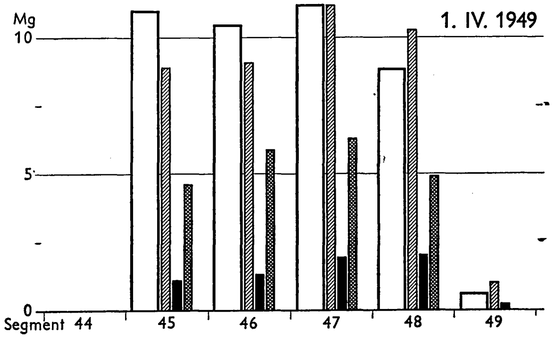


Fig. 23

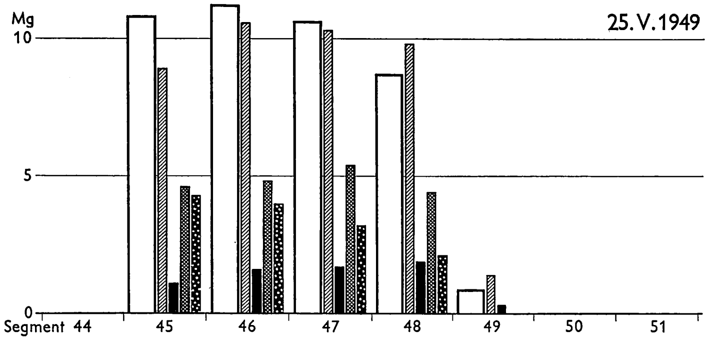


Fig. 24

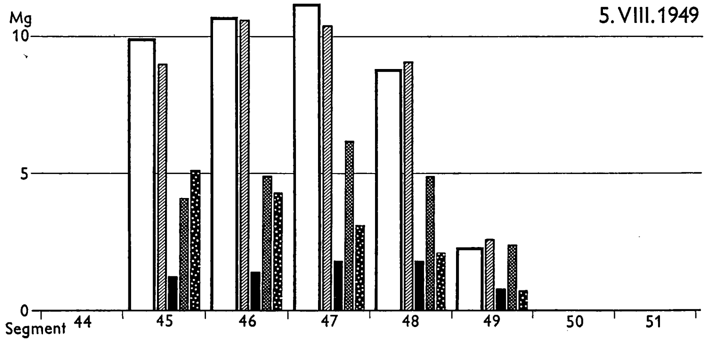


Fig. 25

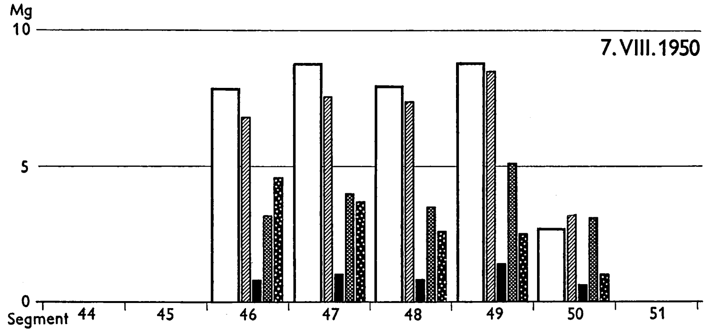
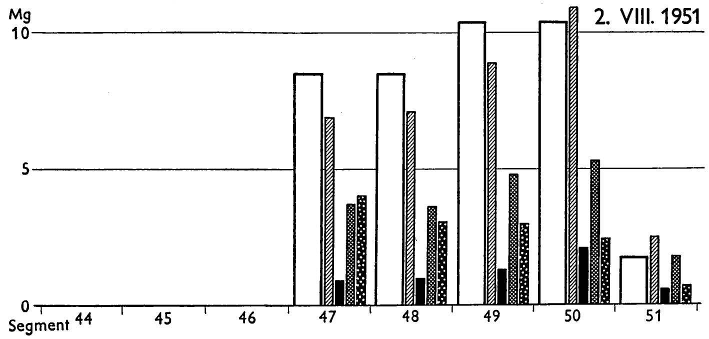


Fig. 26



Figs. 19 to 26. For explanations see overleaf. For symbols, see Fig. 19.

Several conclusions may be drawn from the diagrams in Figs. 19 to 26: 1) The slow decrease in percentages of N, P and K in growing segments is due to the fact that weight increases at a rate slightly faster than the content of these elements. The difference in rate between growth and nutrient uptake is, however, so little that both processes can be considered as running almost parallel. 2) In older segments the absolute contents of these three elements decrease. P and K usually reach their maximum content in segments 2 or 3, while the N content may be approximately the same in segments 2, 3 and 4. As the per cent content of N does not change much in old segments (Tables XI and XII), the decrease of nitrogen in segments older than No. 4 is probably due to loss of leaflets and side-branches, as the segments become brittle. 3) Ca follows a trend very different from that of the other elements, as a rule increasing with age both in absolute terms and, if the bud is excepted, in per cent figures. Most remarkable is the Ca increase in old and dead segments, best illustrated in Figs. 23 to 26; calcium was either not determined in the first samples, or determined by less accurate methods. It must be a real uptake of Ca, which probably continues even in very old segments, as the per cent content of Ca increases with age at approximately the same rate as earlier even where decomposition does not allow a calculation of absolute Ca uptake. The increase in calcium content of segments during their life-time is not especially remarkable, as the same is the case with most other plant organs (see for example refs. given by LUTZ & CHANDLER 1947, p. 180). 4) As the old and dying segments retain most of their nutrient content, in particular their nitrogen, a translocation of nutrients from dying organs can hardly play the same role as in, e.g., deciduous trees. In all probability most of the nutrients taken up by *Hylocomium splendens* are absorbed by the growing organs themselves. Translocation of solutes is probably slow in the moss stem, but may well be of importance for the growth of the young bud, as it must be for the sporogonia.

The relative nutritional independence of the different segments is a result which agrees well with the great growth variation found in Chapter V, and especially with the lack of partial correlation between segment 2 and segment 4 (Table IV). Had the grandparent segment exerted any important physiological influence on the growth of the granddaughter segment, this influence should certainly have appeared in Table IV.

Figs. 19 to 26. Average dry weights of different segments of "unbranched" *Hylocomium* individuals in samples from Site I, collected in different seasons and years; and amounts of nutrients contained in 100 segments. For symbols, see Fig. 19.
The following numbers of specimens have been weighed: 151 (Fig. 19), 136 (Fig. 20), 51 (Fig. 21), 243 (Fig. 22), 277 (Fig. 23), 300 (Fig. 24), 325 (Fig. 25), and 155 (Fig. 26).

Table XIII. Contents of nitrogen, phosphorus and calcium in stems and branches of *Hylocomium splendens* (sample 9, collected 26.V.1949.).

	Per cent dry weight					
	N		P		Ca	
	Stem	Branches	Stem	Branches	Stem	Branches
Living moss (Segment "47")	0.71	0.79	0.16	0.14	0.29	0.32
			0.16	0.14	0.28	0.27
Moss litter (chiefly segments "45" and "46")	0.64	0.74	0.12	0.10	0.39	0.38
			0.11	0.10	0.39	0.39

A comparison of Figs. 19, 24, 25, and 26 (samples taken at yearly intervals) shows that the differences in nutrient contents correspond to similar differences in the relative size of segments in different years, i.e. that nutrient uptake follows growth fairly well. Segments 49 and 50, which were larger than segments 47 and 48 when full-grown, also contained larger amounts of nutrients.

One might suspect changes in the nutrient concentration of old moss segments to be due to a loss of organs (e.g. leaflets or branch tops) differing from the rest in composition. Table XIII shows that the differences between stem and side-branches are small as regards P and Ca content. The observed difference in N content cannot account for the fact that very old moss segments may contain a higher percentage of nitrogen than somewhat younger segments; the more persistent stem contains less N than the more easily lost side-branches. In this case one might rather think of a loss of organic matter at a rate more rapid than the loss of nitrogen. When somewhat younger segments are considered, most of the loss in weight with decomposition is no doubt due to the fact that leaves and branches are broken off, and not directly to differential decomposition of different substances.

Local variation in contents of N, P, K and Ca

We have already found that *Hylocomium* growth increases with light beneath spruce and decreases with the distance to trees (Chapter V). It is now of interest to determine whether there is some relation between the nutrient content and the yield.

Tables XIV and XV show the nutrient contents of the samples from Site II (cf. Tables V and VI) in relation to light, canopy and yield. Both *Hylocomium splendens* and some of the other constituents of the ground layer have been analysed. The relationships found have been illustrated in Figs. 27, 28 and 29. Figs. 27 a and 29 a show that the concentrations of nitrogen and phosphorus

Table XIV. Per cent dry weight of plant nutrients in segment 1+2 of *Hylocomium splendens*, and in annual shoots of other major constituents of the ground layer. Samples from Site II (see map Fig. 10) collected 26.V.1949 (Nos. 1—14) and 25.VII.1949 (Nos. 15—21).

No. of sample	Relation to tree canopy	Light (% of that in opening)	Estimated moss yield mg d.w./dm²	Species analysed	Contents of nutrients				Segment 1 in % of segment 1+2
					N	P	K	Ca	
1	Inside	12.5	380	*Hylocomium* .	2.03	0.36	0.62	0.33	10
					2.03	0.36	0.57	0.31	
				Pleurozium . .	1.62	0.33	—	—	—
2	”	20	460	*Hylocomium* .	1.78	0.34	0.70	0.32	—
					1.82	0.34	0.76	0.32	
				Pleurozium . .	1.48	0.31	—	—	—
3	”	25	430	*Hylocomium* .	1.26	0.29	0.66	0.27	9
					1.28	0.29	0.66	0.28	
				Pleurozium . .	1.00	0.24	—	—	—
4	”	35	660	*Hylocomium* .	1.16	0.25	0.62	0.24	—
					1.15	0.25	0.62	0.23	
				Pleurozium . .	1.26	0.25	—	—	—
5	”	45	780	*Hylocomium* .	1.02	0.22	0.64	0.24	10
					1.00	0.21	0.66		
				Pleurozium . .	0.67	0.18	—	—	—
6	”	50	520 + lichens	*Hylocomium* .	0.90	0.22	0.52	0.28	—
					0.92	0.22	0.52	0.26	
				Pleurozium . .	0.71	0.18	—	—	—
7	Beneath border......	60	580 + lichens	*Hylocomium* .	0.92	0.20	0.58	0.22	10
					0.94	0.21	0.52	0.21	
				Pleurozium . .	0.71	0.16	—	—	—
				Cladonia (whole plants)	0.39	0.06	—	—	—
					0.39	0.06			
8	1 m outside	55	1060	*Hylocomium* .	1.11	0.26	0.70	0.27	12
					1.12	0.25	0.71	0.27	
9	1 ” ”	70	980	*Hylocomium* .	0.91	0.20	0.60	0.29	—
					0.93	0.21	0.55	0.29	
10	1 ” ”	70	600 + lichens	*Hylocomium* .	0.87	0.20	0.48	0.24	11
					0.89	0.21	0.49	0.26	
11	1.5 ” ”	80	930	*Hylocomium* .	0.79	0.19	0.56	0.23	15
					0.79	0.19	0.58	0.23	
				Pleurozium . .	0.71	0.18	—	—	—
				Dicranum . . .	0.98	0.18	—	—	—
12	2 ” ”	70	530	*Hylocomium* .	0.84	0.19	0.47	0.25	—
					0.84	0.20	0.46	0.25	
				Pleurozium . .	0.67	0.17	—	—	—
13	2 ” ”	70	610	*Hylocomium* .	0.99	0.21	0.52	0.23	—
					0.99	0.20	0.53	0.22	
14	2.5 ” ”	65	500	*Hylocomium* .	1.13	0.21	0.50	0.26	12
					1.14	0.21	0.50	0.27	

Table XIV. (Cont.)

No. of sample	Relation to tree canopy	Light (% of that in opening)	Estimated moss yield mg d.w./dm²	Species analysed	Contents of nutrients N	P	K	Ca	Segment 1 in % of segment 1+2
15	Inside	20	620	*Hylocomium* .	1.59 1.60	0.29 0.29	0.78 0.79	0.27 0.27	—
16	,, ...	25	640	*Hylocomium* .	1.59 1.57	0.30 0.30	0.84 0.81	0.27 0.29	—
17	,, ...	30	520	*Hylocomium* .	1.15 1.13	0.22 0.22	0.56 0.57	0.25 0.26	—
18	,, ...	35	750	*Hylocomium* .	1.01 1.03	0.22 0.22	0.57 0.60	0.24 0.25	—
19	Beneath border......	45	670	*Hylocomium* .	0.89 0.88	0.20 0.20	0.58 0.59	0.23 0.22	—
20	Beneath border......	55	910	*Hylocomium* .	0.83 0.83	0.17 0.18	0.46 0.46	0.24	21
21	1 m outside.	55	960	*Hylocomium* .	0.93 0.93	0.20 0.20	0.55 0.54	0.23 0.23	19

Table XV. Per cent dry weight of nitrogen and phosphorus in segment 2 (segment 49) of *Hylocomium splendens* from Site II, collected 28.XII.1949, in relation to tree canopy, light supply and total moss yield.

No. of sample	Reference number (in Table XIV.)	Relation to tree canopy	Light (% of that in opening)	Estimated moss yield mg d.w./dm²	Contents of N	P
565	1	Inside......	12.5	270	1.92	0.37
564	2	,, ...	20	240	2.40	0.40
570	15	,, ...	20	550	2.11	0.33
559	3	,, ...	25	250	1.63	0.33
573	17	,, ...	30	350	1.61	0.30
563	4 & 16	,, ...	30	450	1.55	0.29
572	18	,, ...	35	470	1.02	0.22
557	5	,, ...	45	530	1.18	0.21
571	19	Beneath border......	45	410	1.08	0.23
556	7	Beneath border......	60	430	0.92	0.20
567	10 & 20	0.5 m outside	60	590	0.97	0.22
562	8	1 ,, ,,	55	740	1.31 1.34	0.29 0.30
555	9	1 ,, ,,	70	280	0.82	0.20
561	11	1.5 ,, ,,	80	600	0.93	0.20
558	12	2 ,, ,,	70	600	0.91	0.20
569	13	2 ,, ,,	70	580	1.19 1.17	0.28 0.29
568	14	2.5 ,, ,,	65	350	1.24 1.26	0.22

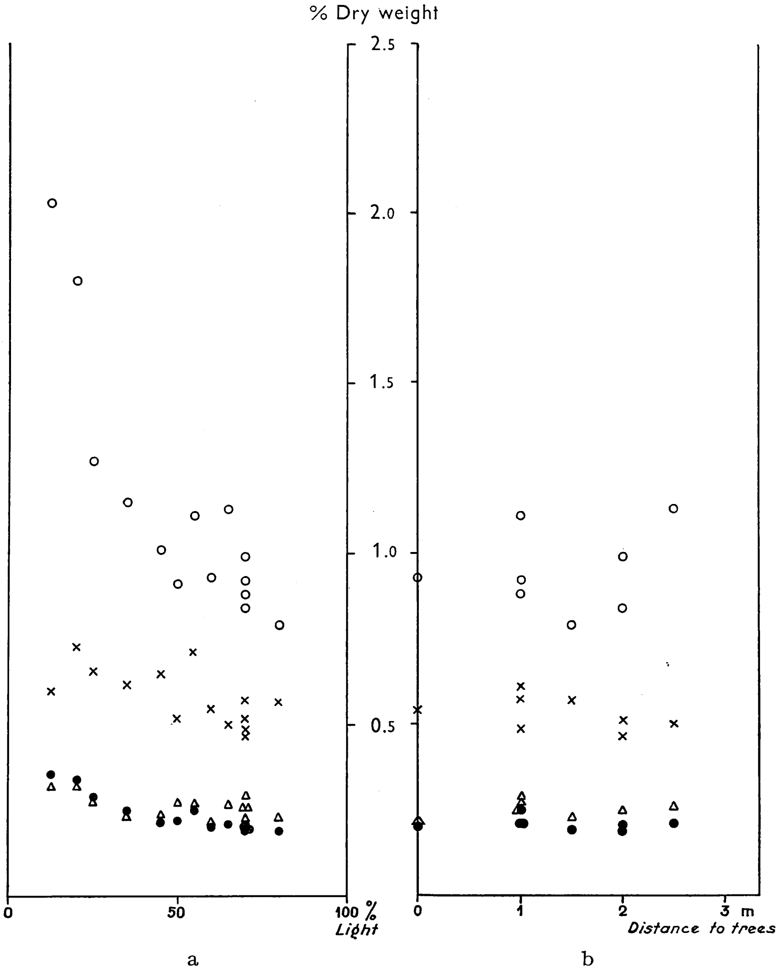


Fig. 27. Nutrient concentration in segment 1 + 2 of *Hylocomium splendens* in relation to (a) light supply and (b) distance to the nearest tree crown projection. Data from Table XIV.

○ N × K ● P △ Ca

in *Hylocomium* increase strongly when the light decreases from about 50 per cent to lower values. Fig. 28 a shows the same for *Pleurozium Schreberi.* At light intensities above 50 per cent (as measured in Site II) there is no correlation between phosphorus concentration and light in both species, while that between nitrogen and light is at least much weaker than at lower light intensities. As the yield decreases when N and P concentrations increase at low light intensity, the uptake of these elements remains almost

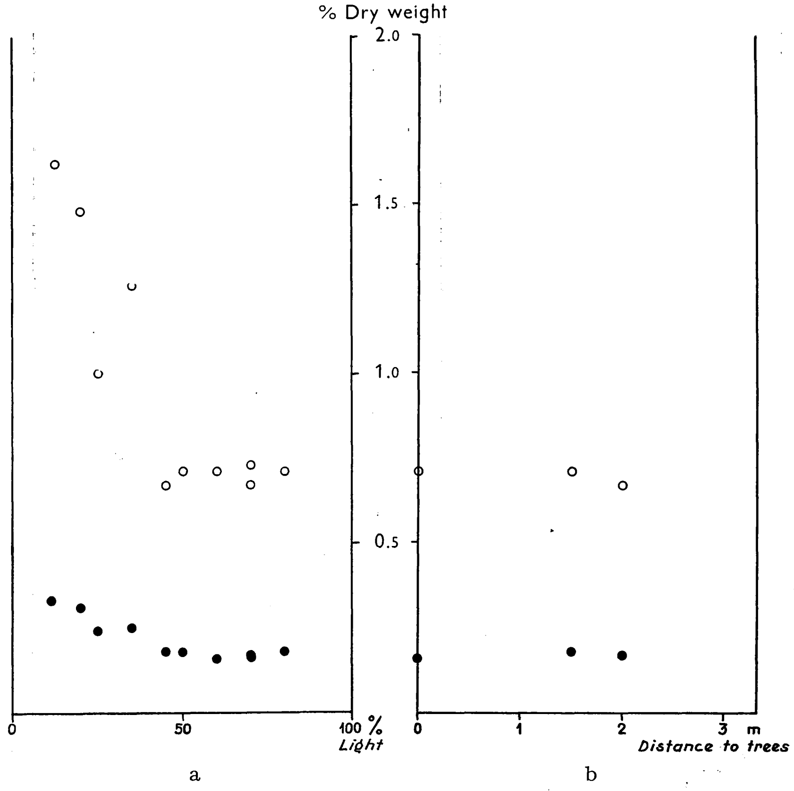


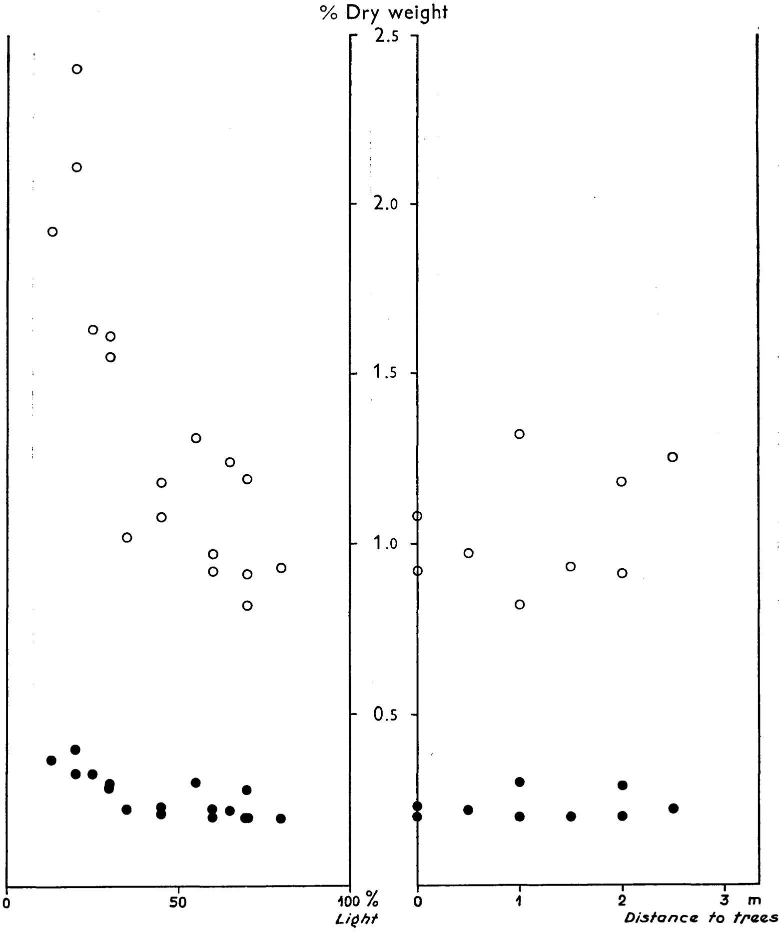
Fig. 28. Nutrient concentration in young shoots of *Pleurozium Schreberi* in relation to (a) light supply and (b) distance to the nearest tree crown projection. Data from Table XIV.

○ N ● P

constant within the different plots beneath trees in Site II, from about 50 per cent to about 20 per cent light.

Because of the small samples available, potassium and calcium could not be determined in *Pleurozium* (Fig. 28) and in the winter samples of *Hylocomium* (Fig. 29). In *Hylocomium* collected in May (Fig. 27) the concentrations of these elements, Ca in particular, show less correlation with the light intensity than N and P percentages. There is, however, a tendency to higher figures at very low light intensities, at least in the case of K. This tendency is evident also in the July series of *Hylocomium* samples (Table XIV).

Figs. 27 b, 28 b and 29 b show that in the openings nutrient concentration is relatively independent of the distance to trees. It may be pointed out that the highest nitrogen and phosphorus values in these diagrams belong to the sample plots 8, 13 and 14 (and the corresponding plots in the winter series,



a b

Fig. 29. Nutrient concentration in segment 2 of *Hylocomium splendens* in relation to (a) light supply and (b) distance to the nearest tree crown projection. Data from Table XV.

○ N ● P

562, 568 and 569, cf. Tables XIV and XV), which possessed a denser dwarf shrub layer than the other plots (cf. p. 41. The independence of the plant nutrient concentration as regards the distance to trees implies that the nutrient uptake per unit area decreases with the distance to trees in the same way as does the moss growth (Fig. 11 b).

Figs. 27, 28 and 29 were based upon analyses of young, growing moss. Very similar pictures would have been obtained if the concentration of any except the oldest segments had been plotted against light. Figs. 30 and 31

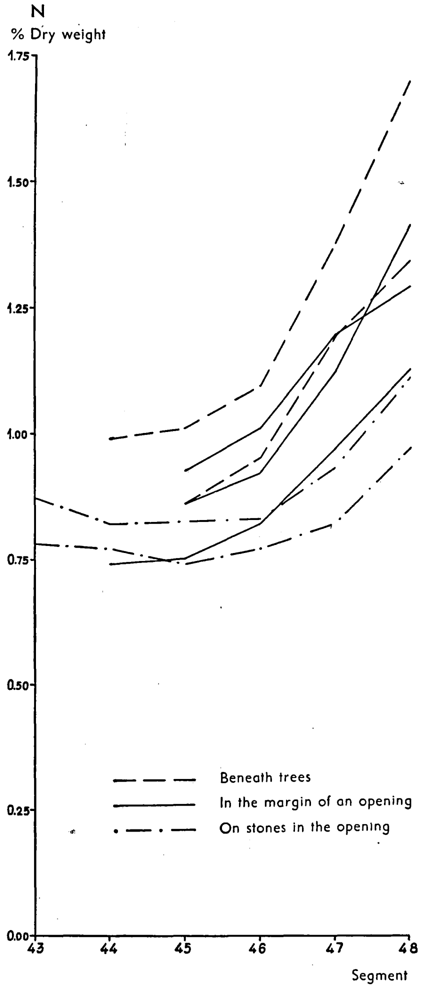


Fig. 30. Nitrogen concentration in different segments of *Hylocomium splendens* from seven different plots within Site I. Samples collected 5. I. 1949.

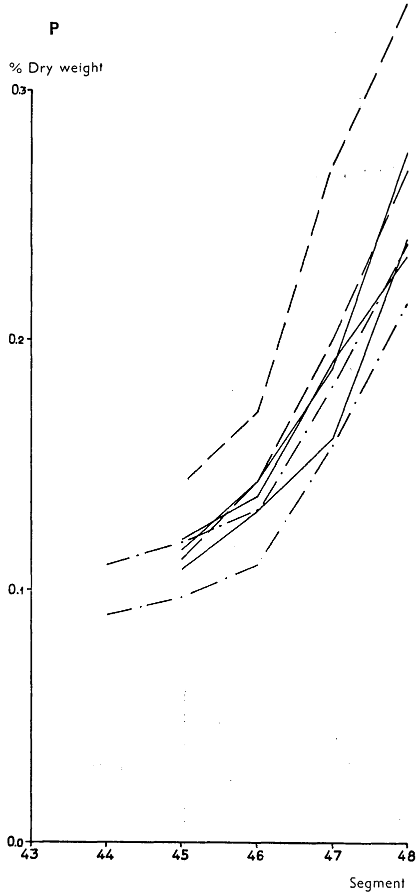


Fig. 31. Phosphorus concentration in the same *Hylocomium* segments as in Fig. 30.

give an idea of the relation between the concentrations of segments of very different age from samples with a different light supply. All values for the most exposed samples (here growing on stones) lie below the corresponding values for samples from beneath trees. As the light was not measured here, we cannot compare the plots directly with those in Site II, but they are certainly well inside the light range of the plots in Figs. 27 to 29.

In Table XVI we again find differences in nutrient concentration between

Table XVI. Nutrient contents in per cent dry weight of

		A. Plots with good									
Plot No.		231	309	320	895	896	631	632	672	649	656
Date of sampling		15.VIII.48.	7.X.48.	5.I.49.	16.VII.51.	2.VIII.51.	9.VI.50.	9.VI.50.	15.VI.50.	12.VI.50.	14.VI.50.
Segment	Element										
1	N	1.50	—	—	1.20	1.93	1.21	1.34	1.35	1.18	1.27
	P	0.25	—	—	0.32	—	0.24	0.28	0.26	—	0.13
	K	0.76	—	—	0.83	—	0.77	0.89	0.78	—	0.52
	Ca	—	—	—	0.31	—	0.23	0.33	0.26	—	0.25
	Na	—	—	—	0.02	—	0.12	0.10	0.12	—	—
2	N	1.10	1.30	1.02	0.77	1.33	0.78	1.03	1.01	1.03	0.96
	P	0.19	0.20	0.21	0.17	0.24	0.10	0.13	0.13	0.08	0.06
	K	0.50	0.75	0.70	0.46	0.42	0.28	0.32	0.39	0.30	0.24
	Ca	—	—	0.29	0.18	0.24	0.17	0.18	0.17	0.25	0.17
	Na	—	—	—	< 0.01	—	0.06	0.06	0.03	—	—
3	N	1.03	1.04	0.82	0.66	1.01	0.78	0.82	0.90	0.98	1.01
	P	0.14	0.13	0.16	0.10	0.15	0.09	0.10	0.10	0.08	0.06
	K	0.45	0.60	—	0.42	0.37	0.27	0.31	0.34	0.33	0.23
	Ca	—	—	—	0.24	0.26	0.19	0.25	0.27	0.29	0.20
	Na	—	—	—	< 0.01	—	0.05	0.05	0.03	—	—
4	N	0.91	0.92	0.77	0.70	0.85	0.76	0.74	0.88	0.91	0.99
	P	0.13	0.10	0.11	0.09	0.11	—	0.09	0.09	0.07	0.06
	K	0.42	0.45	—	0.36	0.32	—	0.25	0.32	0.33	0.22
	Ca	—	—	—	0.32	0.32	—	0.28	0.31	0.32	0.26
	Na	—	—	—	< 0.01	—	—	0.06	0.04	—	—
5	N	0.89	0.80	0.74	0.68	0.80	—	—	0.82	0.87	0.98
	P	0.11	0.08	0.10	0.09	0.09	—	—	0.08	—	0.06
	K	0.38	0.39	0.39	0.32	0.23	—	—	0.24	—	0.22
	Ca	—	—	0.40	0.34	0.41	—	—	0.39	—	0.31
	Na	—	—	—	< 0.01	—	—	—	0.03	—	—
6	N	0.93	0.78	0.77	0.70	—	—	—	0.77	—	0.92
	P	0.11	0.09	0.09	0.09	—	—	—	0.07	—	0.06
	K	0.32	0.36	0.38	0.31	—	—	—	0.20	—	0.17
	Ca	—	—	—	0.36	—	—	—	0.42	—	0.36
	Na	—	—	—	< 0.01	—	—	—	0.04	—	—

Description of plots. **A.** — **Eastern Sweden**: 231 Dry and open pine forest; 309 Opening in a so-called park meadow; 320 Middle of opening in Site I; 895 Open pine and spruce forest; 896 Northern slope of small rock in open pasture. **Western Norway**: 631—632 Open pine forest; 672 Margin of spruce forest; 649 Ombrogenous bog with low pines and *Calluna;* 656 *Calluna* heath on hilltop in outer part of archipelago; 666 Open pine and birch forest in sheltered valley near 656. **North Sweden**: 516—519

exposed and shaded *Hylocomium.* The differences concern all segments, and are most consistent in the case of nitrogen. There are regional differences as well, especially in the case of phosphorus. The P values are much lower in

Hylocomium splendens **from sample plots in Sweden and Norway.**

light supply				B. Plots with low light supply								
666	516—519	775	778	318	492	625	626	627	628	633	634	677
14.VI.50.	15.VII.49.	26.VIII.50.	26.VIII.50.	5.I.49.	14.VIII.49.	5.VI.50.	5.VI.50.	5.VI.50.	5.VI.50.	9.VI.50.	9.VI.50.	15.VI.50.
1.48	0.92	0.92	1.18	—	2.36	2.07	1.78	1.82	2.19	2.04	2.20	1.89
0.19	0.29	0.27	0.23	—	0.38	0.41	0.36	0.33	0.37	0.36	0.34	0.37
0.63	—	0.91	0.83	—	—	0.85	1.18	1.07	0.95	0.85	0.82	—
0.27	—	0.16	0.20	—	—	0.42	0.58	0.61	0.51	0.28	0.30	—
0.10	—	—	—	—	—	—	—	—	—	0.11	0.11	—
1.20	0.74	0.70	0.91	1.69	2.05	1.43	1.37	1.44	1.66	1.66	1.70	2.00
0.10	0.16	0.14	0.12	0.33	0.22	0.21	0.21	0.23	0.23	0.21	0.21	0.27
0.35	—	0.41	0.34	1.00	—	0.52	0.54	0.60	0.62	0.57	0.53	0.62
0.19	0.23	0.15	0.18	—	—	0.24	0.32	0.31	0.29	0.19	0.17	0.26
0.05	—	—	—	—	—	—	—	—	—	0.05	0.06	0.03
1.06	0.68	0.71	0.93	1.38	1.99	1.24	1.32	1.32	1.41	1.32	1.50	1.83
0.08	0.13	0.11	0.10	0.27	0.20	0.16	0.20	0.18	0.18	0.17	0.17	0.21
0.36	—	0.34	0.26	—	—	0.51	0.55	0.52	0.59	0.59	0.48	0.64
0.22	0.26	0.21	0.24	—	—	0.28	0.54	0.45	0.45	0.26	0.24	0.31
0.05	—	—	—	—	—	—	—	—	—	0.05	0.09	0.03
0.91	0.66	0.76	0.92	1.10	1.96	1.27	1.41	1.29	1.38	1.22	1.47	1.56
0.07	0.11	0.10	0.10	0.17	0.22	0.17	0.22	0.20	0.18	0.16	0.17	0.18
0.33	—	0.33	0.25	—	—	0.57	0.61	0.57	0.57	0.44	0.47	0.53
0.26	0.33	0.30	0.30	—	—	0.39	0.65	0.50	0.53	0.40	0.25	0.39
0.07	—	—	—	—	—	—	—	—	—	0.06	0.05	0.03
0.82	0.66	0.75	0.98	1.01	1.72	—	—	—	—	—	—	1.45
0.06	0.10	0.09	0.10	0.14	0.19	—	—	—	—	—	—	0.16
0.28	—	0.30	0.24	0.47	—	—	—	—	—	—	—	0.47
0.33	0.40	0.37	0.35	—	—	—	—	—	—	—	—	0.43
0.07	—	—	—	—	—	—	—	—	—	—	—	0.02
0.81	0.68	0.75	1.00	0.99	—	—	—	—	—	—	—	1.38
—	0.09	0.08	0.09	—	—	—	—	—	—	—	—	0.15
—	—	0.29	0.26	0.28	—	—	—	—	—	—	—	—
—	0.44	0.41	0.43	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—

Open old spruce forest. **Tröndelag in Middle Norway**: 775 Open spruce forest on poor sand; 778 Small opening in highly productive spruce forest.

B. — **Eastern Sweden**: 318 Beneath dense spruce canopy, Site I; 492 Extremely dense spruce forest. **Eastern Norway**: 625—628 Moderately dense spruce forest (Ås, within plot No. 91 of Norwegian Forest Research Institute, described by MORK 1942.) **Western Norway**: 633—634 Beneath dense spruce canopy near 631—632; 677 Beneath dense spruce canopy near 672.

All samples except 309, 320 and 318 were collected during summer.

West-Norwegian than in Swedish samples; within each geographical group the P content is correlated with the exposure. Potassium is usually higher in shaded plots, while the tendency is more uncertain in the case of calcium.

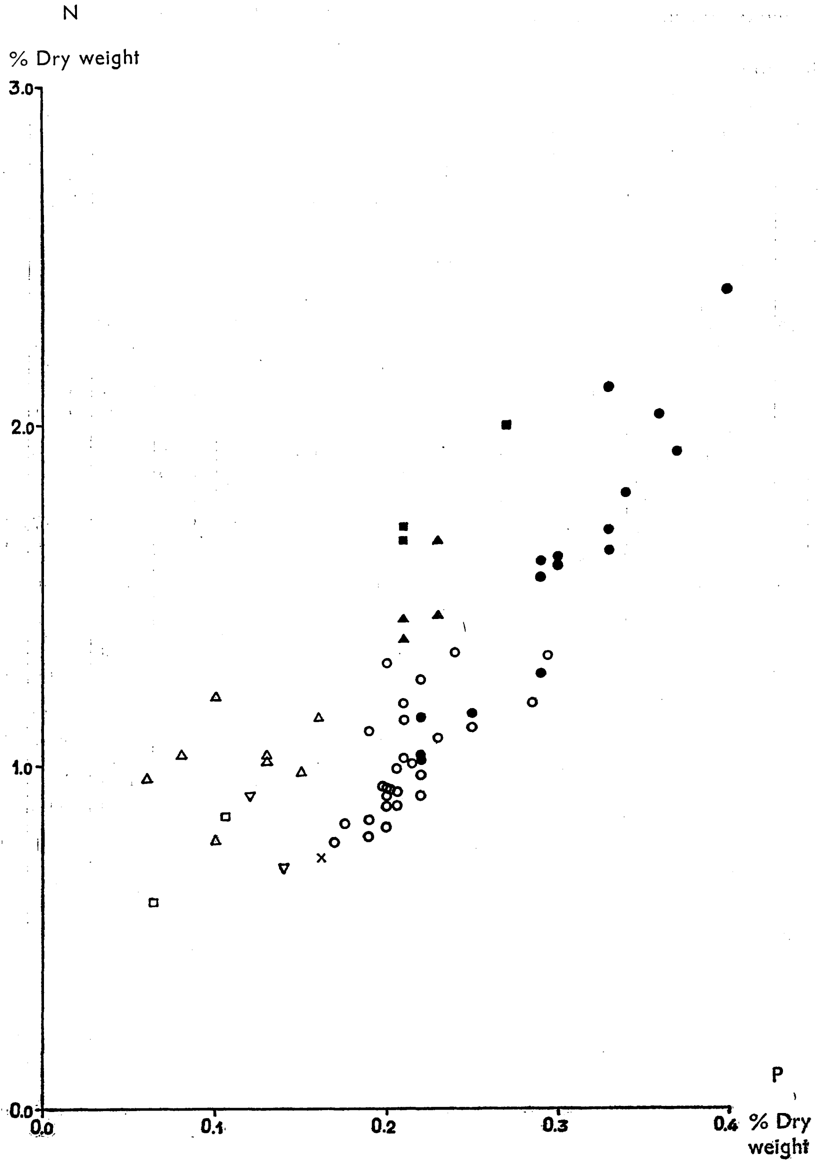


Fig. 32. Nitrogen concentration in segment 2 of *Hylocomium splendens*, plotted versus phosphorus concentration in the same segment. Samples from different regions and exposures:

	Exposed	Shaded
Roslagen	○	●
Western Norway	△	■
Eastern Norway		▲
Scotland (near Fort William)	□	
Västerbotten	×	
Tröndelag	▽	

Fig. 32 shows a strong positive correlation between the concentrations of N and P in *Hylocomium splendens.* This correlation is stronger if the comparison is restricted to samples from either a very wet climate (western Norway and Scotland) or a dry climate (Roslagen and Västerbotten) or a moderately humid climate (eastern Norway and Tröndelag); though in the last case the number of analyses is low. The difference between these regions may be described as a tendency to lower P contents relative to N with increasing climatic humidity.

The data presented in Table XVI can also be used to show the above-mentioned correlation between the nutrient concentration in parent and daughter segment. In this connection it is very important to distinguish between average differences, found between different samples or fractions of samples, and differences found between different individuals. We have already met with similar problems in connection with the growth measurements. They are even more difficult to master where chemical analyses are concerned, as the sensitivity of the methods used does not allow accurate determination of very small amounts of the elements in question.

Figs. 33 and 34 compare the correlation between segments 2 and 3 both for whole samples or sample fractions (a) and for individual specimens (b) in the

Table XVII. Per cent air-dry weight contents of nitrogen and phosphorus in individual *Hylocomium* segments. Sample 679, moderately exposed, collected 15.VI.1950 at Os, Norway. Water content of air-dry sample ca. 8 per cent.

A. Nitrogen				B. Phosphorus			
Segment "48"		Segment "49"		Segment "48"		Segment "49"	
Weight mg	% N	Weight mg	% N	Weight mg	% P	Weight mg	% P
20.0	0.65	30.3	0.71	33.6	0.06	34.0	0.11
23.2	0.82	27.3	0.99		0.05		0.11
22.8	0.86	29.6	0.80	39.1	0.07	17.3	0.09
13.0	0.86	27.1	1.02		0.08		0.09
14.6	0.90	18.5	1.09	23.8	0.07	34.4	0.14
24.2	0.91	34.7	0.82		0.08		0.12
31.8	0.92	50.0	0.99	11.1	0.07	18.6	0.22
21.9	0.93	47.3	0.84		0.09		0.22
20.5	1.06	31.5	1.52	12.0	0.08	21.2	0.07
26.4	1.24	35.5	1.19		0.09		0.08
34.8	1.28	20.9	1.48	11.9	0.10	14.1	0.28
14.6	1.32	16.4	1.65		0.09		0.26
20.7	1.36	14.6	2.15	23.9	0.11	37.0	0.13
15.6	1.40	24.5	1.13		0.10		0.14
				21.8	0.11	30.1	0.10
					0.11		0.10
				13.0	0.17	17.5	0.28
					0.16		0.26

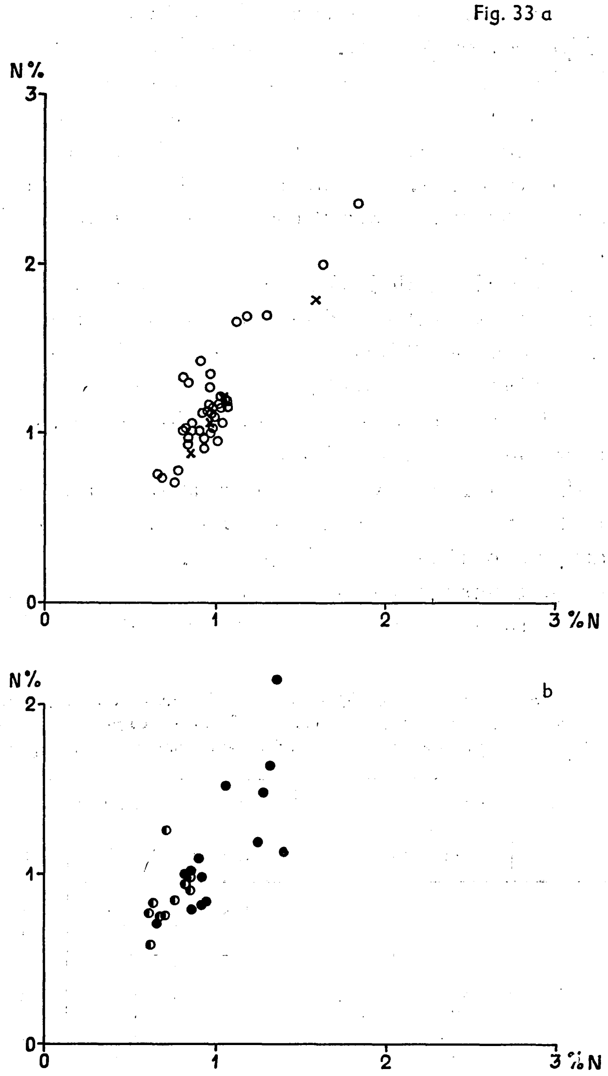


Fig. 33. Nitrogen concentration in segment 2 of *Hylocomium* in relation to the nitrogen concentration of its parent segment.
a. In average samples. × fast-growing fraction ○ normal fraction or whole sample
b. In individual moss plants. ● sample 679 ◐ sample 493

case of N and P concentrations. We find a very close correlation between N and P concentrations of daughter and parent segment in Figs. 33 a and 34 a, while Figs. 33 b and 34 b show a greater variation. The relative error in the determination of the nitrogen values in Figs. 33 b and 34 b is greater

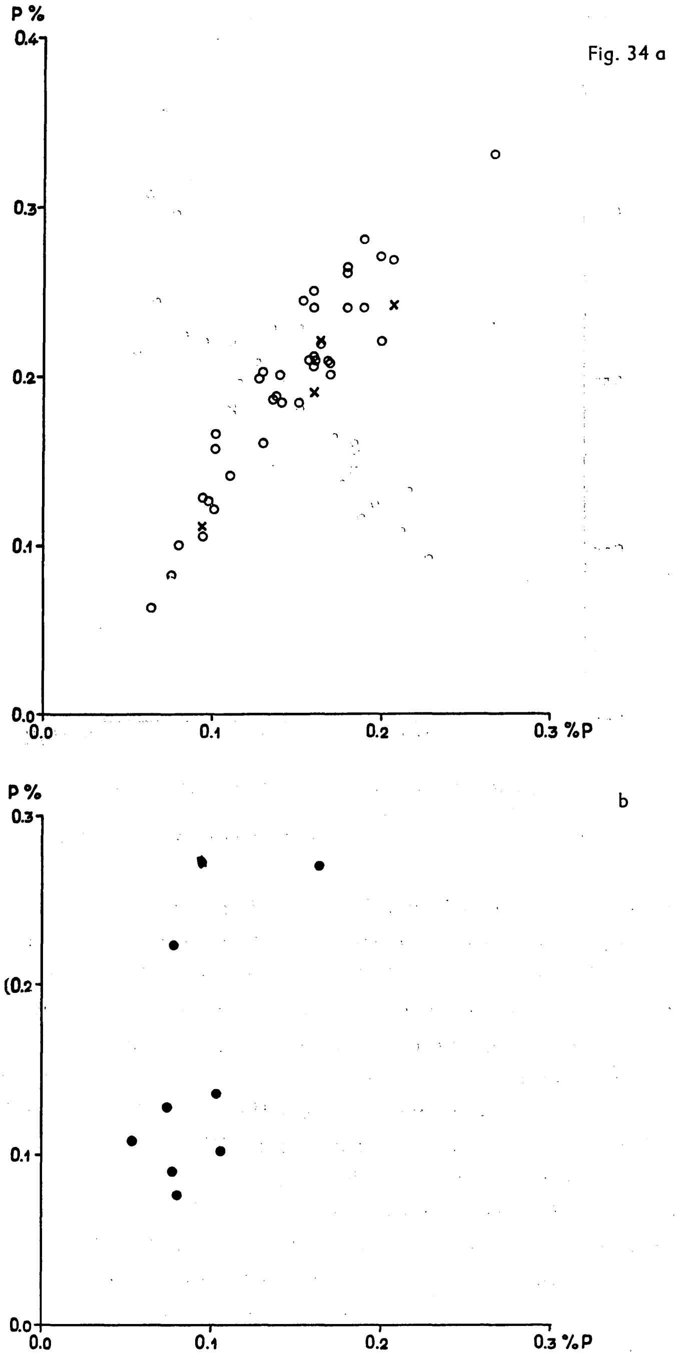


Fig. 34. Phosphorus concentration in segment 2 of *Hylocomium* in relation to the phosphorus concentration of its parent segment.
a. In average samples. × fast-growing fraction ○ normal fraction or whole sample
b. In individual moss plants (sample 679).

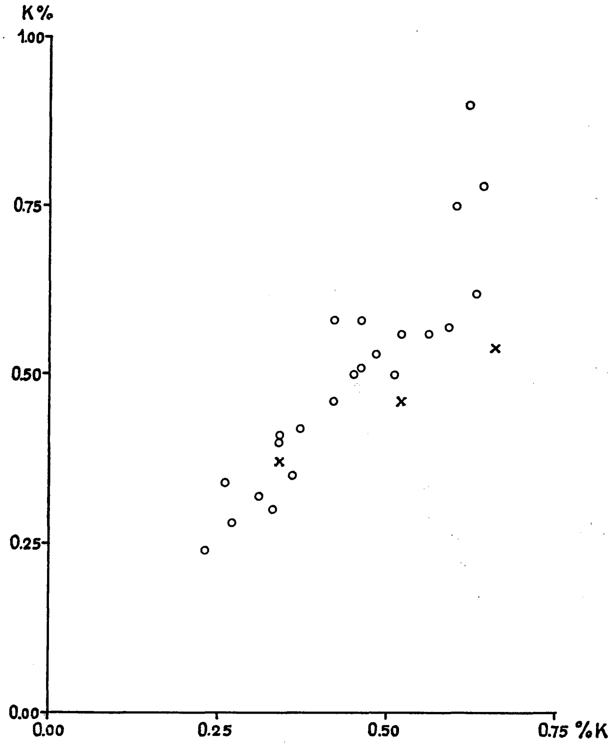


Fig. 35. Potassium concentration in segment 2 of *Hylocomium* in relation to the potassium concentration of its parent segment.
× fast-growing fraction ○ normal fraction or whole sample

than usual on account of the smaller amounts analysed: a standard deviation of about ± 0.01 mg N (p. 14) corresponds to an error of ± 2 per cent if 50 mg are used for the analysis, but to ± 5 per cent if only 20 mg are used. However, this analytical error cannot in any way explain the wide scattering of the dots in Fig. 33 b. The error in the phosphorus determination is larger than in the nitrogen analysis, but on the other hand the colorimetry has been duplicated (see Table XVII), which makes the values fairly reliable.

In the large variations of chemical composition from segment to segment we have a fresh reason for postulating a relative nutritional independence of the different *Hylocomium* segments.

Figs. 35 and 36 show that in the case of K and Ca there is a strong variation about the regression line when we plot the figures for whole samples; it has therefore been considered unnecessary to demonstrate a possibly still greater individual variation.

In Figs. 33 to 36 the values for so-called fast-growing individuals are marked

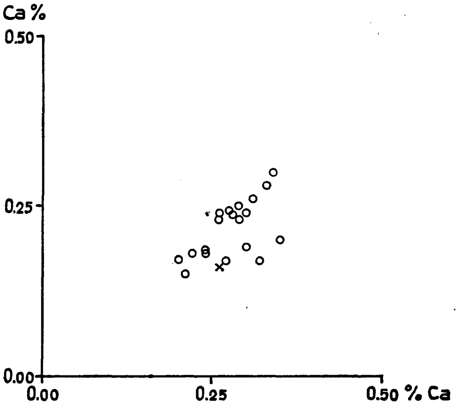


Fig. 36. Calcium concentration in segment 2 of *Hylocomium* in relation to the calcium concentration of its parent segment.
× fast-growing fraction ○ normal fraction or whole sample

with special signs. These specimens were selected from the main fractions of the samples for their large segment 2 in comparison with segment 3. The dots for the fast-growing fractions lie quite near the regression lines in the figures, so it is evident that these specimens agree with the rest where chemical composition is concerned. The properties of the fast-growing moss plants may be studied more in detail in Table XVIII. We see here that there are small differences both in parent and daughter segments between different fractions of the same sample. The cause is probably an uneven distribution of the different kinds of individuals, coupled with local differences within the plot, e.g. regarding exposure. The small differences between the various fractions does not, however, invalidate the conclusion that a growth increase of 50 per cent or more over the normal does not much alter the nutrient concentration in *Hylocomium.* Evidently the stronger growth is associated with an increase in nutrient uptake. Whether a slow growth is likewise accompanied by a slower nutrient uptake is more difficult to decide, as some of the slow-growing specimens may grow slowly on account of some injury which, although difficult to observe, may interfere with nutrient uptake or translocation. There are no clear indications in Table XVII that slow-growing segments contain more nutrients than the average; some slow-growing segments contain indeed very much nitrogen, but that is also true of their parent segment.

The large individual variation observed in the composition of the *Hylocomium* segments should not lead us to conclude that the nutrient concentration in *Hylocomium* always varies within wide limits. A look at Table XVI shows us that the N concentration seldom falls below ca. 0.70 per cent dry weight. In the samples at this low N level, the percentages are approximately the same

Table XVIII. Nutrient contents of fast-growing *Hylocomium splendens* individuals compared with those of normal individuals.

No. of sample	Locality Date of sampling	Fraction	Fraction in % of sample (segm. 3)	Segm. 2 in % of segm. 3	Per cent dry weight							
					N		P		K		Ca	
					segm. 3	segm. 2	segm. 3	segm. 2	segm. 3	segm. 2	segm. 3	segm. 2
324	Site I, Grenholmen 1.IV.1949.	Fast-growing	—	187	1.04	1.20	0.16	0.22	0.66	0.54	—	—
		Normal "unbranched"	—	74	1.03	1.15	0.16	0.22	—	—	—	—
		Normal "unbranched"	—	81	1.02	1.17	0.18	0.25	—	—	—	—
		Mixed sample "branched" and damaged	—	—	0.98	1.16	0.16	0.23	0.56	0.56	—	—
330	Site I, Grenholmen 25.V.1949.	Fast-growing	9	163	0.96	1.05	0.16	0.19	0.52	0.46	—	—
		Normal "unbranched" .	38	83	0.97	1.13	0.16	0.21	0.51	0.50	—	—
		Normal "branched"	23	92	0.84	0.97	0.17	0.20	—	—	—	—
		Damaged...	30	92	0.93	1.13	—	—	—	—	—	—
672	Os, western Norway Exposed plot. 15.VI.1950.	Fast-growing	13	205	0.85	0.89	0.09	0.11	0.34	0.37	0.26	0.16
		Normal.....	87	121	0.90	1.01	0.10	0.13	0.34	0.40	0.27	0.17
677	Os, western Norway Shaded plot. 15.VI.1950.	Fast-growing	18	152	1.79	1.79	0.21	0.24	—	—	—	—
		Normal.....	82	103	1.83	2.00	0.21	0.27	0.64	0.62	0.31	0.26

in living and dead segments. From one of these samples (No. 516) 9 individual segments 3 have been analysed for N. The result was 0.62 per cent N (on the air-dry basis) with a standard deviation of 0.044 (maximum value 0.69, minimum value 0.57 per cent N). If the standard deviation is expressed in mg N the value is 0.010 (average segment weight 22 mg). This value is approximately the same as the standard deviation in all the nitrogen determinations (0.012, see p. 14). We have therefore no proof of the existence of differences in N percentages between the individual segments from sample 516; on the contrary we have established that the sample is as homogeneous with respect to nitrogen content as our method allows us to determine.

We can now summarize our results concerning the variation of N, P, K and Ca in *Hylocomium splendens:* 1) N percentages are highest in young segments and decrease to an approximately constant level in old segments. The absolute amount of N in a segment increases during growth and then remains more or less constant until the decomposing segment goes to pieces. 2) Shaded *Hylocomium* contains more N than *Hylocomium* from plots with a moderate or good light supply. 3) There is a close correlation between the nitrogen percentages of parent and daughter segments, if whole samples are compared; on the other hand there is large individual variation in this respect, at least in some samples. 4) In at least one habitat there is much less individual variation in N percentages than in others; in this case and also in some other samples there is little difference between segments of different age (except the bud which always is higher in N). These samples are characterized by very low per cent contents of N. 5) When fast-growing specimens have been analysed separately, their N content has been similar to that of normal individuals from the same sample. A rapid growth has thus been accompanied by a strong uptake of nitrogen. 6) In the case of phosphorus contents, conditions are on the whole similar to those described for nitrogen, except that both the per cent and the total contents of old segments decrease from year to year. The analytical methods have not been sensitive enough to allow us to find a case with low individual variation in P percentages, but a fairly constant P level appears to be established in different plots in the same locality, when the light intensity is moderate to good. Curiously enough the phosphorus level is different in different areas (e.g. eastern Sweden and western Norway). 7) Potassium behaves essentially as phosphorus, but the decrease with the age is faster still, and there is more irregular variation when the K content is considered in relation to different factors (light supply, content of parent segment, geographical region, etc.). 8) Calcium differs from the other elements in two important respects: there is very little or no correlation between Ca content and the different factors discussed above, and 9) the Ca content increases with age, both in living and dead segments.

These points will be discussed in Chapter X with regard to the causal relationships involved.

Other mineral constituents

The analyses mentioned so far have only concerned the four elements N, P, K and Ca. However important these elements may be as plant nutrients, we have no right to assume that they are more important for *Hylocomium splendens* than are the other essential elements, S, Mg, Fe, and the trace elements. There is reason to believe that at least most of these elements are supplied to the moss carpet in small amounts, as shown in the next chapter. However, the quantitative demand for these elements, and the corresponding concentration levels, are unknown in the case of *Hylocomium splendens*. Being

Table XIX. Composition of different segments of *Hylocomium splendens* from Site I (analysed sample mixed from equal parts of four different samples collected from October 1949 to April 1950) and from Site III (collected 16.VII.1951).

Locality	Segment No.	Average d.w. of segment "unbranched" specimens mg	Per cent dry weight												
			N	Ash	P	K	Na	Ca	Mn	Fe	Al	Insoluble residue	SiO_2	K_{sil}	Na_{sil}
Site I.	1	0.4	—	—	—	—	—	—	—	—	—	—	—	—	—
	2	8.3	1.08	—	0.24	0.77	—	0.27	0.012	0.015	0.009	—	—	—	—
					0.24	0.81	—	0.27	0.012	0.015	0.010				
	3	9.5	0.82	—	0.13	0.48	—	0.28	0.011	0.033	0.026	—	—	—	—
					0.13	0.47		0.27	0.011	0.034	0.028				
	4	9.3	0.78	—	0.11	0.49	—	0.37	0.014	0.034	0.043	—	—	—	—
					0.11	0.50		0.35	0.014	0.038	0.040				
	5	7.9	0.75	—	0.10	0.44	—	0.44	0.022	0.048	0.052	—	—	—	—
					0.10	0.44		0.44	0.020	0.052	0.054				
	6	—	—	—	0.09	0.37	—	0.52	0.027	0.050	0.061	—	—	—	—
	7	—	—	—	0.09	0.31	—	0.63	0.033	0.059	0.063	—	—	—	—
Site III	1	1.2	1.21	—	0.32	0.83	0.02	0.31	0.022	0.010	<0.010	—	—	—	—
			1.18												
	2	9.0	0.77	2.09	0.17	0.47	<0.01	0.18	0.011	0.026	0.020	0.33	0.26	0.010	0.003
			0.77	2.17	0.17	0.45		0.17	0.011	0.026	0.020	0.34	0.28	0.010	0.005
	3	9.8	0.66	2.27	0.10	0.42	<0.01	0.23	0.010	0.038	0.026	0.47	0.38	0.014	0.007
			0.67	2.26	0.10	0.43		0.24	0.011	0.035	0.025	0.44	0.35	0.012	0.004
	4	8.5	0.70	2.41	0.09	0.37	<0.01	0.32	0.014	0.050	0.044	0.62	0.48	0.017	0.008
			0.70		0.09	0.35		0.32	0.013	0.055	0.039				
	5	9.5	0.66	2.61	0.09	0.31	<0.01	0.35	0.015	0.059	0.045	0.78	0.61	0.021	0.011
			0.70		0.09	0.33		0.34	0.012	0.050	0.046				
	6	—	0.69	3.03	0.09	0.31	<0.01	0.36	0.019	0.073	0.063	1.02	0.80	0.024	0.013
			0.71												
	7	—	0.71	—	0.09	0.28	<0.01	0.39	0.018	0.072	0.055	—	—	—	—

purely physiological problems we can hardly solve them by the methods used in this investigation. Moreover, determination of some of the trace elements, e.g. copper, would require special precautions in the preparation of the samples, as contamination is very likely to occur during the separation of the different segments, when every segment has to be handled directly.

We have thus not carried out analyses of elements other than the four discussed above, except in a few samples. In Table XIX we find for two samples (from Sites I and III, Grenholmen) the contents of manganese, iron and aluminium in addition to the usual analyses. In the sample from Site III the ash and silica content have also been determined after dry ashing at 600° in platinum dishes. As only about $^4/_5$ of the acid-insoluble residue after the ignition could be accounted for by silica, it was tested for potassium, sodium and calcium after volatilization with hydrofluoric acid. Calcium was not found in measurable quantities, but potassium and sodium were found to make up a low but almost constant proportion of the residue (K_{sil} and Na_{sil} in Table XIX). As a matter of fact the sodium content of the residue in some cases exceeded the content of acid-soluble sodium, which was well below 0.01 per cent in all segments except the bud. Moreover, potassium in the residue increases with the age of the segment, in contrast to the main fraction of the same element.

The explanation of this apparent contradiction is no doubt that the acid-insoluble residue not only contains the silica taken up by the moss, but also particles of minerals. Such very small particles have sometimes been observed in the wet digestion in addition to the cloudy precipitate normally formed by the silica. This contamination with extraneous material may of course give rise to errors in the conclusions based upon analytical data. However, even if the residue originally had contained chiefly minerals rich in calcium, e.g. Ca-rich plagioclase, and this calcium had been completely dissolved during extraction, the increase in Ca content from segment 2 to segment 5 or 6 could not have been entirely explained in this way. Thus we cannot expect serious errors from this source. This is the more true as even minerals rich in Ca, e.g. labradorite or hornblende, are dissolved to only a small or moderate extent (varying with the coarseness) during acid extraction after dry or wet combustion (personal communication by Mrs. KARIN KNUTSON).

Returning to Table XIX we can establish that manganese in *Hylocomium* shows a trend very similar to that of calcium: relatively high percentage in the bud, low in segment 2 and then increasing with age. Iron and aluminium (probably silica too) show similar curves, except that there is no enrichment in the bud.

The sodium content in these samples was too low for an accurate determination, but some sodium values can be found in Table XVI, showing that sodium in Norwegian samples is highest in the bud and then decreases to a very low and more or less constant level. In all analysed Swedish samples the Na content is lower than in the Norwegian ones. (Of the Swedish samples analyzed for sodium only one is listed in Table XVI.)

From these data we can conclude that the univalent elements potassium and sodium are accumulated in the young moss and then decrease in concentration, sodium very quickly, potassium at a slower rate. The bivalent and trivalent metals show a successive accumulation from year to year in most segments, with or without a previous accumulation in the bud. Aluminium, which is not considered as necessary, appears to behave as the indispensable element iron.

Nutrient uptake per unit area

From the yield data, presented in Tables V, VI, VII, and VIII, and from the chemical analyses (Table XVI) it is possible to estimate the annual consumption of nutrients per unit area by the *Hylocomium* community. This is most easily done in the case of nitrogen, because this element is not subject to leaching (see Chapter VIII). The youngest full-grown segment is segment 3, which also contains that amount of nitrogen which is given off by the moss community as litter in a year. Segment 2 has not always completed its nitrogen uptake; moreover there may be some translocation of N from segment 2 to the bud.

The figures for maximum nutrient consumption within different plots interest us most, as they give us minimum figures for the amount of nutrients which are annually supplied to a well-developed moss carpet. As the moss composition does not differ very much, in particular not in the case of N, in different exposed plots, and as the shaded plots with high nutrient concentration have low moss yields, the maximum nutrient consumptions are found in the same plots as the maximum yields. Minor exceptions from this rule may well appear if more samples are analysed, but at present we only want to determine the order of magnitude of the nutrient supply to the moss carpet.

Our maximum yield was obtained on plot 672, from Western Norway, where segment 3 (together with annual shoots of other species) weighed 1.1 g/dm^2. Segment 3 contained in this samples 0.90 per cent N, and the annual uptake of N can thus be estimated to 10 mg N/dm^2 or 10 kg N/ha, always supposing that the other species do not differ much from *Hylocomium splendens* in their nutrient uptake. The corresponding calculation for phosphorus gives us ca 1.1 mg P/dm^2 per year; for potassium we get 4 mg/dm^2 per year. These latter values may be somewhat too low, as P and K are lost by leaching to some extent (see Chapter VIII). Moreover we know that segment 3 in sample 672 is considerably smaller than segment 2, so that a calculation based upon segment 2 would give higher values, even if we use the same percentages.

In the case of calcium it is a matter of definition how we shall calculate the annual consumption. If we only deal with the living moss, we arrive at values similar to those for potassium, but if we include the uptake by dead moss, we must increase the figures, in some cases perhaps double them.

For the plot with maximum yield in Sweden (No. 8 in Table XIV) we have unfortunately only figures for the composition of the sum of segments 1 and 2. However, we may compare the contents of segments 1 + 2 in sample 8 with the corresponding figure for sample 672, which can be calculated from Tables XVI and IX: 1.05 per cent N, 0.15 per cent P, 0.45 per cent K and 0.18 per cent Ca. In sample 8 we have the following percentages: N 1.11, P 0.25, K 0.7 and Ca 0.27 (Table XIV). Evidently the higher N content compensates for the slightly lower yield so that N consumption per unit area becomes approximately the same within both plots, 10 mg/dm^2 per annum. In the case of the other three elements the yearly consumption has been higher in the Swedish plot, about 1.5 mg P and 6 mg K, all calculated per dm^2 per annum. The composition of segment 3 in sample 8 can also be deduced from a comparison with the samples from Site I, which leads to similar figures for the nutrient uptake.

Of course these figures are subject to annual variation to at least the same extent as are the yield figures. We have already tried to study annual variation in moss composition in Table XI, although the annual variation here was mixed with a more or less random variation. One example of differences between different years can be found in Table XVI, where segment 4 contains more phosphorus and potassium than segment 3 in samples 625 to 628, in contrast to the usual trend. It is tempting to associate the high content of segment 4 (in this case segment 47) with the dry weather during a large part of the year 1947 (see Fig. 45 a, p. 135).

It is also possible to compute the nutrient consumption for plots other than 672 and 8, but these figures will be lower. For exposed plots they will decrease roughly in proportion to the yield, for shaded plots at a much slower rate. The samples from more northern localities (Table VIII) show lower yields and comparatively low nitrogen contents; their nitrogen consumption thus stays around 5 mg/dm^2 per annum, or about half the figures attained in favourable habitats in eastern Sweden or western Norway.

Determinations of both the moss yield and its nutrient uptake have been made earlier by ROMELL (1939) and ANDRÉE (1947). These collections of ROMELL and ANDRÉE were all made in the late autumn, which will lead to an underestimation of the yield, if only the last segment is weighed. ROMELL found a moss yield of 0.7 g/dm^2 for old spruce forest in Orsa, and the value obtained by ANDRÉE is almost identical; the sample plot was a mixed forest of spruce and pine not far from Stockholm. ROMELL reports some determinations carried out by MORK for another locality near Stockholm (mixed forest of spruce and pine), which yielded 0.8 and 0.9 g/dm^2. ROMELL estimates the amount of nitrogen contained in the annual moss growth on the Orsa plot at 6.7 mg/dm^2; ANDRÉE found 7.3 mg/dm^2. ROMELL also gives the corresponding figures for potassium, 4.6, calcium, 2.8, magnesium, 1.0, and for phosphorus 1.5, all in mg/dm^2 per annum.

These figures agree well with those found in this investigation; it must be remembered that the yield is underestimated more than the nutrient uptake, as young segments harvested in late autumn have not attained their full size and contain relatively high concentrations of N, P and K.

Chapter VII. The Supply of Plant Nutrients to the Moss Carpet

In some mosses the existence of a transpiration stream has been demonstrated (HABERLANDT 1886, cf. BUCH 1947). Even if water and salt uptake are different things, it seems reasonable to assume that such mosses behave like most higher land plants, viz. obtain nutrients from the soil. On the other hand we know from experiments (STÅLFELT 1937 a) that water rises very slowly in a *Hylocomium* stem, even if it dips into water. Capillary suction cannot prevent the upper part of the plant from drying out quickly, except in air nearly saturated with vapour. The maximum rate of water uptake by a *Hylocomium splendens* carpet is estimated by STÅLFELT (l.c. p. 185) at 3 g per dm^2 in 24 hours, provided the lower parts of the moss stems are thoroughly in contact with water-saturated soil. As these prerequisites are fulfilled only periodically, and for those moss plants which have an unbroken connection with the subsoil, STÅLFELT considers the capillary uptake of water from the subsoil as clearly insufficient for the moss carpet; he also points out that the nutrient supply by capillary water must be very small.

ROMELL (1939) tried to calculate the phosphorus supplied from below to the mosses, using STÅLFELT's data and a value for the phosphorus concentration in the soil solution of one p.p.m. of P_2O_5. In spite of this very high concentration he arrives at the conclusion that most of the content of phosphorus in the moss must come from some other source; he suggests leaching from leaves and needles lying on the moss carpet.

Simple observation in nature adduces evidence for the view of STÅLFELT and ROMELL, viz. that the mosses obtain their nutrients (or most of them) in some other way than by capillary suction from below. *Hylocomium splendens*,

Fig. 37. *Hylocomium splendens* and *Pleurozium Schreberi* colonizing a stone. Grenholmen 24. IV. 1952.

as well as ecologically similar species, often covers stones and tree stumps where little or no humus has collected beneath the moss carpet (Fig. 37). It is difficult to decide whether mosses grow less vigorously on stones without humus than on the ground, as even on the stones the patches without humus are small and recently invaded by the moss community; after some time both tree and moss litter collects. Humidity, light supply and possibly carbon dioxide concentration are also somewhat different on stones and on the ground. Under favourable conditions there is, however, no great difference in growth of mosses on the ground and on protruding rocks, stones and tree stumps. Fig. 38 shows such a habitat where a dense carpet of *Hylocomium splendens, Pleurozium Schreberi* and *Ptilium crista castrensis* covers most of the ground without being much influenced by the micro-topography. On the other hand, where water comes trickling down steep slopes, *Hylocomium* may form dense pillows, apparently profiting by the rich water supply, or by something contained in the water. Fig. 39 shows a habitat where *Hylocomium* probably receives such water occasionally. (The appearance of *Hylocomium splendens* in this habitat is somewhat abnormal, probably due to a rather strong sun exposure.)

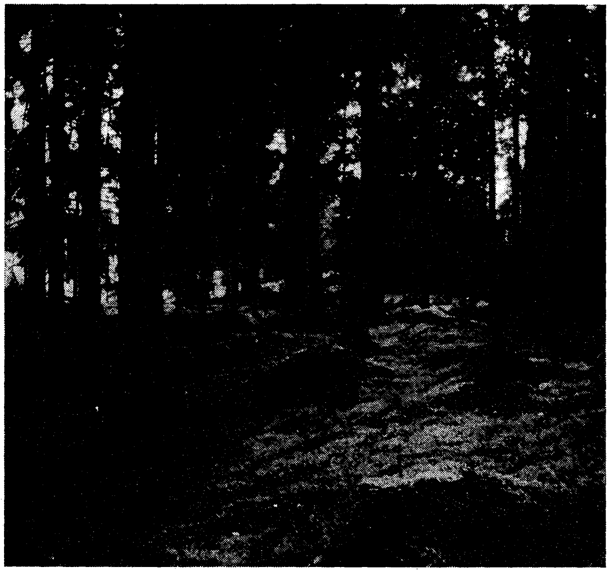


Fig. 38. Spruce forest with a uniform moss carpet covering ground, stones and tree stumps. Field vegetation chiefly scattered *Deschampsia flexuosa;* moss layer consisting mainly of *Hylocomium splendens, Ptilium crista castrensis* and *Pleurozium Schreberi.* Hok, Småland, 7. IX. 1952.

In most *Hylocomium* habitats there is no water trickling along the surface of the ground, except on very unusual occasions. We must therefore find some other source of nutrients for the moss carpets. The dependence of the moss growth on tree canopy offers us a clue. As already mentioned ROMELL (1939) has suggested the tree litter as a source of nutrients, since it often remains on top of the moss for some time before being incorporated into the soil profile. It is well known that leaf and needle litter give off soluble substances, among them most mineral nutrients, when leached with water (RAMANN 1888, SCHRÖDER 1878, WALLACE 1930).

In this litter we certainly have a supply of nutrients to the mosses, one which moreover decreases with the distance to the trees, as does the moss growth. According to the opinion of the present author, however, the litter lying above the mosses cannot be their main source of nutrients. The leaf and needle litter is still more unevenly distributed than is the moss growth, which we have found to vary a great deal from individual to individual. Some of the moss specimens at some distance from trees are unlikely to be hit by a needle or a leaf which persists in a position where the leachate drips down on the moss. The growth of specimens lacking closer contact with litter and water—both are required simultaneously—should be expected to

Fig. 39. Rock sloping towards the north-east, where *Hylocomium* is growing without a tree canopy. Field vegetation scattered grasses and herbs rooting in fissures. Sample plot No. 896 marked with cross. Noor, Roslagen, 21. IV. 1952.

be almost completely inhibited. This is hardly the case, as individuals with little or no young growth usually exhibit visible mechanical or other damages.

We thus need some source of nutrients more evenly distributed than the litter fall. The existence of such a source can be deduced from the quoted work of RAMANN: if fallen litter gives off nutrients to pure water, the same ought to be the case with litter remaining on the tree. The needle litter of conifers often persists on the branches for a long time before it is shed. The rainwater beneath the trees, and on windy occasions also in their neighbourhood, ought to contain some salts leached out from the trees. The question of whether leaching of green leaves and needles, or active excretion of substances from living plants, also is responsible for a nutrient release is much discussed but still unsettled (ARENS 1934, LAUSBERG 1935, ENGEL 1939, cf. also LE CLERC & BREAZEALE 1909). The excrements of aphids, insect larvae and other animals living in the tree crowns may also contribute to the nutrient content of the water dripping down. Irrespective of the mechanism of nutrient release from the tree crowns, some salts must be expected to come down, although the quantities have up to now been completely unknown.

In this connection it should be mentioned that some nutrients are supplied to the ground with the pollen rain, but according to FIRBAS & SAGROMSKY (1947) this supply does usually not account for more than a small fraction of a milligram per dm^2 per year in the open in the case of N, P, K and Ca. Beneath

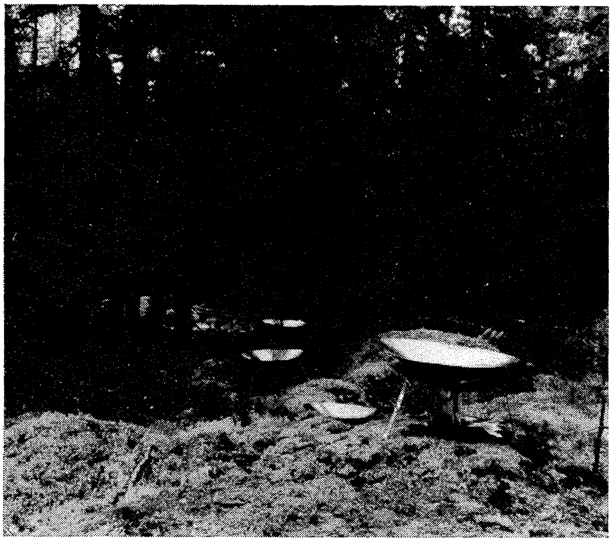


Fig. 40. Arrangement for collection of rainwater in Site II with funnels and flasks of stainless steel. See also the map Fig. 10, p. 40.

trees the quantities may be larger (cf. ROMELL 1946) and contribute to the nutrition of the mosses.

A possibly important source of nutrients to the moss carpet is atmospheric dust. Its role in the nutrition of epiphytic vegetation has earlier been pointed out by DIXON (1881), SERNANDER (1912), DU RIETZ (1932), WALDHEIM (1944), and others. Analytical data pertinent to this question have been published by PESSIN (1925) and WHERRY & CAPEN (1928). Some of the dust is washed down from the air with the rain, some may sediment directly onto the mosses, and still another fraction may be deposited on the surface of the tree crowns, from which it is later washed down by the rain.

In order to decide whether these nutrients supplied by water from above could play a part in the nutrition of mosses, several analyses have been carried out on water samples collected beneath and outside tree crowns. Some preliminary results have already been published (TAMM 1951). Another part of the analyses will be published separately (TAMM & ALVERIN, in prep.), but some data for samples from Site II and its neighbourhood are presented in Tables XX, XXI and XXII.

The samples in Table XX were collected in funnels and flasks of stainless steel placed beneath and outside the spruce trees in Site II (see Fig. 40 and map Fig. 10). The funnels were placed near sample plots, except funnel A in the middle of the opening, and funnel E in the centre of a spruce cluster

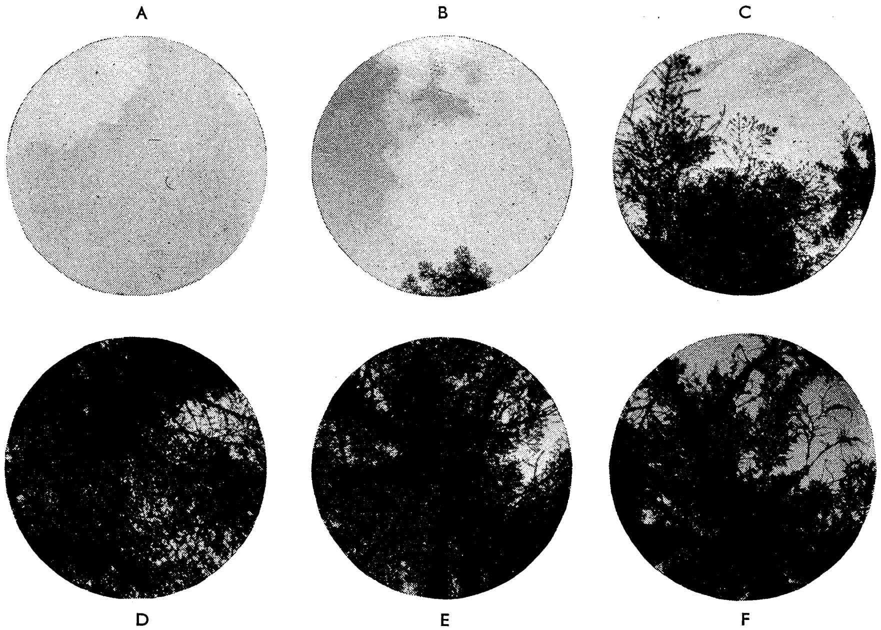


Fig. 41. A—E. View upward from the funnels in Fig. 40. F. View upward from the glass funnel beneath spruce in Table XXI.
Camera made horizontal with a water level. View angle ca. 40°.

where mosses were lacking. The density of the canopy is illustrated in Fig. 41 A—E, a series of photographs taken upwards from the centres of the funnels (view angle 40°). Water was collected from two rains of different type. On July 28—29 3 mm fell after a dry period; on September 19 4 mm of rain was collected in the middle of a rainy period. It would of course be premature to estimate the annual supply of salts to the ground from these two occasions, but a rough idea of the distribution of the salt supply can be obtained. We must remember that an average content of one part per million carries down 5 mg/dm^2 or 5 kg/ha with an annual precipitation of 500 mm. The interception of water by the tree crowns is neglected in this calculation; this is approximately correct when we speak of the outer parts of the tree crowns, where we sometimes have a slight interception, sometimes an increase in run-off (cf. LINSKENS 1951). Both the interception and the increase in run-off occur in Table XX. The interception is larger for isolated showers and the marginal run-off is larger during longer rain periods, when the crown becomes thoroughly moistened. Beneath the centres of the spruce crowns very little water percolates, especially from isolated showers.

The content of different substances in the water increases steadily from the opening toward the centre of the crown; the increase (in p.p.m.) being much

Table XX. Composition of rain water collected in an opening and beneath tree crowns in Site II. Collection a from July 28 to 29, when 2.8 mm fell after a dry period, and collection b from September 19, when 4.1 mm was collected in the middle of a rain period. Funnels and flasks of stainless steel. 1951.

Mark and location of funnels (cf. Fig. 41).	Precipitation % of value in opening		Parts per million of											
			Dry matter, lost on ignition		Ash		P		K		Na		Ca	
	a	b	a	b	a	b	a	b	a	b	a	b	a	b
A. Middle of opening	100	100	9	7	5	2	≤0.01	0.01	0.0	0.3	0.2	0.9	0.3	0.1
B. Opening but near trees; above plot No. 9.	100	104	9	7	4	2	<0.01	n.det.	0.0	0.2	0.8	0.9	0.5	0.2
C. At the margin of spruce crown projections, as plot No. 7.	102	129	295	14	17	(1)	0.12	0.01	5.3	1.0	1.0	0.8	2.1	0.5
D. Beneath spruce, as plot No. 3.	53	72	188	45	29	6	ca. 1	0.06	11.8	3.1	1.9	1.0	3.6	0.7
E. Beneath spruce, very dark.	9	66	437	166	30	36	3.5	n.det.	14.5	9.5	2.3	4.3	4.0	5.4

higher in the July series than in the September series. Presumably the most easily released nutrients are given off in the beginning of a rain period, and were thus already washed down when the funnels were set out on September 19.

The composition of the rain water in funnel B has differed little from that in funnel A. However, we cannot conclude from this that plot 9 (Fig. 10), which is located beneath funnel B, is as poorly supplied with nutrients as the middle of the opening. Neither of the two rains studied came with the more usual south or west winds, which would be expected to carry down more nutrients to funnel B (cf. Fig. 10). In funnels C and D (corresponding to plots 7 and 3, respectively) we meet with nutrient concentrations of the order expected from the moss contents, allowing an uptake of some milligrams per dm^2 per annum for potassium and calcium, somewhat less for phosphorus and sodium. The concentrations are quite naturally highest in funnel E, but the large interception here means that the quantities carried down are not so great.

Table XXI shows that mineral nutrients other than P, K, and Ca are also supplied to the mosses from above. Manganese was found only beneath the spruce, while iron was found both beneath the spruce and in the open; the concentration was higher beneath the spruce, but the amount carried down was about the same because of the interception by the tree crown. The same applies to silica. These results, together with the leaching experiments of SCHRÖDER (1878 p. 94—97) and RAMANN (1888) suggest that most or all elements contained in the tree crown are to some extent washed down by the rain. From a physico-chemical point of view we should expect univalent metals

Table XXI. Composition of rainwater collected beneath spruce and in the open during four different periods. A. 1—17.XI.1951. B. 17.—24.XI.1951. C. 17.VII.—12.VIII.1952. D. 12.—15.VIII.1952. Glass funnels and flasks. (Values from opening within brackets are suspected to be too high on account of contamination, e. g. by birds or insects.)

Location of funnel	Precipitation mm		Parts per million of																		
			Dry matter, lost on ignition		Ash		NH_3-N		P		K		Na		Ca		Fe		Mn		SiO_2
	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A
Open field	21	25	8	6	5	5	0.8	0.2	<0.1	<0.1	0.6	0.3	1.0	0.7	0.7	0.2	0.02	0.02	0.00	0.00	0.4
												0.3		0.7		0.3	0.02	0.03			
Beneath spruce (cf. F in Fig. 41.)	9	10	63	49	56	30	0.0	0.0	ca. 1.6	ca. 1.0	10.3	6.3	3.6	2.6	4.3	2.2	0.06	0.05	0.26	0.11	0.8
												6.5		2.7		2.1	0.04	0.04			
	C	D	C	D	C	D	C	D	C	D	C	D	C	D	C	D	C	D	C	D	
Open field	78	15	—	—	—	—	0.9	0.5	—	—	0.3	0.3	0.3	0.5	0.5	0.2	—	—	—	—	—
Opening in forest	78	14	—	—	—	—	(3.0)	0.4	—	—	(1.0)	0.3	(0.7)	0.3	0.4	0.2	—	—	—	—	—
Beneath spruce (cf. F in Fig. 41.)	38	10	—	—	—	—	0.0	0.1	—	—	5.2	1.7	0.9	0.4	0.8	0.5	—	—	—	—	—

(Na, K) to be leached more readily than bivalent ions (Ca, Mn, Mg, Cu, Zn) and these more so than metals usually forming trivalent ions under the prevailing conditions (Fe, Al). Although scarce, the data in Tables XX and XXI confirm this view. From Table XXII we see that the leaching of potassium is a general phenomenon for different tree species. The concentrations of sodium and calcium are also higher beneath trees, but the amounts carried down are only slightly higher than in the open. This is particularly true of the sodium concentrations; it should be remembered that the amounts of sodium in the tree leaves are not great.

Regarding the elements usually taken up as anions we know that phosphorus is washed down in considerable quantities (Tables XX and XXI and unpublished data). It was also easily leached in the experiments of SCHRÖDER and RAMANN (l.c.). Also sulphur was leached in these experiments, and there is no reason why small quantities of boron should not come down in the same way.

From Table XXII we see that even in the open calcium and potassium are supplied by rain in quantities which may well be of importance for the mosses, 0.9—1.0 kg/ha in 227 mm precipitation. Sodium is carried down in a still larger quantity, 1.4 kg/ha. The interesting question now arises: from where do

Table XXII. Concentration of potassium, sodium and calcium in rain-water collected in the open and beneath different trees; and amounts of these elements supplied to the ground beneath trees in comparison with those supplied in the open.

Rain was collected during five different periods during summer and autumn 1952 at Grenholmen, Roslagen; rain from the open was analysed from all periods; but beneath trees the values are fewer. Glass funnels and flasks, protected against bird droppings (cf. Egnér et. al. 1949).

In the open 227 mm fell during the sampling period, which carried down 0.97 mg K, 1.41 mg Na and 0.91 mg Ca per dm^2 (average of values from three different vessels).

Canopy	Precipitation, % of that in open field (average)	Parts per million of						Amount carried down (amount in open field = 1)						No. of analysed samples
		K		Na		Ca		K		Na		Ca		
		aver.	range	aver.	range	aver.	range	aver.	range	aver.	range	aver.	range	
None.............		0.3	0.2—0.5	0.5	0.3—0.8	0.5	0.2—1.1							5
,, ...		0.3	0.2—0.7	0.6	0.3—1.0	0.5	0.2—1.1							5
,, ...		0.4	0.2—0.8	0.6	0.3—1.1	0.5	0.2—1.2							5
Alnus glutinosa....	77	8.9	0.9—21.5	0.8	0.4—1.5	1.6	0.7—2,1	26.0	3.5—18	1.3	1.0—1.5	2.6	1.8—4	3
Betula verrucosa...	94	2.0	1.2—3.4	0.8	0.5—1.4	1.0	0.5—1.6	7.3	4—9	1.7	1.5—1.9	2.0	1.7—2.7	3
,, ,, ...	83	2.3	0.8—4.5	0.7	0.5—1.1	1.0	0.3—1.7	7.8	2.5—10	1.4	1.0—1.8	1.8	1.3—2.1	3
,, ,, ...	83	4.4	0.5—16.4	0.6	0.3—1.0	1.6	0.3—5.0	12.4	1.5—20	0.9	0.8—1.3	4.4	1.0—13	5
,, ,, ...	83	2.1	0.9—4.6	0.7	0.3—1.1	0.9	0.4—1.9	5.0	3.0—5	1.1	0.8—1.9	1.6	1.3—2.2	5
Corylus avellana...	86	5.1	2.3—8.6	0.6	0.3—0.9	1.4	0.6—1.9	16.8	10—20	1.1	0.8—1.3	2.6	1.6—4	3
Fraxinus excelsior .	82	5.1	2.5—9.0	0.7	0.5—1.0	1.0	0.4—1.9	13.3	9—25	1.3	1.2—1.4	1.4	1.2—2.0	3
Picea abies	44	3.2	1.7—4.2	0.8	0.5—1.2	0.7	0.3—1.2	5.4	2.5—9	0.8	0.5—1.0	0.7	0.7—0.7	3
,, ,, ...	83	1.9	0.6—3.1	0.8	0.3—1.4	0.6	0.3—1.2	3.5	2.5—8	1.1	0.8—1.2	1.0	0.7—1.7	4
,, ,, ...	69	11.5	5.6—25.4	4.8	2.0—7.7	2.8	1.2—5.5	13.8	5—89	4.7	3.5—17	3.7	2.3—7	4
,, ,, ...	63	4.5	1.7—10.3	1.2	0.4—2.2	0.9	0.5—2.2	5.3	3.0—15	1.2	0.7—2.2	1.1	0.7—1.7	5
Pinus silvestris....	81	5.4	1.5—8.3	2.0	0.5—5.1	1.5	0.7—2.6	10.0	5—54	2.8	1.0—3.0	3.8	1.3—5	4
,, ,, ...	101	1.4	0.9—2.8	1.3	0.6—1.9	0.8	0.5—1.0	2.8	1.3—13	2.2	1.8—3.4	1.6	0.8—3.6	5
Quercus robur.....	107	4.0	3.1—5.6	0.9	0.5—1.3	0.9	0.5—1.8	9.2	8—25	1.3	1.2—2.7	2.1	1.5—3.2	3
,, ,, ...	85	4.3	2.4—7.2	1.3	0.8—2.2	1.1	0.3—2.4	11.0	9—22	2.0	1.4—4	1.7	1.6—1.8	3
,, ,, ...	83	3.5	2.4—5.2	0.9	0.8—1.0	0.9	0.4—1.9	9.2	7—17	1.6	1.5—2	1.4	1.3—1.5	3
Sorbus aucuparia..	129	2.4	1.1—3.6	0.4	0.4—0.5	1.0	0.4—1.7	12.8	5—21	1.6	1.2—2	2.2	2.2—2.3	2

these elements come? It has been believed (see e.g. KÖHLER 1925) that much of the salt content of rainwater originates from sea salt spray. Then we should expect the calcium and potassium content to be about 4 per cent of the sodium content, as in sea water (cf. CLARKE 1920); in addition there ought to be 12 per cent magnesium, expressed in the same way. The phosphorus content would be negligible in this connection, but sea salt contains about 1/8 as much sulphur as sodium; in addition to this there may be sulphate formed by oxidation of H_2S escaping from sea sediments (cf. CONWAY 1942).

Already the analyses presented in Tables XX—XXII show that the ratios between the different elements in rainwater can be very different from that in sea water (cf. also references on rainwater analyses given by ERIKSSON 1952—1953). Some of the sodium is probably oceanic—which implies a simultaneous supply of magnesium and sulphur—but most of the calcium, potassium and phosphorus found in rainwater in the open must have some other origin. The same probably applies to the iron and silica found in Table XXI.

There are many indications that this other source of mineral nutrients is dust (EGNÉR 1953). In most of the analyses in Tables XX to XXII strong direct dust contamination is not very likely, as the funnels were rinsed before each short-term collection; the long-term collections were made during long wet periods, when dust is not so prevalent. But precipitation carries down dust from the atmosphere (where dust particles may serve as condensation nuclei for the rain). Dust may also collect in the tree crowns and later be washed down by the rain. It is a suggestive fact that the correlation between the amounts of precipitation and the amounts of minerals supplied per unit area in the open has been rather weak at Experimentalfältet near Stockholm: it appears as if almost as much salt is carried down in months with moderate precipitation as in months with very much rain (TAMM & ALVERIN, in prep.). Considerable amounts of soluble minerals, calcium and phosphorus in particular, have been found in road dust collected in snow at different distances from the source of contamination (TAMM & TROEDSSON, in prep.).

Systematic investigations of the dust deposit in Sweden are unfortunately not available, but in Great Britain average figures have been reported by MEETHAM (1952) for both the country-side and industrial districts. Recalculating the British figures (l.c. Table 22) to kg/ha per year we obtain for the country districts the following rounded averages:

Insoluble matter,	combustible	40
” ”	ash	60
Dissolved matter,	total	280
	chlorides	40
	sulphates	60
	calcium	14

While the country-side of Britain is much more polluted by smoke than the Swedish forests, the quantities of calcium carried down with the dust cannot be neglected, especially as calcium is probably supplied not only from chimneys but also by particles blown up from the soil, particularly from cultivated land or deserts. Such particles are probably responsible for the large Ca deposits (hundreds of kilograms per ha per year) found in Natal by INGHAM (1950). Similar or still higher figures are reported from Hungary (TREITZ 1924) and from a district with chalk rocks in the Alps (BRAUN-BLANQUET & JENNY 1926, p. 317).

We have thus found three main sources of mineral salt supply to the moss carpet: atmosperic dust, sea salt spray and tree leachate (including leachate of animal excrement and of litter and pollen shed from the trees). In all three cases the nutrients are carried down to the mosses by the rain, but the distribution on the ground will vary. Elements originating from sea salt spray and dust will be more uniformly distributed than those leached from the trees, though there will probably be a certain enrichment beneath the trees in the first two cases as well; since the big surface of the tree crowns seems bound to collect dust particles from the atmosphere, which later may be washed out. Elements originating from the trees, either those directly leached or those contained in animal excrements, may be expected to show a strong decrease in quantity supplied in passing from beneath the trees to outside them. Animal excrements, especially those of larger animals such as birds or squirrels, of course fall very irregularly. It is tempting to explain a few abnormally high values in Table XXII by such contamination.

Most mineral nutrients may be supplied in more than one way, though in varying quantities. Potassium shows a strong gradient, decreasing with the distance from the tree crowns; the same is also true of phosphorus, though the reliable data are fewer in this case. These elements, which were also easily leached in the experiments of SCHRÖDER and RAMANN (l.c.), are thus supplied in fairly large and probably sufficient amounts from the trees to the moss carpet beneath them and perhaps also at some distance from the trees. Elements such as calcium, and more particularly iron, are probably to a large extent supplied by dust, being less easily leached from the trees. Sodium, sulphur and magnesium also occur in dust and litter extract, but the sea salt spray probably accounts for a considerable part of their supply.

The steepness of the gradient in mineral supply from an opening to beneath a tree will depend on many factors, and cannot be exactly determined except by extensive series of observations. The intensity and form of precipitation will influence it, and so will the wind force and direction, tree height, shape of tree crown, etc.

Where the supply of nitrogen is concerned, we know that rainwater contains some ammonia and nitrate, the concentration of which is very variable but of the order 0.5 p.p.m. The annual supply at Ultuna, ca. 70 km westward from Grenholmen is about 3 kg/ha according to the investigations of EGNÉR and his collaborators (see ÅNGSTRÖM & HÖGBERG, 1952). In North Sweden the supply is lower (EGNÉR 1953). Since ammonia makes up the largest part of the rain nitrogen, and since leaching of nitrate from tree crowns appeared improbable our analyses have been restricted to the ammonia fraction of the rainwater. Some of the data are presented in Table XXI. It appears that the concentration of ammonia-N is lowered rather than increased under tree crowns. The figures for ammonia-N in Table XXI are fairly reliable in spite of the low values, as each determination has been duplicated at least once. However, the result has not been confirmed by observation on other trees at Experimentalfältet near Stockholm (TAMM & ALVERIN in prep.), where conditions are, however, very different from those in Site II; here more ammonia-N was supplied beneath trees than in the open. Also at Bogesund (TAMM 1951) slightly more nitrogen has been found beneath trees than in the open, though these determinations were carried out by a somewhat different method (possibly including some organic N). We do not know anything about the concentration of nitrate-N in the rainwater beneath the trees, but it is unlikely that the amounts are large, as our forest trees usually do not accumulate nitrate in their leaves (HESSELMAN 1917 p. 416). Of great interest is the possible release of organic compounds containing nitrogen. As can be seen in Tables XX and XXI large amounts of organic matter are carried down with the rain. However, we do not know how much of this nitrogen—if there is any—is available to the mosses. A complete analysis of the different organic compounds in this leachate meets with considerable difficulties, as only small quantities are available for the analysis.

Although our data on the nitrogen supplied by rainwater to the mosses on Site II are far from conclusive, they certainly do not favour the assumption that the rain itself, or its leachate, supplies sufficient nitrogen to the moss carpet. We have earlier rejected the possibility of a nutrient supply from below on a sufficient scale. If this view were the most likely one in the case of mineral nutrients, it would be even more probable in the case of nitrogen, because of the very low concentration of available nitrogen in ordinary mor layers. Most mor plants have an extensive root system, or are associated with mycorrhizal fungi (as a rule both). We have good reason to believe that an extensive and effective absorbing system is necessary for the mor plants, perhaps in the first place to enable them to obtain enough nitrogen. The mosses in question possess no living organs in the soil which can absorb nitrogen or other nutrients.

The nitrogen nutrition of forest mosses may thus appear at first to be rather mysterious. Yet there is the possibility of direct ammonia absorption from the air. Such an absorption was much discussed in the middle of the 19th century (see refs. given by ERIKSSON 1952), although on the basis of not entirely reliable analytical data. Recently EGNÉR (1953) has made new determinations of the air ammonia content. The concentration varies between wide limits, but 5 micrograms per cubic metre appear to be a fairly common value in Sweden. This concentration stands in equilibrium with a solution containing 5 per cent ammonia at pH 4 (EGNÉR l.c.). As the mosses are very acid (cf. extract pH in Table XXV), and contain only small amounts of ammonia, if any, an uptake from the air will doubtlessly take place. The problem is how much ammonia-N the mosses may absorb in this way. The air volumes which come into contact with plants and soil may be estimated from the amounts of photosynthate and the air content of carbon dioxide. On the basis of such calculations EGNÉR (l.c.) considers the direct uptake of ammonia from the air to be several times higher than the supply by rainwater. Figures of twenty kilograms or more per hectare per year may well be possible. It is of course not known how this ammonia absorption is distributed on the different vegetational layers and on the humus layer, but the acid mosses with their large absorbing surface appear to be extremely well adapted to this type of nutrition.

We have thus been able to point out the following sources of nutrients for the moss carpet: tree and litter leachate, atmospheric dust and salt spray (carried down with rain or directly), and air ammonia. Should these sources of nutrients suffice for the moss community, we must assume 1) a very efficient mechanism of absorption from extremely dilute solutions, and 2) a large absorbing surface. The first prerequisite will be discussed in the next chapter, where it is shown that the cation concentration of water in equilibrium with living moss is very low, indicating a strong ability of the mosses to take up at least cations. As for the second point, a large absorbing surface is also characteristic for the mosses in question—in addition to *Hylocomium splendens, Ptilium crista castrensis, Pleurozium Schreberi, Dicranum undulatum, Rhytidiadelphus triquetrus* and many others. It seems quite possible that the ecological role of such organs as the paraphyllia of *Hylocomium* or the rhizoids of *Dicranum* is more to enlarge the nutrient absorbing surface than to take up water by capillary action, as has often been assumed. It should also be pointed out that the surface enlargement is probably equally efficient in absorbing ammonia from the air as in taking up salts from the percolating rainwater.

Conclusions

The mineral supply from rain, atmospheric dust and tree leachate appears to be of the same order of magnitude as the observed moss uptake. Furthermore, the supply is greatest beneath the trees and decreases outward from the tree crowns. The nitrogen nutrition is more obscure, but it seems quite possible that atmospheric ammonia, together with ammonia and nitrate in rain and perhaps also nitrogenous compounds in water coming down from the trees, will furnish sufficient nitrogen to the moss carpet.

Chapter VIII. Behaviour of *Hylocomium splendens* in Contact with Water

The difference in composition between *Hylocomium* segments of different age might be suspected to have something to do with the leaching effect of the rainwater. In order to test this hypothesis experiments were carried out, and later extended in order to elucidate problems in connection with salt uptake by *Hylocomium.*

The results of the first two experiments are given in Table XXIII. Fresh moss samples were divided into equal fractions, of which one was treated for 24 hours with flowing water, either tapwater (5. I. 1949), or distilled water (1. V. 1949). The distilled water was filtered through amberlite IRC 100 to insure complete absence of metal ions.

Nitrogen content seems not to be much affected by soaking, while some potassium and probably some phosphorus is released to the tapwater. The calcium content, on the other hand, is doubled after 24 hours in flowing tapwater, in living moss as well as in moss litter. In distilled water living moss

Table XXIII. Per cent dry weight of nitrogen, phosphorus, potassium and calcium in *Hylocomium* soaked in flowing water for 24 hours, compared with contents in untreated moss.

Medium and date	Condition of sample	Contents							
		N		P		K		Ca	
		soaked	contr.	soaked	contr.	soaked	contr.	soaked	contr.
Tapwater (5.I.1949)	Living	1.19	1.20	0.24	0.26	0.62	0.78	0.74	0.30
	Dead (a)	0.83	0.86	0.11	0.12	0.38	0.44	not determ.	
	Dead (b)	0.78	0.80	not determ.		0.32	0.40	1.15	0.56
Distilled water (1.V.1949)	Living	1.17	1.17	0.23	0.23	0.49	0.52	0.22	0.26
	Dead	0.75	0.76	0.08	0.11	0.22	0.50	0.34	0.48

Table XXIV. Concentration of K, Na and Ca in distilled water extracts of *Hyloco-* exposed plot; sample 9 was collected 26.V.1949

Sample No.	Condition of sample	Temp. C. (average)	Amount of moss g/1000 g water	Per cent air dry weight before expt.		
				K	Na	Ca
553	Young, living......	20°	1.3	0.74	—	0.30
553	,, ,, ...	20°	1.3	0.74	—	0.30
553	Old, dead.........	18°	6	0.38	—	0.39
553	,, ,, ...	18°	4.5	0.38	—	0.39
9	,, ,, ...	25°	10	0.34	0.02	0.49
9	Old, dead & ground.	24°	10	0.34	0.02	0.49
9	,, ,, ,, .	20°	10	0.34	0.02	0.49

loses only small amounts of P, K and Ca, while moss litter releases much potassium and some phosphorus and calcium.

As an experimental model of what happens in nature, the soaking in tapwater appears more adequate than the soaking in distilled water. In nature as in tapwater P and K contents decrease, while Ca increases in both absolute and relative terms. That the calcium increases much more during the 24 hours treatment than during a whole year in nature may well be due to the high Ca content of the tapwater (ca. 30 p.p.m.).

Evidently the calcium uptake from tapwater by the moss is an example of simple ion exchange, as living and dead moss behave so similarly. The prerequisites for this exchange are 1) a low base saturation of the moss—which is illustrated by the low extract pH in Table XXV—and 2) a sufficiently high calcium concentration in the solution surrounding the moss.

In nature we meet with lower calcium concentrations in the water than 30 p.p.m., but the ion exchange will still result in Ca uptake if the average concentration of Ca in the water percolating through the moss carpet is higher than the concentration in equilibrium with the moss. Our next task is then to determine the equilibrium concentration, and compare it with the concentration in the solution supplied from above.

First some experiments have been carried out to determine how fast an equilibrium is established if *Hylocomium* is immersed in distilled water freed from metals. Both living moss and moss litter have been used. The results are presented in Table XXIV.

We see from Table XXIV that living moss releases very little K (a few per cent of its content) and still less calcium to distilled water. An equilibrium appears to be established, with respect to potassium at least, within the first four hours. The analyses after 24 hours were in this case carried out on concentrates, which may explain the slight difference from the 4 hour

mium splendens. Sample 553 was collected 28.XII.1949 near Site I, in a moderately in Site II. Extracts vigorously stirred.

Parts per million in extract														
After 15 min.			After 1 hour			After 4 hours			After 24 hours			After 48 hours		
K	Na	Ca	K	Na	Ca	K	Na	Ca	K	Na	Ca	K	Na	Ca
—	—	—	0.2	—	—	0.3	—	—	0.24	—	0.09	—	—	—
—	—	—	0.1	—	—	0.2	—	—	0.16	—	0.03	—	—	—
—	—	—	—	—	—	13.0	—	1.0	14.5	—	0.9	—	—	—
—	—	—	—	—	—	9.7	—	1.1	10.4	—	0.5	—	—	—
14	0.8	1.0	20	0.8	1.2	28	1.3	1.5	—	—	—	30	1.1	1.7
—	—	—	26	1.2	1.8	—	—	—	26	(> 10)	1.9	20	(> 10)	2.2
—	—	—	24	1.1	1.6	—	—	—	28	2.1	2.9	26	2.4	3.5

value. The concentration of K at the end of the experiment was approximately the same as the usual concentration in rainwater from open field; the much higher concentrations in rainwater beneath trees will undoubtedly allow *living moss* to take up potassium. As bivalent (and trivalent) ions are much more easily absorbed than univalent ions like K, it will certainly not be difficult for living *Hylocomium* to absorb calcium from solutions of the compositions given in Tables XX to XXII. Higher plants may accumulate more K than Ca from such solutions, owing to difficulties in the translocation of the Ca, a factor which probably plays a subordinate role in *Hylocomium,* where most nutrients are absorbed by the growing organs themselves.

If we study the data for moss litter in Table XXIV, we find much higher extract concentrations than in the experiments with living moss. Apparently the living moss possesses a mechanism for ion accumulation in addition to the simple ion exchange mechanism. The potassium concentration appears to approach an equilibrium in 24 hours in the litter experiments, as indicated by the small differences between the last analyses in each series, and by the agreement between analyses of unground and ground moss (Wiley mill 20 meshes per inch). Whether an equilibrium is established during the experiment in the case of sodium and calcium is not quite clear; the grinding appears to increase the concentration, probably by making the diffusion path shorter. In one of the experiments sodium concentration suddenly rises far above what can be accounted for by the original sodium content of the moss. This must be due to some contamination, perhaps through a crack in the glasstube enclosing the stirring magnet. Some of the very small amounts of Na found in the extraction experiments, as well as in the moss analyses, may be due to contamination during the preparation of the samples, which must necessarily be very thorough. This may account for the occasionally very irregular Na values.

As a result of the experiments with moss litter in Table XXIV we may say that within 24 hours an equilibrium is approached with regard to K. The equilibrium concentration depends on the ratio between moss and water, but is for the tested dilutions much higher than in rainwater beneath trees. Potassium must therefore be expected to be released to the rainwater from all segments except the living ones. This is entirely in accordance with our previous results (Table XXIII).

Calcium occurs in the moss litter extracts in concentrations varying from 0.5 to 3.5 p.p.m. If representing a concentration not too far from equilibrium, these figures will allow calcium uptake by both dead and living moss from the more concentrated water samples in Table XX. Two factors make it probable that the concentration necessary for Ca uptake in nature is lower than those found in Table XXIV. Firstly, very often water evaporates from the moss carpet, thereby increasing nutrient concentration in the remaining water. Secondly, the high concentrations of K in the extracts in the experiments must displace some calcium from the moss, thus increasing the calcium concentration in the solution above that established in equilibrium with a flowing solution low in potassium, such as rainwater.

The different effects on the moss of solutions containing the same concentrations of calcium but different amounts of potassium has been tested in a simple experiment. An extract of segment 5 of sample 895 had been found to contain 1.5 p. p. m. of Ca and 20 p. p. m. of K (Table XXV). Another part of this sample fraction was now treated with a flowing solution of calcium chloride, containing 1.5 p. p. m. of Ca. During 40 hours treatment the moss increased its Ca content by 130 per cent but released almost all K. The average flow-rate was 3 cm/min, considerably more than in the distilled water experiment in Table XXIII. At the same time a sample treated with tapwater increased its Ca content by 300 per cent, while the K content was reduced to almost nil. Evidently the treatment also in this case was more effective than that in Table XXIII, probably due to a higher flow-rate.

The time-lag in the establishment of equilibrium with regard to the calcium concentration may also have something to do with the displacement mechanism. It must be remembered that the samples used for the leaching experiments have been composed of segments and individuals differing widely in composition and base saturation. An experiment thus means an equalization between cells and segments by a continuous release and reabsorption, which must take some time.

The equilibration experiments thus lead to the same conclusion as the measurements of salt uptake, in relation to the amounts supplied from above according to Table XX. The higher values in Table XX are most probably above the equilibrium concentration and may well explain the increase of Ca

Table XXV. Contents of cations in different segments of *Hylocomium*, and in water extracts of these segments. Extracts obtained by shaking one part of air-dry moss with 100 parts of distilled water for 24 hours. Extraction in February, 1952; samples the same as in Table XIX + a sample of the humus layer from Site III. Average temperature 17° C.

Locality	Segment No.	Composition of moss per cent air-dry weight			Composition of extract, p.p.m.			pH of extract	Per cent of cation content of moss extracted in experiment	
		K	Na	Ca	K	Na	Ca		K	Ca
Site I	1	—	—	—	—	—	—	—	—	—
	2	0.70	—	0.25	56	2.0	2.4	4.1	78	10
		0.74		0.25						
	3	0.43	—	0.25	32	1.0	2.0	4.2	74	8
		0.44		0.25						
	4	0.44	—	0.33	33	0.9	2.3	4.4	73	7
		0.45		0.32						
	5	0.40	—	0.40	29	0.9	3.8	6.2	73	10
		0.40		0.40						
	6	0.33	—	0.47	25	0.9	3.9	6.7	76	8
Site III	1	0.74	0.02	0.28	—	—	—	—	—	—
	2	0.40	< 0.01	0.16	26	1.5	1.3	4.7	63	8
		0.42		0.15	27	0.8	1.0	4.9		
	3	0.38	< 0.01	0.21	25	0.6	1.1	4.9	64	5
		0.39		0.22	24	0.6	1.0	4.9		
	4	0.33	< 0.01	0.29	22	1.2	1.3	5.3	70	5
		0.31		0.29	23	0.6	1.5	5.1		
	5	0.28	< 0.01	0.31	20	0.6	1.5	5.1	69	5
		0.30		0.31						
	6	0.28	< 0.01	0.32	18	0.6	1.5	5.7	64	5
	7	0.25	< 0.01	0.35	17	1.0	2.7	5.4	68	8
Humus layer		0.11	0.01	0.37	5.6	0.6	1.9	4.4	52	5
		0.11	0.01	0.35	5.8	0.5	1.8	4.4		
		0.11	0.01	0.37	5.8	0.6	1.8	4.3		
Contents of blanks in extraction					0.0	0.1	0.2			
					0.1	0.2	0.3			

content with age of moss litter. As stated previously they can also account for the observed salt uptake per unit area. The lower values, found in the open field or in other places where the rain is not much affected by the tree crowns, may be below the equilibrium concentration. If we analyse *Hylocomium* samples from such places, e.g. sample 895 (Table XXV), which was collected from a position rather similar to sample 9 and funnel B (Table XX), we find only a slow calcium accumulation in old segments, suggesting that the average concentration of Ca is not far from the equilibrium value. There is thus hardly any contradiction between our results and the hypothesis that the increase in Ca content of moss litter with age is due to uptake, by ion exchange, from the water coming down.

Leaching experiments may also provide some information concerning the other possibility for moss nutrition—uptake from below, by either capillary rise or, on flat ground, occasional flooding. We have already pointed out the importance of moving water on slopes. Such a supply from below would imply base saturations approximately the same in the humus layer and the old moss litter, or possibly changing continuously as we move upward toward the living segments. It may be argued that such a continuous transition between moss layer and humus layer can be explained in other ways; on the other hand a discontinuity may be a strong argument against such a salt supply from below.

In Table XXV we can study the concentrations in extracts of different segments from two moss samples, and of the humus layer forming the substrate of one of the samples. We find extract concentrations of the same order as in Table XXIV; falling slowly with age in the case of K and increasing slowly in the case of Ca. Evidently young segments stored dry for a long time as in this experiment behave more like old segments than if they are soaked immediately after collection (cf. Table XXIV). The percentages of Ca and K which are released during the experiment are remarkably constant within each sample, but higher in the sample from Site I, which contained more nutrients to begin with. This constancy may perhaps be taken as a point in favour of the view that an equilibrium is established in 24 hours. The fact that the percentage of the K content released is about ten times that of Ca is probably only a direct expression of the stronger absorption of the bivalent ion Ca^{++} in comparison with the univalent K^{+}. We also find an increase in pH with age, running parallel with the increase in calcium content of moss extract (and ash content of moss, cf. Table XIX). The young moss gives rather acid extracts, which may be significant as regards direct ammonia uptake from the air (cf. p. 94).

The thing that interests us most is the comparison between the old moss segments and the humus layer in Site III. The calcium contents are about the same, both when considering extracts and dry samples. However, potassium in the humus layer and its extracts is only one-third that of the moss and moss extracts. Moreover, the pH is one unit lower in the humus extract than in the extracts of the oldest moss segments. No doubt a similar result would have appeared in Site I if the humus layer had been investigated, since the pH has been determined to 4.8—5.4 in the upper part of the humus layer in Site I. In dilute extracts — corresponding to those in Table XXV — values of 5.5 to 5.9 have been found.

We have thus found a sharp discontinuity between the moss litter and the humus layer underlying it in at least two properties, pH and K concentration. This discontinuity could hardly be maintained if there were a rapid movement of substances in both directions: water from above and salts from below. We thus have a new argument for the moss carpet's nutritional independence of the soil.

If might be asked how this discontinuity can arise, as the humus layer is to a considerable extent formed by moss litter. A possible answer is that roots and particularly hyphae from mycorrhizal fungi remove ions, thus making the humus layer less base-saturated than its parent substances.

Conclusions

As a summary of our experiments on the behaviour of *Hylocomium* in contact with water, we may state that nutrient supply to the *Hylocomium* community from above seems quite reasonable, and provides a simple explanation of the peculiar accumulation of calcium (together with Mn, Fe and Al) in moss litter. The old view that *Hylocomium splendens* and similar mosses obtain their nutrients and water from below meets with serious difficulties when it comes to the interpretation of the experimental results.

Chapter IX. Some Other Factors of Possible Importance for the Growth of Forest Mosses

In the preceding chapters we have dealt with the importance to the *Hylocomium* community of the supply of light, water, and nutrients. Although these factors indubitably affect the mosses, there may also be other environmental influences on moss growth and development. We are, however, not so much interested at present in how all the different factors may affect mosses—this is more a physiological problem, much too great to deal with in the present study (cf. in this connection the investigations of PLANTEFOL, 1927, and DAVY DE VIRVILLE, 1927—1928). On the other hand we ought to know which ecological factors vary within the habitats studied. We have found the moss growth to be correlated with light supply and nutrient supply, and a lack of close correlation between moss growth and humidity of climate. Before we can draw conclusions about the causal relationships with any certainty, we must show that there are no other factors related to light or nutrient supply, which could be responsible for the observed relations. For the explanation of the internal growth variation within small areas we also need a very detailed knowledge of the factors operating.

Carbon dioxide concentration

The contents of carbon dioxide in the air are known to be higher near the ground than on a level with the tree crowns (in the day-time), where photosynthesis may remove a part of the carbon dioxide content of normal air (cf. ROMELL, 1932, HUBER, 1947, LUNDEGÅRDH, 1949). Near the ground carbon dioxide may be above normal on account of "soil respiration". It is not believed that this gradient in carbon dioxide concentration is of very great importance for the forest trees (ROMELL l.c.), but it is possible that the mosses are favoured by this factor, since they grow very near the carbon dioxide source. From this point of view mosses growing on stones may be at a disadvantage in comparison with those growing between the stones, where more litter is accumulated and decomposed. While many of the plots in Site II lie on very shallow soil, others occur on deep soil (for example No. 8 with the maximum yield). Thus we cannot exclude the possibility that some of the scatter of values in Fig. 11 is due to this factor. On the other hand the yield/light relationship (Fig. 11 a) cannot be explained in this way, since the carbon dioxide production ought to be greatest beneath the centres of the spruce crown projections, where the supply of litter is most abundant. In all probability the influence of the carbon dioxide factor on the moss production is much less than the influence of the light factor (cf. in this connection DAXER 1934 p. 413).

The carbon dioxide factor also fails entirely to explain the variation in growth between moss individuals a short distance apart (often a few cm or dm). The turbulence of the air, together with the rapid diffusion of gases, makes differences of ecological importance at such small distances most unlikely. Reversals in carbon dioxide concentration between different years, such as must be postulated to explain the changes in individual moss growth, are also extremely improbable. Nor can the absence of *Hylocomium*, or its low competitive capacity at large distances from a canopy, be explained by the carbon dioxide factor, concentration seldom falling much below the "normal" value, which allows photosynthesis by all land plants.

We may therefore conclude that the variation of carbon dioxide content in the air can probably be regarded as of minor importance with respect to *Hylocomium* growth.

Temperature

The temperature factor cannot explain the internal variation within the moss community either, since it affects the plots too uniformly. That temperature is nevertheless of great importance for moss growth has been shown by STÅLFELT (1937 b) in physiological experiments. Temperature decrease lowers respiration more than photosynthesis, making it possible for the moss to maintain a positive balance of photosynthesis over respiration in short and dark autumn and winter days. The net gain in dry weight at 8,000 lux is, however, smaller at low temperatures than at "optimal" temperatures (15°—20° C., STÅLFELT l.c. Fig. 3 b).

Fig. 42. *Hylocomium splendens* suffering from sun exposure after felling a sheltering tree. Most branches have lost their leaves. *Climacium dendroides* in the upper part of the picture seems to have endured one summer's exposure better. Slightly enlarged. Grenholmen 17. IX. 1952.

The differences in yield between different plots in the same habitat cannot be explained by the temperature factor, as according to STÅLFELT small or moderate differences in temperature—and others are not to be expected for example within Site II—only cause small or moderate differences in photosynthesis.

Sun exposure

Closely connected with the question of the temperature factor is that of sun exposure. *Hylocomium splendens* does not stand direct and prolonged sunshine, at least not in the dry climates characteristic over large parts of Sweden. On a clear felling *Hylocomium splendens* soon looks dead and "burnt" except where sheltered by stones, tree stumps or field vegetation (Fig. 42). Other mosses, for example *Dicranum undulatum* and *Ptilium crista castrensis*, also suffer severely from the sudden changes. *Pleurozium Schreberi* endures the new conditions somewhat better, although growth is checked in comparison with that in the forest (cf. KUJALA 1926).

It should be mentioned that in certain situations *Hylocomium* appears to be more tolerant. In a wet climate, such as that of western Norway, it may persist on clear fellings, though growth is apparently less vigorous. Even in the drier conditions of eastern Sweden, *Hylocomium* may be found in open

Fig. 43. Dry talus formation facing west near lake Vättern in the province Östergötland close to Småland. The stones are partly covered with mosses. In the open *Homalothecium sericeum, Antitrichia curtipendula, Leucodon sciuroides* and *Hypnum cupressiforme* predominate. In the neighbourhood of trees, also on rather exposed stones, *Hylocomium splendens* and *Rhytidiadelphus triquetrus* occur more or less abundantly. 31. V. 1952.

places, at least if they do not slope SE., S. or SW. Fig. 39 shows such an occurrence of *Hylocomium* on a gentle north-east slope; but it must be admitted that the morphology of *Hylocomium splendens* in this habitat is somewhat abnormal; the individuals are all small with the segment size averaging 1 mg. Fig. 43 shows another slope facing west, with *Hylocomium* occuring in the neighbourhood of trees, even where the ground is rather exposed. There may thus be a difference in tolerance between *Hylocomium* growing in sheltered and in exposed habitats.

At present we cannot decide the direct cause of the death of *Hylocomium splendens* and other mosses on clear fellings. We must choose between direct radiation injury, excessive temperature or rapid and strong exsiccation after rain and dew interfering with photosynthesis, nutrition or other processes. Very probably a combination of these and possibly other factors is concerned. It would be interesting to know whether *Hylocomium* is more susceptible to injury when dry, and whether intermittent exsiccation strengthens the sunshine effect or weakens it. As plasmolysis is difficult to observe in *Hylocomium* (on account of the narrow cells with strongly refracting walls) some other method ought to be devised to distinguish between living and dead cells.

Snow cower

The snow cover is a factor varying strongly between different years, different regions and different plots. In western Norway there is very little snow on the ground in winter. The remarkable similarity in behaviour of *Hylocomium* in this region and in eastern Sweden does not suggest a great dependence of moss growth on the snow cover in the latter region, although it must of course check photosynthesis to some extent. According to the growth curves, however, moss growth is already slowed in late autumn (Figs. 3 and 4), before a snow cover is established. In the spring some patches may melt a week or more before others; this may favour the mosses in the former patches to some extent. In the spring of 1952, however, the last melting snow-drift covered the highly productive plot 9 in Site II, while most other plots were free from snow. In any case, moss growth is slow during spring according to Figs. 3 and 4, which makes the time when the snow melts less important for the annual yield. Under certain circumstances the snow cover may act as a shelter for the moss community, but if so the primary factor must be something else—for example sun or wind exposure.

It is most unlikely that snow cover is responsible for the internal growth variations at small distances, since it acts rather uniformly over a plot of small size.

We thus have no evidence that differences in snow cover exert any important influence on the forest moss carpets under normal conditions.

Litter fall

In the fall of litter we have a factor which may influence the moss carpet both as a source of nutrients and as an obstacle, shading the moss plants and depriving them of the water coming from above. The negative effect is often dominant in deciduous forests, where the leaves may form a thick carpet impenetrable to the *Hylocomium* shoots. In such habitats we often find abundant *Hylocomium splendens* on stones and other places where the leaves do not accumulate. A similar behaviour is also characteristic for *Pleurozium Schreberi, Dicranum undulatum* and *Hypnum cupressiforme,* while *Rhytidiadelphus triquetrus* appears to endure at least a moderate litter fall fairly well, probably because of its stiff, upright shoots at some distance from each other (KUJALA 1926 p. 39). The horizontal shoots of *Hylocomium splendens* or the dense pillows of *Dicranum* are apparently not so tolerant of such conditions.

If the leaf litter is more scattered the effect on the *Hylocomium* community will of course be much lessened and more irregularly distributed. In fact we have here one factor which may account for the irregular growth of *Hyloco-*

mium within small areas. In Site II the number of birch leaves per dm^2 has varied from none to several within the sample plots. On the other hand, we also have an irregular growth variation within plots 672 and 677 in western Norway, which were situated in pure spruce forest without any deciduous trees in the neighbourhood (except a few small birch shrubs at some distance). Thus the individual growth variation here cannot be explained by leaf litter fall. On the other hand this litter *may* be responsible for the fact that the individual growth variation was stronger in Site II than in the Norwegian plots studied.

In coniferous forests the litter usually does not form such dense carpets; moreover the needles fall somewhat more evenly over the year (cf. MORK, 1942, and LINDBERG & NORMING, 1943). The heaviest litter fall is found at the centres of the spruce crowns. In the very same places *Hylocomium* is often absent or scarce and the ground covered only by a needle carpet. There are, however, other circumstances unfavourable for the mosses in such places: the low light supply and the small quantity of rainwater penetrating the dense spruce crowns. We have already found that the water supply seems to be a factor of secondary importance, as exactly the same behaviour is found beneath spruce in extremely wet western Norway and in dry eastern Sweden. With respect to moss growth in relation to litter fall two observations seem remarkable. 1) It is mainly beneath spruce with branches drooping near the ground that mosses are really lacking, except in very overstocked stands. But there is hardly any reason why the litter fall should be less beneath a spruce without low branches than beneath one with such branches, if both have crowns of similar size and width. 2) Beneath drooping branches, the mosses usually grow beneath their distal parts, but may be absent beneath the proximal parts even if the light supply appears to be similar. As spruce needles persist on the branches for many years (often six or seven), the litter is not shed from the distal parts of the branches. This may be the reason why the mosses grow better there. Another explanation would be that *Hylocomium* may persist for some years after light supply becomes scarce; this alternative, however, does not account for cases where the boundary of *Hylocomium* is fairly distinct towards the centre of the tree.

The observations reported under 1) and 2) can be explained in a simple way by assuming that litter fall is detrimental only where *Hylocomium* growth is slow on account of light deficiency. In such cases it must be difficult for the moss to keep pace with the litter accumulation. Some support for this hypothesis may be found in the observation that *Hylocomium,* like other shade-tolerant mosses which occur beneath dense spruce (e.g. *Plagiothecium* species), often grows better on stones and other places where the needles do not accumulate.

Plasma-active organic substances

Physiologically active organic substances can be leached from different kinds of litter and also from green leaves (STÅLFELT 1948). These substances exert a remarkable influence on the protoplasmic viscosity even in extreme dilution (10^{-9}) and may affect other physiological processes. At present we know nothing about their importance for the mosses, except that they must be tolerated at the concentrations usually met with in rainwater penetrating tree crowns.

Hydrogen ion concentration

The pH of rainwater beneath trees was determined potentiometrically on several occasions, most extensively on the material in Table XXII. Beneath trees it varied between 4.0 and 6.7. The first value was obtained beneath a birch; on another occasion a pH of 6.2 was obtained in the same place. The highest value (6.7) came from beneath an alder, where, however, water of pH 4.4 has also been obtained (at the same time as the low birch value). In the open field pH varied between 4.3 and 5.9, if a probably polluted record of 6.5 is excluded. This range also covers most of the samples from beneath trees, and is very similar to the range for moss extract pH in the extraction experiments. Moreover, it is a pH range tolerated by most mor plants. In the experiments of IKENBERRY (1936) the pH range 4 to 6 was found to allow spore germination and protonema growth of almost all mosses tested; for most species the range was wider. We have therefore no indication that the hydrogen ion concentration in the water percolating through the moss carpet is of any ecological importance for *Hylocomium splendens* in "normal" habitats. Conditions may be otherwise if an alkaline soil solution occasionally rises over the moss carpet, or in industrialized areas where rainwater is heavily polluted and may have an abnormal reaction in addition to contents of possibly poisonous substances (cf. MAC INTYRE & YOUNG, 1923).

Injuries from animals and parasites

Influences from larger animals will necessarily be very irregularly distributed and are thus difficult to study. Such factors may well contribute to the growth variation within small plots. However, for most animals *Hylocomium splendens* seems to be little if at all palatable and seldom eaten. More important perhaps is the role played by aphids and insect larvae in the tree crowns, where their excrements may account for some of the soluble salts found in the rain-water beneath tree crowns.

Ant paths soon become free from mosses. The ants may also—together with earthworms and other soil animals—transport soil particles upward into the moss carpet, where the analyses (Table XIX) have suggested the presence of small amounts of mineral particles.

Injuries due to the activities of fungal parasites may also occur in the *Hylocomium* community. In fact a white mould-like fungus has sometimes been observed on the *Hylocomium* segments, especially in samples collected from December to May. The fungus is a basidiomycete and grows especially in the underside of the green segments. These usually appear unaffected and normal, but sometimes look bleached.

A possible detrimental influence of lichens upon *Hylocomium splendens* has been mentioned earlier. In addition to simple competition we may meet with excretion of poisonous substances (cf. BURKHOLDER et al., 1944, 1945) or even parasitism (MC WHORTER 1921, cf. RICHARDS 1932).

Chapter X. A Discussion of the Observed Ecological Relationships, and of Factors Determining the Structure of the *Hylocomium* Community

In the preceding chapters we have examined the behaviour of the *Hylocomium splendens* community in relation to certain external factors. A causal ecological analysis must of course be confined to cases where we find variations in moss properties correlated with environmental factors (or promoted by experimental treatment). This limitation of the problem does not imply that other factors are without importance for moss growth, only that they act in a different way—usually more uniformly—than the factors which cause the variation we observe within or between sample plots. A second prerequisite for a causal analysis of an ecological problem is a satisfactory knowledge of the physiology of the plant in question. In the case of *Hylocomium splendens* we have, thanks to STÅLFELT (1937 a and b), a fairly good knowledge of its water relations, its photosynthetic activity and its respiration under varying conditions. Some information has been presented in Chapters VI and VIII on its nutritional physiology.

We may now discuss the following points with regard to the causal relationships:

1) The decrease in moss growth with lessening light supply beneath trees, and the accompanying increase in nutrient concentration.

2) The parallelism between moss growth and nutrient uptake in several cases.

3) The very strong growth variation within small areas, which has been attributed (entirely or partly) to the influence of external factors.

4) The strong variation in composition of the moss within at least some sample plots.

5) The remarkably low frequency of very small individuals in well developed *Hylocomium* communities.

6) The frequent purity of the *Hylocomium splendens* community.

7) The differences in composition of *Hylocomium* of different age.

8) The differences in composition of *Hylocomium* from different regions.

To start with point 1), the relation between moss growth and light, strong evidence supports the view that light deficiency really limits moss growth in darker places. Other possibilities, such as low precipitation and abundant litter fall, have no general applicability. Moreover, this view is quite consistent with the results of STÅLFELT on the photosynthesis of *Hylocomium splendens* (STÅLFELT 1937 b). He found that the rate of photosynthesis increases rapidly as light increases up to a moderate value (about 4,000 lux). Further increases in light intensity bring about only small increases in the rate of photosynthesis until a constant or even diminishing rate is attained. Beneath the spruce crowns light intensities of less than 4,000 lux can be expected during the greater part of the year. Maximum light intensity in the open on clear summer days is of the order of 100,000 lux; the average intensity is of course much lower, but probably great enough to supply openings in the forest with more than 4,000 lux during long periods, including the August and September days when moss growth is most rapid.

If the rate of photosynthesis is the factor limiting moss growth, nutrients are then present in excess of the necessary amounts. High concentrations of nutrients in the moss then result. According to Figs 29 a, 30 a and 31 a we have such a "luxury consumption" at low light intensities. Thus there seems to be little doubt that light deficiency limits moss growth beneath a dense canopy as suggested in an earlier publication (TAMM 1950). An analogous case concerning a higher plant *(Scilla non-scripta)* has been described by BLACKMAN & RUTTER (1946, 1947), cf. also DAXER (1934) and FILZER (1939).

2) A more or less complete parallel between moss growth and nutrient uptake has been found in three cases: when following the seasonal course of both processes, when comparing normal and fast-growing individuals, and finally when comparing growth and nutrient uptake of sample plots outside the tree crown projections. In all cases it is only the average values which follow each other (cf. 4). A parallel also exists between the uptakes of the different nutrients; especially close is the correlation between N and P concentrations in samples from the same region.

The simplest theory which can explain these relationships is that the supply of one or more nutrients determines moss growth. The correlation between the different nutrients makes it more or less impossible for us to decide which nutrient is directly limiting, particularly as we know that the different mineral nutrients are supplied together and thus correlated to one another.

The correlation between the different nutrients can of course also be the result of an uptake determined by the growth, independently of the nutrient supply. This hypothesis supposes an ample supply of nutrients, from which the moss only takes a part. It might also explain the fairly constant nutrient content of *Hylocomium* in many places at the same time as it explains the parallel between growth and nutrient uptake. There are, however, serious objections to this hypothesis. Beneath trees nutrients are taken up in excess, compared with in the open. Why should not the mosses in the open absorb the excess of nutrients, if any, when shaded mosses do? And would not fast-growing specimens contain lower percentages of nutrients than normal individuals, if nutrient supply were a factor without close connection to the growth-determining one?

A still more conclusive proof against the hypothesis of an ample supply of nutrients can be found in the distribution of different ions in the moss. We have found that young moss is generally very unsaturated with respect to calcium and presumably bases in general; an unsaturation which is partly equalized during the course of time. Had the supply of calcium been ample, the unsaturation would very soon be equalized and an equilibrium established where equal amounts of Ca were taken up and released. If both bivalent and trivalent ions are supplied to the moss from above, we must expect the trivalent ions to be absorbed and retained much more strongly than the bivalent ions, which in turn are more strongly absorbed than the univalent ones. We have now found the same relative increase with age for both bivalent and trivalent ions (Table XIX); the reason apparently being that the absorbing capacity of the moss also suffices to retain most of the bivalent ions which come into contact with it. The possibility that a large excess of bivalent ions displaces the trivalent ions is excluded by the low base-saturation in the moss. On the whole our figures for the nutrient supply to the moss community suggest scarcity rather than abundance, at least in openings and beneath light canopies.

The last objections militate also against a third hypothesis, viz. that both *Hylocomium* growth and nutrient supply depend upon some other factor, say precipitation. This assumption would account for the parallelism between growth and nutrient uptake observed in the seasonal and individual variation, but hardly for the relationship between growth and distance to trees. The high precipitation in western Norway does not bring about a corresponding increase in moss yield, nor does the annual variation in moss growth stand in direct relation to the variation in precipitation.

We must then conclude that our first theory, of nutrient supply as a factor often limiting moss growth, seems to be by far the most probable of the alternatives discussed.

3) and 4) The individual variations in growth and composition of *Hylocomium splendens* have been considered as the result of the action of external factors, at least to a large extent. We have in the preceding paragraphs found that the agreement between the average composition of fast-growing and normal *Hylocomium* individuals could be used as an argument for the limiting effect of nutrient supply. The existence of a strong individual variation in composition may appear to contradict this theory to some extent, even if it has not been proved that the individual variation in the most deficient element is very great.

A simple explanation of both the growth variations and the nutrient content variation can be obtained from what we know about the nutrient supply from the tree crowns, assuming the validity of our conclusion about nutrient supply often limiting moss growth. The heavy drops falling from tree branches in rain will certainly not be uniformly distributed over the ground. Some spots will be favoured, but these spots will change from year to year, both outside the tree crowns, where the prevailing winds will decide where the drops shall fall, and beneath the branches, which elongate and thereby change the places from which the drops preferentially fall. The variations in moss growth and concentration are just such as might be expected if our theory is right: as a rule individuals receiving much nutrients grow faster than the average, but if other factors are scarce (e. g. light supply during winter), the result may instead be a high content of nutrients.

Water is also supplied at the same time as nutrients, but two circumstances will make this water of minor importance for the growth variations, especially outside the trees (cf. p. 48). Firstly, when drops start to fall from the trees, the moss carpet in openings will as a rule already be moistened, and excess water has little physiological effects. Secondly, water falling in heavy drops on the moss carpet will probably either dry out or equalize by capillary forces fairly soon. The translocation of nutrients by capillary suction is certainly slower than that of water, as in an absorption column or a paper chromatogram.

The distribution of light over the moss carpet is not always uniform, as the location and courses of sunny spots may change from season to season and from year to year. Some segments may also receive less light than the rest due to an unfavourable direction of growth. The place and growth direction of the young buds appear to vary in a fairly random way, although they may be affected by external factors—as pointed out for one case on p. 50—and possibly by internal factors. The apparent randomness of the direction of growth may contribute to the growth variations, as individuals rising over their neighbours will either be favoured by a larger light supply, or disfavoured by faster exsiccation. Individuals lower than the average will probably be disfavoured in most cases. It may be pointed out that the variation in chemical composition between different individuals from the same plot is so large that it is difficult to explain it as caused by the small difference in what higher and lower moss individuals may receive from above.

In the samples receiving the most detailed study (Table IV) there appears to be a slight difference in individual variation between shaded and exposed habitats; which may be an indication that conditions are more uniform when light is deficient than when nutrients are scarce. However, this relationship does not show up in Site II, where the individual variation is very great in all sample plots, perhaps because of the occurrence of birch leaf litter on these plots.

The dependence of the individual growth variation mainly on the nutrient supply in exposed habitats and on the light supply in dark habitats is not proved, but appears very probable. In many cases we may have additional growth variation due to litter fall.

5) The low frequency of small plants is easily understood from the preceding paragraphs. The surface of the *Hylocomium* community rises every year by the average height of the annual segments; on the other hand the oldest and decomposing segments are compressed by the weight of the moss layer and of the snow. Individuals not able to develop segments of normal height are inevitably suppressed and soon die. Very small individuals may persist for some time, if they develop very slender segments of normal height. This means, however, that they must use a larger part of their photosynthate and nutrients for stem elongation and less for leaf development, which will weaken then furthermore. Competition thus sets a lower boundary for segment size by disfavouring very small individuals. It must be admitted that this conclusion is somewhat theoretical, as in most samples very small individuals (segment size < 1 mg) have been too scarce to permit reliable estimations of their average growth. There is of course also an upper limit to segment size, but this boundary may be more an internal physiological property. As translocation seems to be slow in the moss stem, the apical dominance may be weakened in large segments, which therefore branch more often than smaller segments.

6) The great purity so often characteristic for the *Hylocomium* community shows that *Hylocomium splendens* competes successfully with any other moss species throughout the whole range of conditions within the community in such habitats. On the other hand we have in paragraphs 3) and 4) just concluded that conditions may change from spot to spot and from year to year, thereby of course changing the intensity of competition at the same time.

Apparently we must consider two kinds or "phases" of competition: one between plants colonizing a more or less barren area, and one between plants in a closed, "stable" community. In the first case the dispersal of disseminules and their germinative capacity determines which species invade. At least in the beginning plants with a rapid development will be favoured (cf. ROMELL, 1938 p. 296 ff., p. 435 ff.). Later on, competition will be more like that in a closed community, where plants once established have a great advantage in comparison with "seedlings", both of the same and new species. This may hold even if the intensity of competition fluctuates within rather wide limits. Changes may of course occur in closed communities, but they are usually slower than shortly after colonization. The abilities of different species to spread (mainly vegetatively) under severe competition now strongly affect the direction and rate of the changes, even if they are induced by changes in primary factors.

Where forest moss communities are concerned, it appears that the mode of growth has a considerable competitive importance. It may well be as difficult for a species with horizontal fronds, like *Hylocomium splendens,* to invade a dense tussock of *Dicranum undulatum,* as it is for the latter to invade a *Hylocomium* carpet. Mechanical resistance as well as differences in average height growth may here play a role. On the other hand mixed communities also occur; in particular it has been observed that *Hylocomium splendens* spreads at the expense of *Pleurozium Schreberi* during the growth of a young forest. The morphology is not so different in this case; the driving force for development must of course be sought in different optima or at least different tolerances in the two species.

Detailed observations on permanent plots are needed to follow the exact course of competition (cf. KUJALA 1926 p. 39—42). As long as we lack an accurate description of the phenomena, our discussion must remain rather speculative.

7) The differences in composition between *Hylocomium* segments of different age have already been discussed in Chapter VI. The high percentages of N, P and K in young moss are probably the result of active accumulation, while the decrease in phosphorus and potassium concentration with age was attributed to leaching (Chapter VIII). The relative constancy of nitrogen concentration in old segments is connected with the probable absence of marked translocation of substances in the moss. The increase of calcium with the age of the segment was explained as the result of ion exchange between the base-unsaturated moss and a solution containing Ca in a concentration of the order one part per million, such as has been found in the rainwater beneath trees. Mn, Fe and Al are enriched in a similar way.

8) As a rule the local variation in concentration of different elements in the moss is much larger than the differences between comparable samples from different areas. Some notable features in the geographical variation

may, however, be pointed out. In Fig. 32 we found a difference in the ratio of N to P between dry eastern Sweden and wet western Norway. The phosphorus concentrations are remarkably low in western samples; the nitrogen contents often fairly high, while the opposite is true of samples from eastern Sweden. The samples from areas of intermediate humidity fit well between the two extremes.

As we know that phosphorus is leached to some extent from living segments, while nitrogen is not, we may attribute at least some of the difference to leaching. The precipitation is between 3 and 4 times higher in western Norway than in eastern Sweden. Moreover the sea salt content of the rain may be expected to be higher near the Atlantic, which may increase the leaching. The influence of the sea salt is also visible in the higher sodium content toward the west.

As phosphorus is the element which shows the most constant level in exposed plots in Site II (Figs. 27—29) it would be tempting to consider the P level found there (ca. 0.20 per cent in segments 1+2, corresponding to 0.18 per cent in segment 2) as a minimum level and P as a limiting factor.

In sample 672, however, with the highest yield of all sample plots, segment 2 contained only 0.13 per cent P. As three quarter of a year had elapsed since the maximum growth period, it is not entirely impossible that the difference is due to leaching or accumulation, respectively, after this period. It is of course when growth is intense that we expect the nutrient level to exert its influence. It is, however, more probable that the minimum P level in *Hylocomium* lies somewhere in the neighbourhood of the lowest Norwegian and Scottish values, 0.06 per cent P for *Calluna* heath, 0.08 for ombrogenous bog. Both these types of habitats are known to be phosphorus deficient in certain cases, at least (FRASER 1933, BRANDTSEG 1948, MALMSTRÖM 1952, TAMM unpublished).

Where nitrogen is concerned, conditions are different from those in the case of phosphorus. Forest samples of *Hylocomium splendens* from all areas studied show rather constant N percentages, if the more exposed plots are considered. The minimum values are 0.75 in Västerbotten, 0.70 in Tröndelag, 0.72 in Site II (recalculated from Table XIV) and 0.78 in western Norway (Rådalen), all in segment 2. The only aberrant value is 0.60 for *Hylocomium* from a Scottish *Calluna* heath (near Fort William), which, however, was not a typical *Hylocomium* community, only scattered individuals being present among *Pleurozium Schreberi* and other mosses. It cannot be decided whether this low value is caused by a real nitrogen deficiency, as found for other plants in similar sites by LEYTON (1952), or whether something has interfered with the N uptake by *Hylocomium*.

In the habitats with N concentrations in the moss around or slightly above

0.7 per cent, all segments have very similar N percentages. In one case the individual variation was tested and found to fall within the analytical error (which unfortunately was not as small as might be desirable). These observations could be explained by the assumption that nitrogen supply is a limiting factor for moss growth in these habitats. Moderately increased N supply to a moss individual would then act first by increasing growth; the increase in N percentage may be small as long as there is still a severe N deficiency (cf. MACY 1936).

A very important task is to supply more evidence of how nitrogen is supplied to the moss carpet. As the ammonia content of the air is suspected to be one of the main sources of N to the mosses, we await with great interest the results of the investigations on air ammonia concentration which are being made by EGNÉR and his collaborators at Ultuna. The problem of whether different forest plants can obtain nitrogen in this way appears to be of such fundamental importance for forest ecology that a special investigation ought to be devoted to it.

The concentrations of potassium and calcium in the moss have differed little in samples from different areas, even if the geology has been very different (e. g. samples 775 and 778, Table XVI). In most cases the differences within each habitat are much greater than those between different areas.

Regarding other elements we have already mentioned the higher sodium content toward the west. Sodium in rainwater appears to stand in a kind of equilibrium with the moss, as there is neither accumulation nor release from old segments (Table XVI). Where iron and manganese contents are concerned, we have very few data available for comparison. From Germany EBERMAYER (1876, Tab. V.) reports some iron determinations, 0.04 per cent Fe in *Hylocomium splendens* and 0.13 per cent in *Pleurozium Schreberi*. MAYER & GORHAM report some iron and manganese determinations on woodland mosses of the English Lake District, unfortunately not on *Hylocomium splendens*. They point out the remarkable fact that mosses often contain more Fe than Mn, while the reverse is more common among higher plants in natural vegetation, in particular among woody plants. This observation is confirmed in the present investigation, where iron has been found to exceed manganese in all *Hylocomium* segments except the bud. The explanation for the iron accumulation in mosses, and manganese accumulation in trees on the same site, cannot be uptake from below by the mosses, except in slopes with water trickling down, nor can it be leaching from the trees, which contain little iron and release manganese more readily (cf. Table XXI). A possible source of iron in the moss is, however, the dust, which may contain much iron (cf. JACOBSON, 1945 p. 239). As shown in Table XXI, some Fe was found in rainwater also in the open. The low iron content in leaves of woody plants (MAYER & GORHAM, l.c.) may be connected with the relative immobility of iron in plants. This phenomenon does not much affect iron percentages in mosses, where ion translocation seems to play a subordinate role (except in the bud).

Regarding the possible use of the *Hylocomium splendens* nutrient concentration as an index to site properties, the prospects are hardly promising. The nutrient concentration in *Hylocomium* has been found to indicate chiefly light supply to the ground, a property more easily determined directly. This negative result is, however, not without value, as it seems very probable that other plants also behave like *Hylocomium splendens*, cf. BLACKMAN & RUTTER (1946, 1947), and that correlations between site quality and nutrient contents should therefore be studied only where light supply is comparable. In practice we should confine such investigations to plants with a good light supply. Plants from the field layer or ground layer can be used only in open habitats; samples from trees should be collected from well-exposed branches.

As mentioned aboved the sodium content of *Hylocomium* may perhaps be considered as an expression of the sea salt supply to the habitat. Definite conclusions should not be based upon moss analyses only, as the sodium supply from the tree crowns may have different origins.

The phosphorus concentration in exposed *Hylocomium* appears to have something to do with humidity or precipitation. Leaf analyses from trees can probably tell us more about the possible difference in phosphorus supply from the soil. It is, however, suggestive that the lowest P values (0.06—0.08 per cent dry weight in living segments) have been found in habitats which for other reasons are considered as phosphorus deficient (cf. p. 114).

Concluding remarks on the relations between the *Hylocomium splendens* community and the environment

In some of the eight points just discussed we have pointed out where we have found a heterogeneity in the *Hylocomium* community, and also tried to find the factors responsible—questions asked in the introduction. We may now attempt to put our results together to form a picture of the ecology of the *Hylocomium splendens* community.

The growth of *Hylocomium splendens* is determined by the supply of different growth factors (in a broad sense), but the "limiting" factor may be different on different occasions. A necessary prerequisite is moisture; during dry periods the water supply limits growth. When water supply is adequate, light and nutrient supply become the most important factors, together with temperature. The carbon dioxide content of the air has been left out of this discussion, since it can probably be regarded as relatively constant within small areas, at least when growth is measured over long periods.

Moss yield determined as annual production represents the integrated result of all these factors and their interaction with the moss organism. The apparent lack of close correlation between yield and humidity shows us that the growth-checking during dry periods is later more or less equalized, the supply of something else then becoming more important. Beneath the trees the light is more or less deficient, and outside the trees the nutrients appear to be scarce. The low temperature in winter is at least one of the causes of the slower growth then; another might be the weaker light, which is further cut off by snow cover.

Morphologically speaking the growth of *Hylocomium splendens* is definitely rhythmical: one segment is formed annually. There is a possibility that this "internal" rhythm may interfere with the environmental factors, so that growth may be partly limited by internal factors during certain periods. Such a hypothesis, supposing an internal periodicity in moss growth with the main growth periods in autumn and spring, has been advanced by HAGERUP (1935). As has been shown by STÅLFELT (1937 a) and ROMOSE (1940), HAGERUP'S winter rest and summer rest periods are to a large extent, perhaps entirely, controlled by external factors. We have at present no evidence of the importance of "internal" factors for the total moss yield. We must, however, admit that it is the physiological activity of the different segments which determines where in the plant photosynthesis and dry weight increase take place.

The external factors of most importance for the moss growth—light and nutrient supply—affect the individual moss plants in a very irregular way. This is especially true of the supply of salts from the tree crowns by rain. The strong individual variation shown by *Hylocomium splendens* in the open thus finds a simple explanation. The effect of competition (cutting off nutrient supply) is probably small in comparison with that of the randomness of the nutrient supply. Where light supply is deficient we have also found a great individual variation. The light supply to the ground is also somewhat irregular; moreover we must expect an effect of competition (mutual shading), which in turn is greatly influenced by the height and direction of the segment, properties which may be affected by internal factors.

The effect of competition seems to be best shown by the purity of many *Hylocomium* communities, particularly in habitats where fairly pure tussocks of *Hylocomium splendens* alternate with equally pure communities of other mosses, e. g. *Ptilium crista castrensis, Pleurozium Schreberi* or *Dicranum undulatum.* This relative purity suggests an ability of these mosses to exclude other species when growing under favourable conditions. The scarcity of very small individuals is another indication of the severe competition within a closed moss community.

We must then conclude that important structural features of the *Hylocomium splendens* community, especially the large individual growth variation, depend to a large extent directly on the action of external factors, though competition modifies the community structure in certain respects. Among the "external' factors is included the forest canopy, which has been shown to affect the moss carpet in so important a way that it can be regarded as a prerequisite for a well-developed community of *Hylocomium splendens* or ecologically similar species in many habitats. The trees may be replaced by shrubs, but no case has been encountered during this investigation where a *Hylocomium* community grows independent of a canopy of some kind, except in slopes with water trickling down. It would be interesting to investigate on the spot the moss growth and nutrition in cases where *Hylocomium splendens* is reported to occur on open ground (for example in Iceland, HESSELBO, 1918, p. 593).

The *Hylocomium splendens* community as a model for other plant communities

Our conclusion that the structural heterogeneity of the *Hylocomium* community is directly dependent upon external factors is connected with the peculiar nutrition of the moss community, which makes it independent of root competition. Thus we cannot generalize to other communities. There are, however, certain results of this investigation which have a more general application.

1) The sources of nutrients to the *Hylocomium* community, rainwater salts, atmospheric dust and ammonia, and leachate from tree crowns and litter must of course favour also other plants, especially epiphytic and epilithic vegetation. Earlier authors have pointed out the importance of one or more of these nutrient sources for such plants, but it is necessary to consider them all together. The role of minerals leaching from trees has often been overlooked. The observations reported by WENT (1940) on the nutrition and sociology of tropical epiphytes are of great interest in this connection.

2) The changes in composition with the age of old moss segments show some of the effects of the processes by which a humus layer is formed of the litter. The litter is percolated by a dilute water solution, to which soluble substances are released—or from which substances may be absorbed, depending on the concentration of the solution and on the absorption capacity of the litter. The presence and nature of the organic matter in the water coming down is also important for the soil-forming processes, as has recently been stressed by BLOOMFIELD (1952).

3) The growth of a shoot of a plant is controlled both by the physiological status of the plant and of environmental factors. In *Hylocomium* we have found a rather loose correlation between the growth of a segment and the

size of its parent segment. The physiological basis for this loose dependence is apparently the fact that of the nutrients and photosynthates used by the young segment in its growth, relatively little is supplied by the parent segment. In many plants the young shoots are mainly built up of substances translocated from older parts of the plant. In this case we would expect a lower sensitivity for variations in external factors, and a close correlation between the size of shoots of different age. The two extreme types are a) plants which economize well with nutrients and/or carbohydrates, but are less well adapted to make use of a sudden increase in the supply of some deficient factor, and b) plants of which only small parts without much storage substances survive the unfavourable season, but on the other hand are able to spread rapidly when conditions are suitable. Of course there are all kinds of intermediate types, and the same plant may economize with some nutrients but not with others. In any case, the character of the competition within a plant community is very much determined by the type of plants in the respect discussed above. As a rule plants of type a) are favoured in closed communities, and those of type b) in more open and unstable ones. *Scilla non-scripta* appears to be a good example of a plant belonging to type a) (BLACKMAN & RUTTER 1949, Figs. 1 and 2), while most "nitrate plants" belong to type b).

An investigation of the individual growth variation of the constituents of a community may help us to find differences in physiological type, which later may be studied in more detail with other methods. If the individual growth variation within the same species is different in different habitats, we must suspect variations in the mode of action of the external factors.

4) However important an investigation of the contents of plant nutrients in different species and organs may be, when the nutrition of a community is discussed, percentage values for different elements may prove clearly unsatisfactory. The absolute amounts of nutrients taken up should also be considered. It is therefore desirable to measure growth and nutrient content simultaneously.

Conclusion 4) is supported by the results of foliar diagnosis, applied as a means to determine the nutrition of crop plants, see for example MACY (1936). In most cases nutrient percentages increase with increased supply of the nutrient in question, due to the fact that the most common case in agriculture is a moderate deficiency. When the supply is ample, nutrient percentages in the plant may also increase with increased supply, but often slowly. The uptake is then a luxury consumption. At very low available concentrations of some nutrient a supply of this nutrient may not result in increased percentages but in a growth increment proportional to the additional uptake (or perhaps even larger, STEENBJERG 1945, 1951). This case is already known in agriculture, and may well be frequent also in natural vegetation, where the productivity of many plants, or even habitats, is limited by a deficiency in one or more nutrients.

Summary

The growth and chemical composition of a forest moss, *Hylocomium splendens,* has been studied in order to evaluate the importance of different environmental factors, and of competition, for the yield and structure of the *Hylocomium splendens* community. The moss yield has been found to be closely related to light supply when this is low, and to nutrient supply when light is abundant.

The nutrients are to a large extent supplied from the following sources: leachable salts in the tree crowns, dust and atmospheric ammonia and nitrate. Ammonia and some nitrate are contained in rain, which at the same time carries down soluble substances from the tree crowns and dust from the air. Dust also sediments directly on the mosses, as well as on tree crowns. The importance of these sources of nutrients for different plant communities is stressed.

The amounts of ammonia in rain-washings cannot account for all the nitrogen in the moss. It is therefore suggested that there may be a direct absorption of ammonia from the air.

There is a large and irregular variation in the individual growth-rate of *Hylocomium splendens,* which is considered as mainly due to the irregular way in which both nutrients and light are supplied, at least in many places. Competition may to some extent interact with light supply in shaded sites, but is hardly the most important cause of the growth variations. It has, however, an effect on the mode of propagation, inasmuch as it is bound to suppress very small individuals more than large ones.

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Note. The names of most periodicals are abbreviated according to the rules of Chemical Abstracts (See List of Periodicals, publ. in Chemical Abstracts, Columbus, Ohio, 1951). The following Swedish journals are abbreviated according to the rules of Botaniska Notiser:

Botaniska Notiser, Lund	BN
Reports of the Forest Research Institute of Sweden, Stockholm	Medd. SS.
Svensk Botanisk Tidskrift, Stockholm	SBT
Svenska Skogsvårdsföreningens Tidskrift, Stockholm	SST

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Sammanfattning

Tillväxt, produktion och näringsekologi i mattor av en skogsmossa

Föreliggande undersökning behandlar tillväxt, näringsförhållanden och struktur under olika ytterbetingelser hos ett enskiktat växtsamhälle, bestående av husmossa, *Hylocomium splendens* eller *proliferum*, med större eller mindre inblandning av andra mossarter.

Arbetet är ett försök att utreda sammanhangen mellan detta växtsamhälles olika egenskaper — t. ex. totalproduktionen och växlingarna i individuell tillväxt — och yttre faktorers inverkan, varvid särskild uppmärksamhet ägnas samspelet mellan å ena sidan de yttre faktorerna, å andra sidan konkurrensen och andra »inre» egenskaper hos växtsamhället självt. Vi vet mycket litet om i vad mån ett växtsamhälles egenskaper formas direkt av ståndortsfaktorerna, och i vad mån konkurrensen och andra biotiska faktorer modifierar dessas verkan. Det är också mycket svårt att angripa sådana problem i ett flerskiktat samhälle, t. ex. en skog, och därför har det enklast byggda av de i skogen ingående enskikts-samhällena utvalts för undersökning, nämligen mosstäcket. Vi kan visserligen icke vänta oss att de andra komponenterna i skogssamhället — framför allt trädskiktet och fältskiktet — skall uppföra sig i allo likadant som mosskiktet. Det föreligger emellertid en intim växelverkan mellan de olika enskikts-samhällena på samma ståndort, och redan därför kan en undersökning av ett skikt ge upplysningar om de andra skiktens ekologi. Vidare kan en grundlig undersökning av ett växtsamhälle — låt vara ett kvantitativt obetydligt sådant — hjälpa oss att finna de nyckelpunkter där undersökningen av andra växtsamhällen lämpligen bör sättas in för att visa vad som är karakteristiskt och ekologiskt viktigt när det gäller olika typer av samhällen.

När det gäller skogsmossornas ekologi framstår särskilt deras näringsförsörjning som ett olöst problem efter STÅLFELTS (1937 a) och ROMELLS (1939) arbeten. Dessutom är husmossan en mycket lämplig art för en undersökning av detta slag, eftersom den dels ofta bildar tämligen rena samhällen, dels genom sin karakteristiska tillväxt gör det möjligt att bestämma års- och arealproduktionen.

Kap. I. Terminologi och metoder

Några termer måste här definieras. Husmossan växer som bekant i »våningar», varav i regel en bildas varje år (fig. 1). Dessa »våningar» kallas i fortsättningen »segment». Varje segment börjar sin tillvaro som en liten knopp på modersegmentet. Vi har daterat segmenten efter den höst då de utvecklas från knopp till »våning», t. ex. segment 49 = det segment som växte ut hösten 1949. När segment ur prov tagna olika år skall jämföras, är det emellertid bättre att numrera på annat sätt: knoppen kallas då segment 1 (ålder under 1 år). Segment 2 är då det segment som är mellan ett och två år gammalt, o. s.v.

Ibland utvecklas flera segment från ett modersegment. Sådana exemplar har för korthetens skull kallats »grenade» och övriga, med en rak sympodiekedja, »ogrenade», trots att bägge slagen naturligtvis har sidogrenar av olika ordning.

Provtagningsmetodiken har varit enkel. Stycken av mosstäcket från ställen där husmossan dominerade har samlats in; i de fall där arealproduktionen skulle bestämmas skars mosstäcket ut efter en ram, vanligen med måtten 25 × 25 cm. Sedan uppdelades proven efter arter, och husmossfraktionen sedan i segment av olika ålder. När det gällde att bestämma arealproduktionen uttogs även av andra mossarter vad som ansågs vara en årsproduktion. I många fall kunde man se gränsen mellan årsskott ganska bra, t. ex. på kammossa och väggmossa; i andra fall måste uppdelningen ske mera på en höft. I sådana fall klipptes ca hälften av de gröna delarna av och vägdes, utom i fråga om vissa arter där de gröna delarna föreföll att också innehålla skott äldre än två år. I sådana fall togs en tredjedel. Dessa bestämningar är således tämligen osäkra, men i regel utgjordes de osäkra fallen endast en liten del av proven.

Vid den följande kemiska analysen har använts de metoder som numera är gängse på Statens skogsforskningsinstitut. I vissa fall måste metoderna modifieras med hänsyn till de ofta mycket små provmängder som stått till förfogande. Kväve har bestämts med en mikro-Kjeldahl-metod, fosfor med kolorimetriska metoder, kalium, kalcium och natrium i regel lågfotometriskt. Järn, mangan och aluminium har bestämts med gängse kolorimetriska metoder.

Kap. II. Undersökta lokaler

Mosstäckets utbredning och egenskaper har studerats på ett stort antal platser i Sverige och Norge, men insamling av prover för analys har endast skett inom följande områden: 1) Östra Mellansverige, särskilt Roslagen. 2) Östlandet i Norge (Ås söder om Oslo). 3) Vestlandet i Norge (Bergenstrakten). 4) Västerbotten (Kulbäcksliden). 5) Nordtröndelag (nära Snåsa).

Ett stort antal prover har insamlats på gården Grenholmen i Roslags-Bro socken. Skogen ifråga är en delvis örtrik barrblandskog. Provlokalerna har valts ut inom de torftigare delarna av denna skog, där bärris och kruståtel dominerat (Lokal II och III; fig. 9) eller åtminstone utgjort ett framträdande inslag i fältskiktet (Lokal I, fig. 2). Mossproven har både här och på andra håll företrädesvis tagits inom fläckar utan fältskikt eller med glest sådant.

Av de norska proven har några från Os prestgårdsskog (omkring 2 mil söder om Bergen) bearbetats särskilt ingående. De härstammar från planterad, högproduktiv granskog, dels från en starkt beskuggad yta inne i beståndet, dels från bättre belyst mark i beståndskanten.

Kap. III. Husmossans tillväxt under olika årstider

För att bestämma tillväxten under olika årstider har prov insamlats från samma plats (lokal I) vid olika tider på året. Därefter har medelvikten av olika segment av husmossan bestämts för ett stort antal »ogrenade» exemplar ur varje prov. Ur dessa siffror kan man sammanställa en årskurva för tillväxten (fig. 3), som dock lider av en viss osäkerhet, eftersom det förekommer en avsevärd variation i medelvikt mellan olika prov. Man kan få bort denna variation genom att uttrycka segmentvikterna i procent av det segment som under året håller sig mest konstant. Även detta beräkningssätt lider av en viss osäkerhet, men torde dock vara att föredraga, särskilt som man då kan få med även de »förgrenade» exemplaren, som visat sig växa något snabbare än de »ogrenade» (tab. I och II). I fig. 4 visas årskurvor som erhållits på detta sätt.

Vi kan nu beskriva tillväxten hos husmossan på följande sätt, som närmast gäller lokal I, men som i stora drag även passar på många andra håll. Ett segment är först synligt som en liten knopp så snart modersegmentet på hösten vuxit ut. Det ökar sedan långsamt i storlek och vikt under året, tills det nästa eftersommar hastigt växer ut och bildar sidogrenar. Sidogrenarna av första ordningen kommer redan på sommaren, de av högre ordning följer något senare. Tillväxten saktar av fram på hösten, men segmentet kan troligen icke betraktas som fullvuxet förrän nästa höst, då också sporogonen växer fram. Dessa mognar på våren. Segmentets färg är ljust grön under vintern och våren efter utväxandet, men blir småningom brungrön och senare brun eller gråbrun. Nedbrytningen sätter också så småningom in, men åtminstone på lokalerna I—III föreföll i allmänhet segment 3 och 4 tämligen välbevarade. Mycket stora skillnader finner man ifråga om färgen, som kan vara olika både på olika lokaler och på olika exemplar på samma lokal. Även tidpunkten när tillväxten sätter igång på sommaren växlar med väderlek och ståndort.

Kap. IV. Individuell variation i storlek och tillväxt hos husmossan

Fig. 5 och 6 visar hur husmossindividen fördelar sig på storleksklasser i två prov, det ena från en väl belyst lokal och det andra från en starkt beskuggad. Vi ser direkt att medelstorleken är större på den ljusa lokalen. Påfallande är också att små individ är förhållandevis sällsynta; detta syns bäst i fig. 5, men skulle ha kommit fram även i fig. 6 om klassbredden varit mindre i förhållande till medelstorleken (jämför även fig. 8).

Om små individ är sällsynta i ett samhälle av perenna växter, tyder detta på att föryngringen sker huvudsakligen vegetativt, genom förgrening (TAMM 1948). Vi har säkert rätt att dra denna slutsats i fråga om husmossamhället, särskilt som diagrammen 7 och 8 visar att man icke kan säga att de mycket små individen växer fortare än andra. Några husmossindivid som uppenbarligen utvecklat sig ur protonemata har ej heller påträffats i de undersökta slutna samhällena; i stället har det visat sig att en stor del av de små individen uppstått som sidoskott på större segment.

Fig. 7 och 8 visar också att tillväxten varierar oerhört kraftigt från individ till individ. Hos samma individ varierar den också från år till år på ett mycket oregelbundet sätt. Variationens storlek åskådliggöres bäst med användning av statistiska metoder. I tabell IV återges därför korrelationskoefficienterna, dels mellan två på varandra följande segment, dels mellan ett segment och dess »dotterdottersegment». Såväl de direkta korrelationskoefficienterna har uträknats som de partiella. I det senare fallet har inflytandet av variationen i det tredje segmentet eliminerats. Vi ser att sambandet mellan två närliggande segment förblir statistiskt mycket tillförlitligt, även om man eliminerar den del av sambandet som kan tillskrivas det närmast yngre eller äldre segmentet. Däremot erhålles endast i ett av fyra fall en statistisk tillförlitlighet för den partiella korrelationen mellan två segment där inflytandet av det mellanliggande segmentet eliminerats. Detta tyder på att något nära fysiologiskt samband knappast föreligger annat än mellan moder- och dottersegment.

Beträffande den individuella variationen i husmossans tillväxt skulle man gärna vilja veta om den är en variation från fläck till fläck, eller om det är en individuell variation i egentlig mening. En möjlighet att svara på denna fråga kan man få tack vare förekomsten av »förgrenade» exemplar. I de flesta fall har de »förgrenade» utgjort en alltför liten procent för en undersökning inom en mindre fläck. I prov 672 (Os, Norge) fanns det emellertid 38 mossindivid (med minst två utvecklade segment vardera) som parvis utgick från gemensamma modersegment. Inom de 19 paren kan endast miljöbetingade eller rent slumpartade skillnader tänkas, däremot ej genetiska skillnader; sådana är däremot tänkbara mellan paren. Förhållandet mellan segment 2 och segment 3 var i genomsnitt för alla 38 exemplaren 1.35 med en standardavvikelse av 0.54. Räknar man i stället ut standardavvikelsen inom par erhåller man siffran 0.43 (tab. III). En stor del av variationen kvarstår sålunda även om man jämför exemplar av *samma genotyp växande på några få centimeters avstånd.*

Kap. V. Växlingar i husmoss-samhällets produktion och struktur under olika ytterbetingelser

Bottenskiktets totalproduktion har uppmätts inom ett stort antal provytor inom lokal II. Det har visat sig att under träd är mossproduktionen positivt korrelerad med ljustillgången, utanför trädkronorna däremot oberoende av ljuset men sjunkande med stigande avstånd till träd (fig. 11). En tydlig korrelation produktion/ljus har också påträffats på norska Vestlandet. Det extrema fallet, när mossor helt saknas under täta trädkronor, är en vanlig företeelse. Det är något svårare att påvisa ett generellt samband mellan närheten till träd och mossproduktionen, eftersom fältskiktsvegetationen i regel är yppigare utanför trädbeståndet och påverkar mosstäcket mer eller mindre i samma riktning som detta. På stenar och hällar kan man dock ofta se att skogsmossorna trivs bäst i närheten av träd (fig. 9).

Mossproduktionens beroende av fuktigheten har studerats dels genom att jämföra tillväxten under år med olika väderlek, dels genom att jämföra prov från ett fuktigt klimat med sådana från ett torrare (tab. VII jämförd med tab. V). Något klart samband mellan mossproduktionens storlek och humiditeten har icke framkommit. Den mest produktiva ytan, nr 672 (över 1 ton torr mossa per ha och år) ligger visserligen på norska Vestlandet med omkring 2000 mm årlig nederbörd, men maximiproduktionen på lokal II i Östsverige med omkring 550 mm är endast obetydligt lägre (yta nr 8).

Även om fuktigheten sålunda icke synes betyda så mycket för årsproduktionen hos mosstäcket är det ändå uppenbart att den påverkar tillväxtens förlopp. Fuktiga somrar börjar tillväxtperioden tidigare än torra somrar, och även på samma lokal kan tillväxten börja senare hos individ som växer uppe på stenar än hos sådana som växer på marken och lättare håller sig fuktiga. Denna motsägelse beträffande fuktighetens betydelse kan vara skenbar och förklaras om det förhåller sig så att en tidigare tillväxt medför en hastigare förbrukning av det som i verkligheten begränsar årsproduktionen.

När det gäller husmossans morfologi och samhällets struktur förefaller de yttre faktorernas inverkan att vara rätt begränsad, åtminstone så länge förhållandena ej är mycket extrema. T. ex. inom lokal II är husmossan ganska ensartad till sin morfologi inom flertalet ytor (jfr fig. 12—13), och när det gäller i samhällets struktur har heller icke några tydliga olikheter påträffats (tab. X, fig. 14—18). Å andra sidan föreligger det en tydlig skillnad i medelstorlek mellan de olika belysta proven 672 och 677 (fig. 5—6). Tillväxtvariationen har möjligen också varit mindre på den mörka ytan (tab. IV). Mest växlar i allmänhet mossans färg mellan olika ytor.

Kap. VI. Husmossans näringsinnehåll och näringsupptagande

Kemiska analyser av mossegment av olika ålder visar att de yngre segmenten är rikare på kväve, fosfor och kalium än de äldre segmenten. Däremot stiger kalciumhalten med åldern (tab. XI och XII).

När det gäller att bestämma näringsupptagandet räcker det ej med att känna procenterna av olika element. Man måste dessutom känna tillväxten samt veta om det förekommer någon transport av näringsämnen inom växten. Diagramserien fig. 19—26 hjälper oss härvidlag. Vi ser här medelvikterna för ogrenade exemplar från lokal I (olika årstider och år) samt deras absoluta näringsinnehåll. Beträffande kväveinnehållet ser vi att det tämligen väl följer torrvikten, särskilt i äldre exemplar. Uppenbarligen sker ingen nämnvärd kvävetransport ur gamla segment till de växande två yngsta segmenten. I så fall skulle man vänta sig en genomgående sänkning i kväveinnehållet när ett segment dör. Nu sjunker ej kväveinnehållet tydligt förrän torrvikten sjunker; vid denna tidpunkt är segmenten så sköra att blad och grenar ofta bryts av och går förlorade. Fosfor och kalium förhåller sig rätt lika med kvävet, men halterna sjunker kontinuerligt i äldre segment. Kvävehalterna blir nästan konstanta med tiden.

När det gäller kalcium stiger ej endast kalciumprocenten, som vi nyss konstaterat, med åldern, utan även totalinnehållet kalcium stiger ända tills segmentet börjar falla i småbitar.

I diagrammen fig. 27—29 visas hur näringshalterna i en serie mossprov ändrar sig med belysningen och avståndet till träd på lokal II. Vid mycket låga ljusstyrkor är näringshalterna (särskilt kväve och fosfor) höga och sjunker med stigande ljustillgång, men när ljuset kommit upp till ca 50 % (= i gläntor) förefaller näringshalterna att vara tämligen oberoende av ljustillgången. Lika litet betyder avståndet till träd för *näringshalterna*, däremot sjunker naturligtvis näringskonsumtionen med avståndet till träd, eftersom mossproduktionen sjunker och halterna är tämligen konstanta.

I tab. XVI återges analysvärden för mossprov från olika trakter. Överallt finner vi en skillnad mellan belysta och beskuggade ytor. Dessutom finns det en tendens till lägre fosforvärden hos proven från det humida norska Vestlandet, jämfört med proven från Östsverige. De norska proven innehåller också något mera natrium än de svenska.

En tydlig korrelation föreligger såväl mellan halterna av olika näringsämnen i samma segment (fig. 32) som mellan halterna av samma ämne i olika segment från samma planta (fig. 33—35; fig. 36 visar föga korrelation beträffande kalciumhalterna). Korrelationerna är starka endast om man jämför blandprov, innehållande många mossindivid. I flera fall (tab. XVII, fig. 33b och 34b) är korrelationen ytterst svag när det gäller enskilda mossplantor. Snabbväxande mossindivid tycks skilja sig mycket litet från genomsnittet i sin sammansättning (tab. XVIII). På vissa lokaler förefaller det som om husmossan hade mera ensartad sammansättning än som framgår av tab. XVII; det gäller särskilt i fråga om kvävehalten på vissa ytor med låg genomsnittlig kvävehalt i mossan (0.7 %).

Järn, mangan, aluminium och kiselsyra visar i stort sett ungefär samma fördelning som kalcium i mossan, ökad halt med åldern (tab. XIX).

Ur siffrorna för mosstäckets tillväxt och näringsinnehåll kan vi nu beräkna den årliga näringsförbrukningen. För den mest produktiva ytan (prov 672, Os) på Vestlandet får vi en förbrukning av 10 mg N, 1.1 mg P och 4 mg K per m^2 (eller kg/ha) och år, om vi utgår från vikten (1.1 ton torr mossa/ha och år) och sammansättningen av segment 3 (48). Segment 2 skulle ge något högre siffror. På lokal II i Roslagen får vi för yta 8 ungefär samma kvävekonsumtion som på yta 672, samt något högre fosfor och kaliumförbrukning, 1.5 resp. 6 mg per dm^2 och år. Kalciumförbrukningen är svår att mäta, eftersom den försiggår i både levande och döda organ. Den är emellertid av samma storleksordning som kaliumförbrukningen. — Dessa siffror stämmer ganska väl med tidigare publicerade (ROMELL 1939, ANDRÉE 1947).

Kap. VII. Tillförseln av växtnäring till mosstäcket

Husmossans förmåga att suga upp vatten från underlaget har undersökts av STÅLFELT (1937 a), som fann att den var ganska ringa, samt att många mossplantor saknade förbindelse med underlaget, varför man knappast kunde förklara mossans näringsförsörjning med vad som kunde sugas upp underifrån. Samma åsikt har framförts av ROMELL (1939), som misstänkte att mossan kunde få sin mineralnäring ur den förna som i varje fall någon tid ligger ovanpå mosstäcket. ROMELL hänvisar till äldre försök över urlakningen ur förna med destillerat vatten eller regnvatten.

Utan tvivel får mosstäcket på detta sätt ett näringstillskott, men frågan är om det räcker till. Förnan faller nog också ojämnare än vad mosstillväxten är, trots vad som förut sagts om dennas variabilitet. Man kan därför misstänka att det finns ytterligare någon näringskälla. En sådan har också påträffats vid analys av regnvatten som droppar ned från träd (tab. XX, XXI, XXII). Samma ämnen som visat sig lätt urlakbara ur förna (RAMANN 1888) kommer också ned ur trädkronorna med regnvattnet, t. ex. kalium, fosfor och mangan. Regnvattnet innehåller en del salter även om det insamlas på öppet fält. Dessa mineralämnen härrör troligen dels från havet (natrium, helt eller delvis), dels från dammpartiklar i atmosfären (t. ex. kalcium och järn). Sådana dammpartiklar avsätts också direkt på mossan och i trädkronorna. Tillsammans torde dessa på olika sätt tillförda näringsmängder ungefär svara mot mossans maximiförbrukning enligt ovan.

Kvävetillförseln till mosstäcket ter sig oklarare än mineralförsörjningen. Regnvatten innehåller något ammoniak- och nitratkväve, men enligt tab. XXI tycks trädkronorna snarare beröva regnvattnet ammoniak än tillföra det sådant. Det är emellertid möjligt att andra kvävehaltiga ämnen urlakas och kommer mosstäcket tillgodo. Dessutom förefaller det enligt nyare undersökningar (EGNÉR, 1953) sannolikt att växterna — och då troligen icke minst mossorna — kan ta upp vissa mängder ammoniak direkt ur luften.

Kap. VIII. Husmossan i kontakt med vatten

Om husmossa behandlas med rinnande vattenledningsvatten under ett dygn urlakas något kalium och fosfor, medan kvävehalten förblir ungefär densamma. Kalciumhalten fördubblades under denna tid i ett försök (tab. XXIII). I destillerat vatten urlakas kalcium liksom fosfor och särskilt kalium lätt ur mossförna, medan levande mossa håller kvar sitt näringsinnehåll bättre. Unga mossegment som legat länge torra förhåller sig däremot som mossförna.

Förändringarna i mossförnans sammansättning vid behandling med vatten beror uppenbarligen på enkelt jonbyte, varvid tvåvärda joner som Ca^{++} tas upp lättare än envärda sådana som K^{+}. Härigenom kan ökningen i kalciumhalt hos mossförnan med åldern förklaras. Levande mossa har dessutom en aktiv upptagningsmekanism, som medger anrikning av joner ur ännu mera utspädda lösningar. Kalciumhalten i lösningar som skakats med mossförna ett dygn rör sig om ett eller annat mg/l, (tab. XXV) alltså samma storleksordning som vi redan funnit i regnvatten under träd.

Kap. IX. Några andra faktorer som kan inverka på skogsmossornas tillväxt

Luftens koldioxidhalt är under dagen i genomsnitt högre nära marken än i höjd med trädkronorna (se bl. a. ROMELL 1932, HUBER 1947). Detta är en gynnsam faktor för mosstäcket, men vi kan icke förklara den individuella tillväxtvariationen härmed, eftersom koldioxiden verkar ganska likformigt på alla mossindivid inom små ytor. Temperaturen är också en faktor av betydelse för mossans livsprocesser, men liksom koldioxidfaktorn verkar den tämligen homogent på små ytor. Stark insolation skadar husmossan, i synnerhet om den plötsligt utsättes därför (fig. 42). Det förefaller emellertid som om den tålde solljuset bättre om den från början växt mera exponerat (fig. 39 och 43). En del av de mera produktiva ytorna på lokal II är mera solexponerade än några av de lågproduktiva ytorna utanför träden, varför man knappast kan förklara korrelationen i fig. 11 b som en följd av mossans krav på solskydd.

Snötäcket bör rimligtvis hindra mosstäckets assimilation under vintern, men denna årstid är tillväxten ändå liten, icke minst på grund av den låga temperaturen. Snön verkar också homogent inom mindre ytor.

En faktor som däremot kan vara orsaken till en del av den individuella tillväxtvariationen är förnafallet. Detta verkar gynnsamt genom att tillföra mineralämnen (om regn inträffar vid lämplig tidpunkt), ogynnsamt genom att beskugga mossan. Bladförna skuggar mera än barrförna och detta är troligen orsaken till att husmossan i lövskog, om den alls förekommer, ofta är inskränkt till fläckar där förna ej samlas, t. ex. på stenar.

Bland ytterligare tänkbara faktorer kan vi nämna plasmaaktiva ämnen avgivna från trädkronan (STÅLFELT 1948), samt inverkan av parasiter eller olika djur. I intetdera av dessa fall har vi anledning att anta någon verkligt betydelsefull inverkan på mosstäcket.

Kap. X. Diskussion av de funna ekologiska sambanden och av de faktorer som bestämmer mosstäckets struktur

När det gäller att diskutera orsakssammanhangen bakom de samband vi funnit i tidigare kapitel torde följande punkter vara av särskilt intresse:

1) Nedgången i mossproduktion med sjunkande ljusstyrka under träd.
2) Parallellismen mellan tillväxt och näringsupptagande i flera fall.
3) Den stora individuella tillväxtvariationen, som åtminstone till stor del är betingad av ytterfaktorer.
4) Den åtminstone på vissa ytor stora individuella variationen i kemisk sammansättning.
5) Den påfallande låga frekvensen av mycket små mossplantor i slutna samhällen.
6) Den ofta påfallande renheten hos husmossmattorna, även där fläckar med andra moss-samhällen omväxlar med husmossfläckar.
7) Skillnaderna i kemisk sammansättning hos segment av olika ålder.
8) Skillnaderna i kemisk sammansättning hos husmossa från olika trakter.

Punkt 1) förklaras säkerligen med att ljustillgången begränsar mossans tillväxt på mörka lokaler. Punkt 2) förklaras enklast med att näringstillgången begränsar husmossans tillväxt på ej för mörka ytor.

När det gäller punkt 3) och 4), den individuella variationen i tillväxt och kemisk sammansättning, ligger det nära tillhands att söka förklaringen i det sätt varpå näringen tillföres mosstäcket. En viktig del av denna näring tvättas av regnet ut ur trädkronorna och faller ned ojämnt fördelad, särskilt under de yttre delarna av kronorna och strax utanför kronorna, dit vinden för en del droppar. Även ljuset kan vara ojämnt fördelat, särskilt under trädkronorna.

Punkt 5), den låga frekvensen av mycket små mossplantor — speciellt »groddplantor» — kan förklaras ur svårigheten för sådana små plantor att följa med i mosstäckets årliga höjdtillväxt på en eller annan centimeter. Punkt 6), den ofta påfallande renheten hos husmoss-samhället, har säkerligen också med konkurrensförhållandena att göra. Trots att tillväxtbetingelserna för den enskilda mossplantan kan växla starkt från år till år är konkurrensen tydligen tillräckligt stark för att utestänga inkräktare av andra arter lika väl som små plantor av den egna arten. Vissa mossarter med likartad morfologi förekommer emellertid blandade, t. ex. husmossa och väggmossa.

Punkt 7) gällde skillnaderna i sammansättning mellan mossegment av olika ålder och orsakerna därtill har något diskuterats i kap. VIII.

Den regionala variationen i husmossans sammansättning — punkt 8) — är i regel mindre än den lokala, men vissa drag framträder dock. Fosforhalterna är påfallande låga i västnorska prov, särskilt när det gäller väl belysta ytor. Detta kan möjligen bero på starkare urlakning på grund av den höga nederbörden, men sammanhänger kanske också med en viss fosforfattigdom på dessa lokaler, jämfört med de svenska lokalerna. Natriumhalten i de norska proven tyder på inverkan av av luftburet havssalt.

Några möjligheter att använda husmossans sammansättning som indikator på ståndortsegenskaper föreligger ej. I första hand beror mossans sammansättning på belysningen, som är lättare att bestämma direkt.

Undersökningen har visat att husmoss-samhället — och säkerligen flera andra skogsmoss-samhällen — har en näringsekologi som i hög grad skiljer sig från den hos samhällen av högre växter. Några slutsatser av generell räckvidd kan dock dragas ur undersökningen:

1) De näringskällor som försörjer husmoss-samhället kan ej gärna sakna betydelse för andra växter och växtsamhällen, särskilt för epifytiska och epilitiska samhällen, som säkert drar nytta av vad som urlakas ur trädkronor och vad som tillföres med regn, damm och i luften (ammoniak).

2) Mossförnans förändringar med åldern belyser en viktig sida av de processer som leder till bildningen av ett humuslager ur förnan. En urlakning sker av vissa ämnen, men samtidigt kan andra ämnen anrikas.

3) Den individuella variationen i tillväxt inom ett växtsamhälle är en betydelsefull egenskap, som kan ge oss upplysningar om hur både yttre och inre faktorer verkar. Sannolikt sammanhänger en växtarts tillväxtvariabilitet i hög grad med det sätt varpå den ekonomiserar med sitt näringsförråd. I detta hänseende hör husmossan till de arter som är starkt beroende av yttre faktorer, eftersom större delen av ett segments näringsförråd måste tas upp utifrån under segmentets tillväxt. Hos många andra växter tillhandahåller moderplantan en stor del av de näringsämnen och kolhydrat som ett skott behöver för sin tillväxt.

4) Även om uppgifter om procenterna av olika näringsämnen i en växt eller ett växtorgan kan vara mycket värdefulla, är de dock ej alltid tillräckliga. Man måste ta hänsyn även till de upptagna absolutmängderna. Detta kan ske genom att undersöka tillväxten parallellt med näringshalterna.

DIAGRAMS AND TABLES

Fig. 44 a

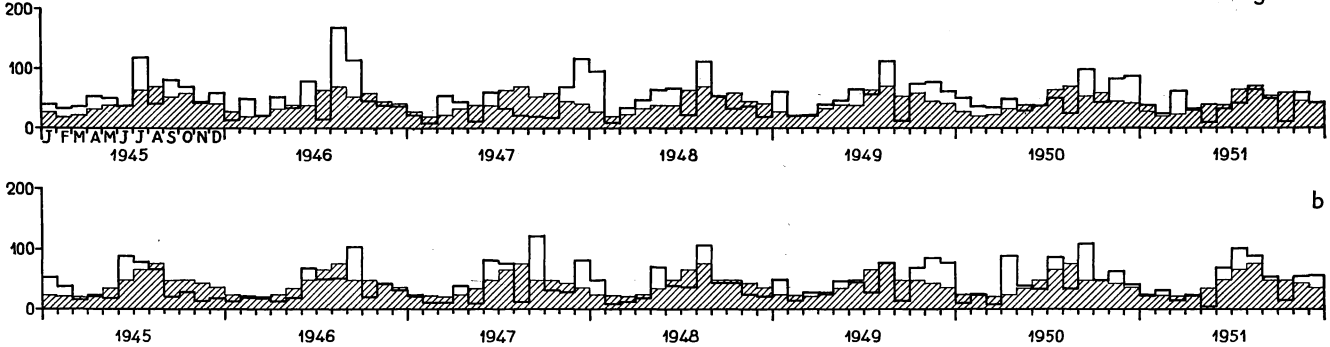

Fig. 44. Monthly precipitation in mm 1945 to 1951 in two Swedish stations, compared with the average precipitation during the period 1901 to 1930. Heavy line marks actual precipitation; hatched area normal precipitation.

a. Väddö, Roslagen. Lat. N. 59°58′, long. E. 18°49′.

b. Kulbäcksliden, Västerbotten. Lat. N. 64°12′, long. E. 19°34′.

Fig. 45. Monthly precipitation in mm 1946 to 1950 in three Norwegian stations, compared with the average precipitation during the period 1901 to 1930. Heavy line marks actual precipitation; hatched area normal precipitation.

a. Ås, eastern Norway. Lat. N. 59°40′, long. E. 10°46′

b. Bergen II, western Norway. Lat. N. 60°24′, long. E. 5°19′.

c. Kjevli i Snåsa. Nord-Tröndelag. Lat. N. 64°10′, long. E. 12°29′.

Fig. 45 a

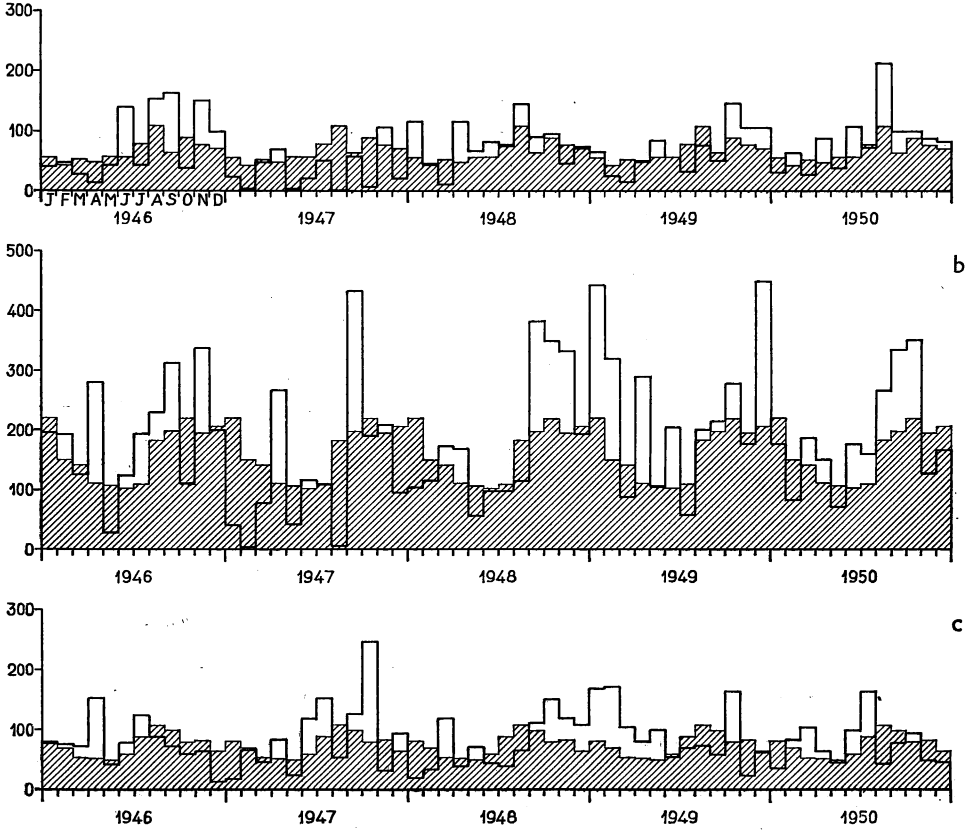
300
200
100
0
J F M A M J J A S O N D
1946
1947
1948
1949
1950
b
500
400
300
200
100
0
1946
1947
1948
1949
1950
c
300
200
100
0
1946
1947
1948
1949
1950

Table XXVI. **Monthly and annual mean temperatures at some stations within the different regions where *Hylocomium* growth has been studied. (Data obtained from Det norske meteorologiske institutt and Sveriges meteorologiska och hydrologiska institut.)**

	Jan.	Febr.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year
Väddö, Roslagen. Lat. N. 59°58'. Altitude 10 m.													
1944.....	—2.4	—1.5	—1.2	2.2	7.5	12.3	17.9	17.8	11.3	7.3	2.6	1.2	6.3
1945.....	—3.1	—1.3	0.7	4.2	7.8	12.7	18.1	16.9	10.4	5.7	0.9	—2.4	5.9
1946.....	—2.8	—5.4	—2.1	5.2	8.2	13.4	17.8	15.6	12.4	5.0	2.2	—0.8	5.7
1947.....	—4.3	—11.7	—6.0	3.9	10.8	15.4	17.6	16.7	14.1	5.9	—0.8	—2.0	5.0
1948.....	—5.3	—3.8	1.7	5.7	9.0	13.6	17.5	15.2	11.6	5.4	0.9	1.8	6.1
1949.....	—0.4	0.3	—1.1	4.7	10.7	12.2	15.8	14.6	14.6	7.1	3.8	—0.2	6.8
1950.....	—6.3	3.1	—0.6	4.3	9.0	14.4	15.2	16.8	11.8	7.3	1.1	—2.8	6.1
1951.....	—4.2	—3.1	—5.7	2.8	5.6	12.6	15.6	16.8	12.7	7.5	3.3	0.4	5.4
Mean 1901 —1930.	—2.9	—2.9	—0.9	2.7	7.8	12.4	15.8	14.4	9.9	5.8	1.0	—1.7	5.1
Umeå, Västerbotten. Lat. N. 63°50'. Altitude 11 m.													
1944.....	—6.6	—5.9	—2.7	0.2	5.7	11.2	15.8	15.1	9.8	5.7	0.5	—0.2	4.1
1945.....	—8.4	—4.7	—3.4	3.0	6.8	12.8	17.5	16.5	8.0	1.4	—1.5	—7.3	3.4
1946.....	—4.9	—9.8	—5.4	2.6	7.3	11.9	16.8	14.5	11.3	2.8	—1.2	—1.4	3.7
1947.....	—6.5	—14.7	—9.5	1.2	8.8	14.5	17.9	15.4	10.8	2.7	—2.9	—6.1	2.6
1948.....	—10.9	—6.8	0.2	3.3	9.0	12.3	16.6	12.8	9.2	2.6	—1.2	—1.1	3.8
1949.....	—3.7	—2.3	—3.2	2.0	8.7	12.0	15.3	13.5	11.2	3.5	1.5	—2.3	4.7
1950.....	—11.6	—6.7	—1.5	3.0	8.2	14.1	15.4	15.6	9.9	4.7	—0.9	—6.9	3.6
Mean 1901 —1930.	—7.4	—7.4	—4.3	0.6	6.3	11.9	15.6	13.3	8.6	2.9	—2.6	—6.0	2.6
Bergen II, Western Norway. Lat. N. 60°24'. Altitude 43 m.													
1946.....	2.5	1.4	2.9	6.3	11.0	12.2	15.6	14.7	12.4	7.9	5.7	3.6	8.0
1947.....	0.6	—4.1	0.0	4.9	13.3	14.2	16.1	17.2	12.6	7.4	4.0	2.3	7.4
1948.....	0.9	1.9	4.7	7.5	10.8	13.0	15.2	14.0	11.3	6.9	5.6	6.0	8.2
1949.....	3.4	4.1	2.3	6.2	9.3	12.3	15.0	13.3	15.2	9.5	6.8	3.2	8.4
1950.....	2.2	2.5	4.3	5.6	11.3	12.4	15.5	16.1	11.6	8.4	4.8	0.9	8.0
Mean 1901 —1930.	1.7	1.6	2.8	5.7	9.2	12.0	14.2	13.5	11.1	7.5	4.1	2.5	7.2
Ås, Eastern Norway. Lat. N. 59°40'. Altitude 95 m.													
1946.....	—4.6	—4.2	—2.0	6.3	11.1	13.0	17.0	14.3	11.5	3.3	2.2	—1.2	5.6
1947.....	—4.3	—13.4	—5.1	3.5	13.6	16.3	18.0	19.4	13.3	5.4	—3.1	—4.7	4.9
1948.....	—8.5	—5.0	0.8	6.4	11.3	14.0	17.1	14.6	11.0	4.6	—0.1	0.6	5.6
1949.....	0.0	0.2	—0.9	5.9	11.2	14.8	18.2	15.0	13.7	6.4	2.1	—1.9	7.1
1950.....	—5.6	—2.5	1.0	5.5	11.7	14.4	15.8	15.8	10.6	6.0	—1.3	—5.1	5.5
Mean 1901 —1930.	—4.0	—3.5	—0.7	3.9	9.5	13.8	16.4	14.3	10.3	5.2	0.0	—3.3	5.2
Kjevli i Snåsa, Nord-Tröndelag, Norway. Lat. N. 64°10'. Altitude ca. 195 m.													
1946.....	—4.7	—8.2	—2.7	2.6	7.4	11.0	14.7	13.3	10.2	4.4	0.5	—1.7	3.9
1947.....	—4.9	—11.2	—6.6	1.6	8.4	13.1	15.0	13.2	9.2	3.3	—3.7	—4.7	2.7
1948.....	—9.7	—2.5	2.3	5.4	7.6	10.5	15.4	10.2	8.3	2.6	—0.3	0.2	4.2
1949.....	—3.3	—1.1	—3.2	2.9	8.1	10.7	11.7	10.9	11.5	4.3	1.6	—3.1	4.2
1950.....	—7.3	—3.9	—0.6	3.4	6.6	11.2	13.9	15.4	9.3	5.5	—1.2	—5.0	3.9

Table XXVII. Botanical composition of the ground layer within different sample plots in Site II. Plots listed in the same order as in Tables V and VI.

Plot No.	Major constituents (> 10 mg/dm²), cf. Table 5.	Minor constituents (< 10 mg/dm²)
1	*Hylocomium splendens* *Pleurozium Schreberi* *Dicranum sp.**	
2	*Hylocomium splendens* *Pleurozium Schreberi* *Aulacomnium palustre*	
3	*Hylocomium splendens* *Pleurozium Schreberi*	*Dicranum sp.** *Rhodobryum roseum*
4	*Hylocomium splendens* *Pleurozium Schreberi* *Aulacomnium palustre*	
5	*Hylocomium splendens* *Pleurozium Schreberi*	*Ptilium crista castrensis* Liverworts
6	*Hylocomium splendens* *Pleurozium Schreberi* *Cladonia rangiferina* *Cladonia sylvatica*	*Dicranum sp.**
7	*Hylocomium splendens* *Pleurozium Schreberi* *Ptilium crista castrensis* *Dicranum sp.** *Cladonia rangiferina* *Cladonia sylvatica*	Liverworts
8	*Hylocomium splendens* *Pleurozium Schreberi*	*Dicranum sp.**
9	*Hylocomium splendens* *Pleurozium Schreberi* *Aulacomnium palustre* *Dicranum sp.**	
10	*Hylocomium splendens* *Pleurozium Schreberi* *Dicranum sp.** Liverworts *Cladonia rangiferina* *Cladonia sylvatica*	*Aulacomnium palustre*
11	*Hylocomium splendens* *Pleurozium Schreberi* *Dicranum sp.**	*Aulacomnium palustre* *Ptilium crista castrensis* Liverworts
12	*Hylocomium splendens* *Pleurozium Schreberi* *Dicranum sp.**	*Aulacomnium palustre*
13	*Hylocomium splendens* *Pleurozium Schreberi*	*Dicranum sp.**
14	*Hylocomium splendens* *Pleurozium Schreberi*	*Dicranum sp.** *Mnium medium* *Ptilium crista castrensis*

* *Dicranum scoparium* or/and *D. undulatum* (mainly *D. scoparium*).

Table XXVII. (Cont.)

Plot No.	Major constituents (>10 mg/dm^2), cf. Tables 5 and 6.	Minor constituents (<10 mg/dm^2)
15	*Hylocomium splendens* *Pleurozium Schreberi* *Dicranum sp.**	*Aulacomnium palustre*
16	*Hylocomium splendens* *Pleurozium Schreberi* *Aulacomnium palustre*	*Dicranum sp.** *Ptilidium pulcherrimum*
17	*Hylocomium splendens* *Pleurozium Schreberi* *Dicranum sp.**	*Brachythecium Starkei* *Mnium affine* *Ptilium crista castrensis* *Ptilidium ciliare*
18	*Hylocomium splendens* *Pleurozium Schreberi*	
19	*Hylocomium splendens* *Pleurozium Schreberi* *Aulacomnium palustre*	
20	*Hylocomium splendens* *Pleurozium Schreberi*	*Aulacomnium palustre* *Brachythecium curtum* *Dicranum sp.** *Ptilidium ciliare*
21	*Hylocomium splendens* *Pleurozium Schreberi* *Dicranum sp.**	
565	*Hylocomium splendens* *Pleurozium Schreberi*	
564	*Hylocomium splendens* *Pleurozium Schreberi*	
570	*Hylocomium splendens* *Pleurozium Schreberi*	*Aulacomnium palustre* *Dicranum undulatum*
559	*Hylocomium splendens* *Pleurozium Schreberi*	
573	*Hylocomium splendens* *Pleurozium Schreberi* *Ptilium crista castrensis*	*Dicranum scoparium* *Mnium affine*
563	*Hylocomium splendens* *Pleurozium Schreberi*	*Aulacomnium palustre*
572	*Hylocomium splendens* *Pleurozium Schreberi*	*Aulacomnium palustre* *Brachythecium sp.*
557	*Hylocomium splendens* *Pleurozium Schreberi* *Ptilium crista castrensis*	*Dicranum scoparium* *Lophozia ventricosa*
571	*Hylocomium splendens* *Pleurozium Schreberi*	*Aulacomnium palustre* *Dicranum undulatum*
556	*Hylocomium splendens* *Pleurozium Schreberi* *Dicranum scoparium*	*Aulacomnium palustre* *Dicranum undulatum*

* *Dicranum scoparium* or/and *D. undulatum* (mainly *D. scoparium*).

Table XXVII. (Cont.)

Plot No.	Major constituents (>10 mg/dm^2), cf. Table 6.	Minor constituents (<10 mg/dm^2)
567	*Hylocomium splendens* *Pleurozium Schreberi*	*Aulacomnium palustre* *Dicranum scoparium* *Brachythecium sp.*
562	*Hylocomium splendens* *Pleurozium Schreberi*	
555	*Hylocomium splendens* *Pleurozium Schreberi* *Dicranum scoparium*	*Aulacomnium palustre* *Barbilophozia lycopodioides* *Brachythecium sp.*
561	*Hylocomium splendens* *Pleurozium Schreberi*	*Aulacomnium palustre* *Brachythecium sp.* *Dicranum undulatum* *Rhytidiadelphus triquetrus*
558	*Hylocomium splendens* *Pleurozium Schreberi* *Dicranum undulatum*	*Dicranum scoparium*
569	*Hylocomium splendens* *Pleurozium Schreberi*	*Brachythecium Starkei* *Hypnum cupressiforme*
568	*Hylocomium splendens* *Pleurozium Schreberi*	*Brachythecium sp.* *Barbilophozia lycopodioides* *Ptilium crista castrensis*

Table XXVIII. Botanical composition of the moss layer within different sample plots. Weights of annual shoots (when distinguishable, otherwise 1/2 to 1/3 of green parts; in the case of *Hylocomium splendens* segment 2) are given in mg dry weight per dm^2. For total moss production per unit area, cf. Table VII and VIII, for chemical composition and description of plots cf. Table XVI.

Sample No.	Constituents (marked tr. when below 10 mg/dm^2)
516	*Hylocomium splendens* 340, *Pleurozium Schreberi* 147, *Ptilium crista castrensis* 246, *Dicranum scoparium* 80, *Barbilophozia lycopodioides* 21.
517	*Hylocomium splendens* 248, *Pleurozium Schreberi* 170, *Ptilium crista castrensis* 89, *Dicranum scoparium* 41, *Barbilophozia lycopodioides* 26.
518	*Hylocomium splendens* 287, *Pleurozium Schreberi* 78, *Ptilium crista castrensis* 275, *Dicranum scoparium* 148, *Barbilophozia lycopodioides* 40.
519	*Hylocomium splendens* 276, *Pleurozium Schreberi* 149, *Ptilium crista castrensis* 178, *Dicranum scoparium* 138, *Barbilophozia lycopodioides* 47, *Polytrichum commune* tr.
625*	*Hylocomium splendens* 523, *Ptilium crista castrensis* 46, *Pleurozium Schreberi* 25, *Dicranum scoparium* tr., *Rhytidiadelphus squarrosus* tr.
626*	*Hylocomium splendens* 346, *Rhytidiadelphus squarrosus* ssp. *calvescens* 97, *Brachythecium Starkei* 48, *Pleurozium Schreberi* 17, *Mnium undulatum* tr.
627*	*Hylocomium splendens* 444, *Plagiochila asplenioides* 140, *Brachythecium Starkei* 63, *Ptilium crista castrensis* 13, *Pleurozium Schreberi* 11, *Dicranum scoparium* tr., *Rhytidiadelphus squarrosus* ssp. *calvescens* tr.
628*	*Hylocomium splendens* 704, *Brachythecium Starkei* 72, *Rhytidiadelphus squarrosus* 12, *Pleurozium Schreberi* 10, *Dicranum scoparium* tr., *Ptilium crista castrensis* tr.
631	*Hylocomium splendens* 354, *Pleurozium Schreberi* 36, *Hypnum cupressiforme* 26, *Dicranum scoparium* 11, *Lophocolea bidentata* tr., *Plagiochila asplenioides* tr., *Plagiothecium undulatum* tr., *Thuidium tamariscinum* tr.
632	*Hylocomium splendens* 540, *Dicranum scoparium* tr., *Hypnum cupressiforme* tr., *Pleurozium Schreberi* tr., *Ptilium crista castrensis* tr., *Thuidium tamariscinum* tr., Liverworts (not det.) tr.
633	*Hylocomium splendens* 481, *Thuidium tamariscinum* 124, *Pleurozium Schreberi* tr., *Ptilium crista castrensis* tr., *Rhytidiadelphus loreus* tr.
634	*Hylocomium splendens* 248, *Ptilium crista castrensis* 21, *Thuidium tamariscinum* 19, *Dicranum scoparium* 17, *Rhytidiadelphus loreus* 14, *Plagiothecium undulatum* tr.
640	*Hylocomium splendens* 515, *Dicranum scoparium* 16, *Hypnum cupressiforme* tr.
672	*Hylocomium splendens* 827, *Rhytidiadelphus loreus* 203, *Ptilium crista castrensis* 122, *Thuidium tamariscinum* 58, *Dicranum scoparium* 46, *Plagiothecium undulatum* 26, *Plagiochila asplenioides* tr., *Plagiochila major* tr., *Pleurozium Schreberi* tr., *Polytrichum commune tr.*
677	*Hylocomium splendens* 242, *Hypnum cupressiforme* 27, *Ptilium crista castrensis* 20, *Pleurozium Schreberi* tr., *Rhytidiadelphus loreus* tr., *Thuidium tamariscinum* tr.
679	*Hylocomium splendens* 530, *Pleurozium Schreberi* 40, *Dicranum scoparium* 31, *Hypnum cupressiforme* 12, *Ptilium crista castrensis* 10, *Plagiothecium undulatum* tr., *Thuidium tamariscinum* tr.
775	*Hylocomium splendens* 612, *Dicranum scoparium* 78, *Ptilium crista castrensis* 55, *Pleurozium Schreberi* 17, *Barbilophozia lycopodioides* tr.
778	*Hylocomium splendens* 260, *Pleurozium Schreberi* 115, *Rhytidiadelphus loreus* 32, *Ptilium crista castrensis* tr.
896	*Hylocomium splendens* 743 (determined from a sample plot 0.8 dm^2, lacking other species; in the neighbourhood occurred *Dicranum scoparium* and *Ceratodon purpureus* together with the lichens *Cetraria islandica* and *Peltigera malacea*). See fig. 39.

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* Within plot No. 91 of Norwegian Forest Research Institute. For tree growth and litter production, see MORK (1942).