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Forest Ecological Studies on Drained Peat Land in the Province of Uppland, Sweden
Parts I–III

Skogsekologiska studier
på dikad torvmark i Uppland
Del I—III

by

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Part I

The vegetation and its development within the special area Jägarmossen

INTRODUCTION

The purpose of this investigation is to give an account of the vegetation and the habitat conditions of some drained peat land, in the eastern part of central Sweden, which carries stands of forest trees at various developmental stages and of various composition.

Mires have long held a leading place as an object of study in Scandinavian vegetation research; a natural consequence of their significance in terms of area in the vegetation as a whole. These investigations have been in various directions. Mire plant communities and their classification and regional distribution have been studied, or the relation between the conditions of the habitat and the occurrence of a particular plant community or species. Peat land has attracted great interest as a historical record, particularly since the development of pollen analysis. With its help it has been possible to follow back the post-glacial development of the vegetation and the dispersal of certain species. Studies of more practical nature have also been carried out, for instance regarding the utilization of the mires for forest production or for agricultural purposes, and the inherent problems involved (see Ch. 1).

Ditching and draining of an area of mire usually leads to very considerable changes in physiognomy as well as nutrient economy. However, the peat substrate is a common factor before and after draining, and has a lasting effect.

In the work that has been practically inclined (Malmström several papers; Melin 1917; etc.) most attention has in Sweden generally been given to peat land which has given poor response to drainage with the aim of afforestation, little or no forest growth resulting. These investigations laid the foundations for the research on fertilization of peat land, recently carried out in order to find economically practicable methods to stimulate forest growth.

The peat lands regarded as good from a forestry point of view usually presented no major problems of forest cultivation. Drainage often gave rapid positive results at least at first. Later development was in different directions; some drainage schemes gave results continuing to be favourable, while others showed stagnation of growth of the young forest.

It was partly with the aim of finding the causes underlying these differences in development that the present work begun.

The main part of the investigations described here have been made on the drained mire Jägarmossen in the Forest Society's Ekebyholm complex in the parish of Rimbo in eastern Uppland. In addition, survey observations have been made in Uppland on drained mires in the regions of Gimo, Dannemora, Tierp, immediately east of Lake Tämnaren and in the area between Gysinge and Tärnsjö in the western part of Uppland. Some data for comparison have also been collected from Jämtland, Västerbotten and some other places. The bulk of these additional data could not be included in the present publication. The conditions found for Jägarmossen can be regarded as fairly typical. Naturally other types of vegetation show up in this larger material.

The localities in Uppland are situated in a climatically favourable part of the country. The fen peat land in this region is often characterized by high contents of certain nutrients. These circumstances are favourable for forest production on the sites.

In connection with the planning of the work (including a survey of the literature), during the process of the field work, and when the first analytical results became available, it became increasingly clear that this type of fen peat land as a site for growing forest was a very variable object for study, and could provide interesting information about the nutrient ecology of such areas. Because of this the scope of the work early became wider than had originally been planned.

A complete survey of the literature was not practical as there is so little written with a direct bearing on the problem but a great deal about adjoining fields of investigation.

On almost no occasion has the intention been to attempt to solve predefined problems. Nor have the various factors of the habitat been studied by means of experimental methods. Rather has the aim been to record the various phenomena and then to find out how they are related to one another. It can be said, more directly, that the work in its present form mainly consists of the classification of a number of observations, some of which are visual and some based on chemical analysis or physical measurements.

The presentation of data is in the following primary divisions:

I. Vegetation and its development within the specially investigated area.
II. Habitat conditions of the specially investigated area.
III. Forest production, and its relation to habitat conditions of good, drained peat land.

The vegetation studies in part I refer exclusively to Jägarmossen, choosen as a representative type. The appropriateness of this choice has been well confirmed by the mentioned investigations in other areas. The descriptions of the vegetation have been made in full detail. There are two reasons for this. Firstly, these vegetation types are relatively little known; this may depend on their artificial nature. Secondly, a description of the present state makes it possible to study the subsequent phases of succession in the plant community when returning to the locality on a later occasion. Knowledge of the later stages would have theoretical as well as practical interest. During the present investigation the lack of more complete comparative data from an earlier period of the development has presented difficulties on several occasions, especially in the preparation of the section on the vegetational development (Ch. 5), in this paper. However, the unpublished manuscript by G. Ullén, Master of Forestry, has been of great value from this point of view. (See Ch. 5. A).

Part II and III also deal with data from the specially studied area, but certain diagrams in part II contain supplementary information from other regions.

Acknowledgements. Professor G. Einar Du Rietz, former head of the Institute of Plant Ecology, Uppsala, introduced me to the field of plant ecology by his stimulating teaching. Professor Hugo Sjörs, present head of the Institute of Plant Ecology, Uppsala, has been of invaluable help to me for many years. In his lectures and during excursions, during my first years at Uppsala university, I received much useful information from him. During his time at the Royal College of Forestry, Stockholm, I had the opportunity of discussing many plant ecological problems with him. Then and later, in the laboratory as well as in the field he has given me many useful suggestions and he has also critically read the manuscript.

Professor Carl Olof Tamm, head of the Department of Forest Ecology, Royal College of Forestry, Stockholm, has in every way facilitated my work from its beginning when he stimulated its initiation. He has always shown an interest in my investigations and has given me much useful advice. He has critically read most of the manuscript and suggested improvements. He has also placed the facilities of his department at my disposal and thus made the present investigation possible.

I have had the advantage of accompanying Professor Carl Malmström on

many of his field investigations. This has given me many opportunities to benefit from his long experience of the ecology of drained peat lands.

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Chapter 1. Features of the development of forest drainage in Sweden and some of the connected problems

The nutrient-rich parts of the mires were early used for cultivation. Peat lands have usually required comparatively little labour in order to be utilized, primarily for grazing but also for haymaking (see Stålfelt 1960, p. 153). These circumstances have meant, for example, that certain types of peat land (eutrophic fens) have had a higher economic value than productive forest land (see Ch. 3. D.; Stålfelt 1960). The primary requirement for this type of exploitation has been to regulate the water table to a suitable level. For forestry it is of major significance that the surface layer of the land should be drained, if a peat land or other type of land with a high water table is to be converted to productive forest land.

In Sweden, forest ditching and draining of mires for forestry was first carried out relatively recently; in the same way, forestry as an industry is also a late development. Hence, in available forest statistical reports the annual increase in the length of ditches for the period 1873—1890 (the first available information) is given as 50—60 km; whereas the corresponding figures for the period when ditching was most intensive (1920—1940) reach 4 000—8 000 km (Fig. 1).

From Great Britain, for example, there are reports of forest cultivation on peat lands in the first half of the 18th century (Zehetmayr 1954, p. 5).

It was first at the end of the 19th century that forest drainage and forest cultivation became significant in extent here in Sweden (see Lindberg 1956; Lundberg 1914, 1926; Malmström 1942, 1946; Olofsson and Nordlund 1898). This means that at most there is experience only of one tree generation on drained peat land. Melin (1917) has come across a forest drainage scheme from 1830, which was, however, intended to provide land for cultivation. This was soon abandoned and the land became forested.

Once forest drainage had commenced it was stimulated by the very marked positive effects which it often had on tree growth. At the end

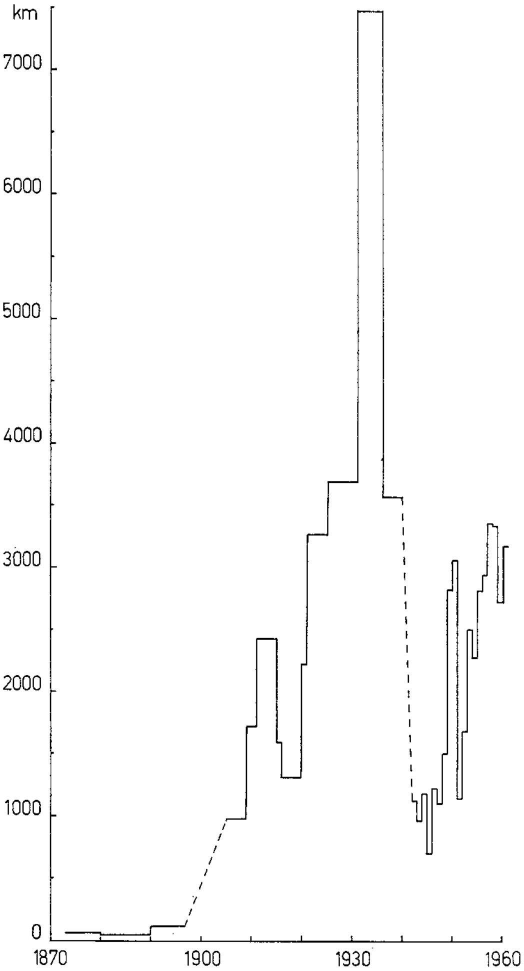

Fig. 1. The length of forest ditches dug in Sweden 1873—1960 according to official statistics. The height of the columns represents the yearly average for the different length periods.

of the 19th century interest in various ways of increasing the growth rate of forest trees heightened because of the rising demand for wood products and wood pulp.

Fig. 1 shows the development of forest drainage, and the violent fluctuations to which it has been subject. Up to the time of the first World War there was a steady increase in the total length of the ditches which had been laid down. This was interrupted by the war, after which the increase continued again, at first caused by the measures introduced in the 1920s to combat unemployment. The world economic crisis at the end of the 1920s and beginning of the 1930s is reflected by the colossal increase in forest drainage at that time. This was a consequence of steps taken to decrease unemployment. With improvement in the economic situation and a changed view of forest management there followed a period of continuous falling-off in the amount of the drainage undertakings completed. The minimum was reached during and directly after the second World War, but after this, with some interruptions, there has again been an increase, so that during the 1950s about the same level of drainage activity has been reached as that of the 1920s. This has probably to a large degree been caused by the extensive mechanization which is developing in forestry, and which has made ditch-digging very much easier, but which, on the other hand, has meant that areas which are less suitable for ditching have been used.

During the period 1873—1960, a total of at least 115 000 km of ditches has been laid down, according to official sources of information. On the basis of 6 hectares area drained per km length of ditch, the measure usually adopted in practice, the total area of forest land gained is 650 000—700 000 hectares, i.e., an area equivalent to the whole of the county of Stockholm or about 3 per cent of the country's total area of forest land. For comparision it may be mentioned that in Finland, "the world's most mire-rich country" (Sjörs 1956, p. 179), where 32.6 % of the area is mire (Tirkkonen 1952)—12.6 per cent of the area of Sweden is mire (AöS)—111 000 km of ditches were laid down between 1900 and 1950, calculated to have given 750 000 hectares of forest land (Tirkkonen 1952). In Finland forest drainage has continued with increased intensity so that the drained area in 1961 is estimated at 1.4 million hectares and the annual increase at 110 000 to 130 000 hectares (Heikurainen 1961).

But in spite of all the labour and capital which has been invested in forest drainage, on numerous occasions the result has been far from as successful as has been expected, even when the water run off has been satisfactory. Various aspects of this problem have been treated at different times. Hesselman (1906, 1910) was the first in Sweden to consider systematically some of the habitat conditions important for forest growth in relation to drainage of peat land. Among other things he studied the frost heaving of the tree seedlings.

Melin (1917) collected the experience which had been gained up to that time. Because of the great and one-sided emphasis on the significance of thorough drainage, without taking nutritional factors sufficiently into account, this paper gives a very biased picture of the relations between vegetation and habitat. Neither did Melin's ideas agree with the experience gained by "peat societies" in connection with the agricultural trials made on drained mires. The impression was given that there remained many unsolved problems in the use of mire land for forestry.

In Scandinavia it was not before 1935, in a paper by Malmström, that sufficient emphasis was laid on the fundamental significance of plant nutrients. Malmström (1935) showed, with the help of an older experiment by V. Ålund, who added wood ashes to a nutrient-poor, well-drained peat land, that good and persistent tree production could be supported by an otherwise barren *Trichophorum caespitosum* mire, if a comprehensive nutrient source was provided. In Central Europe and in Great Britain, more or less refined experiments in which nutrients had been added to peat land had already been carried out (see, for example, Zehetmayr 1954, p. 67).

Refering to Malmström's investigation, Björkman (1941) discussed the development of mycorrhiza and its significance for the uptake of nutrients by trees on ash-fertilized and non-fertilized parts of a mire. After Ålund's successful result, there have been more and more experiments on the nutrient supply of trees, and the methods used have been more and more refined.

But there are still many unsolved problems about the relation between a plant and its habitat. The significance of regulating the water table to a level suitable for trees has already been pointed out. A good drainage is a primary and essential requirement if a mire is to be used in rational forestry practice. Next to this, nutrient supply is the question to be considered, but for unfertilized peat information is scanty. Without anticipating the discussion of this topic (parts II—III), it may be pointed out that we know too little about the relations between forest productivity and reserves of plant nutrients in the soil, or about the position of the lower limit for total amount per unit area or concentration per unit volume of the various plant nutrients, for tree growth in general under natural conditions. We can also reformulate the problem and say that we have no suitable means to express the results of chemical analysis, etc., to define these properties with greater precision.

Chapter 2. Some of the terms used in studies of peat land

Because of their artificial nature, mires which have been drained for forest cultivation, take a place which is not clearly defined in scientific terms. Their more or less successional plant communities have points in common both with the mineral soil plant communities and with the original mire.

It seemed logical to proceed from the study of mires in general, and to use expressions put forward by certain groups of biologists. These terms often consist of words of common usage which have been defined more precisely. Among several schemes, the terminology used at the Institute of Plant Ecology at Uppsala University has been adopted.

The term 'myr' (mire) is used as a collective designation for peat land with its vegetation. There are two subdivisions, 'kärr' (fen) and 'mosse' (bog). Through work by Du Rietz (1933, 1949, 1954), Osvald (1937), Thunmark (1940, 1942), Sjörs (1946, 1956), etc., the terms 'kärr' and 'mosse' have been defined and distinguished on the basis of the differentiation of the vegetation on either side of the 'fastmarksvattengränsen' (mineral soil water limit) (Thunmark op. cit.) or the 'kärrväxtgränsen' (fen plant limit) (Sjörs 1946, p. 14). In later work Sjörs (1961b, 1963) has treated this subject in full detail. The boundary is thus drawn partly on the basis of the occurrence of the mineral soil water and partly on the type of vegetation on both sides of the boundary. In practice the differences in the vegetation are usually the only basis for drawing the boundary, although Malmer (1962a, pp. 42—43) claims that the two subdivisions be defined directly from the presence or absence of mineral soil water.

Parts of a mire which are cut off from the mineral soil water supply are called 'mosse' (bog) whereas other parts are called 'kärr' (fen). In those parts of the country where typically-formed bogs, according to this definition, are numerous and often cover a large area (i. e. the southern and central provinces of Sweden with extensions into Västerbotten and Jämtland) it is usually not difficult to make such a distinction.

The term 'mosse' (bog) was used in a wider sense by Malmström (1923, 1925, 1928, 1935, 1937, etc.), Melin (1917), Almquist (1929) etc., and by most British and American authors (see Gorham 1957, Heinselman 1963), but this has not been adopted here. In consequence, the usage of the term 'kärr' (fen) has been wider than in the quoted work. When these authors are cited the terms are naturally used in their original sense. Sjörs (1948, pp. 46—60) gives a more complete discussion of the concepts and terms used in the study of mires.

Using the terms bog and fen as defined above, the term 'myr' (mire) may now be examined more critically. The question to be answered is: what are the required characteristics of an area to be given this name? Obviously a mire is in most cases an area covered by peat. But the concept cannot be defined so simply, although the formation of a peat layer is important. It is therefore relevant to consider critically the term 'torv' (peat) as well as 'myr' (mire).

An unusually broad interpretation of the concept 'peat' has been put forward by Du Rietz (1945), who considers that peat comprises both the material of which mires are built up and the superficial wholly organic material on top of mineral soil profiles (see also Nilsson 1902, p. 132 and Stålfelt 1960, p. 149).

An example of an older definition is put forward by Zailer and Wilk (1907, p. 190), who cite an earlier definition by Weber, namely that peat is "ein aus abgestorbenen, zellulosareichen Pflanzen ... durch ... Vertorfung entstandenes, in Berührung mit Luft braun oder schwarz gefärbtes ... organisches Mineral, dessen eigentümlichen Färbung auf seinem Gehalt an Ulmin beruht". However, such a definition is not especially satisfactory because, for example, peat is not a material which is particularly rich in cellulose. It often contains mostly lignin, hemicelluloses, etc. (see for example Waksman and Stevens 1928). In addition, ulmin is not a well-defined substance.

Malmström has used the mode of formation and qualitative properties as the main features for characterization of peat (1923, 1928). He wrote, for example (1928, p. 340; transl.), "in water or on wet ground, more or less porous soil types, which consist mostly of humified plant remains". An area covered by this soil type is then called peat land ('torvmark').

Sjörs (1961a) now emphasizes that peat, in contrast to mor and mull, is characterized by accumulation (at least potentially). "Humus accumulated as growing deposits in wet sites is regarded as peat (although accumulation of peat can be interrupted, so the deposits are not always growing at present). The other types of humus do not accumulate after equilibrium between deposition and decomposition is reached, except on certain sites in very cool or wet climates, and are developed on terrestrial (or semi-terrestrial) sites" (op. cit. p. 8).

From a purely pedological point of view, Gjems (1962, p. 112;

transl.) writes that "we speak of organic soil or peat when the content of organic material in the uppermost 30 cm of the soil profile exceeds 40 %".

It is, however, surprising that often very little or nothing is mentioned about the fact that the formation of peat to an overwhelming degree goes on in the complete absence of air, although this is generally known and has been described in different contexts (Stålfelt 1960, p. 149). The turnover in the humus layer in mor and mull usually takes place in fairly well-aerated conditions, whereas in turnover in peat an anaerobic state prevails or gradually develops (see Lundberg 1914, p. 10; Malmström several papers; Sjörs 1956, p. 67; Stålfelt 1960, p. 162).

There are also various opinions about the meaning of the terms 'myr' (mire), and peat land. Complications arise because the terms mire and peat land ('myrmark, torvmark') may be used as synonymous (e.g. Osvald 1937, p. 65) or not synonymous (e.g. von Post and Granlund 1926). However, it is mostly the interests of the author concerned which determines the precise interpretation.

In a paper by Weber (1908) it is pointed out that the term mire (Moor) has changed from a purely botanical concept to a geological one, and that a mire consists of an extensive area "das mit einer im entwässerten Zustande mindestens 20 cm dicken Humusschicht bedeckt ist" (op. cit. p. 91). He considers the geographical quality of the mire, besides the feasible introduction of drainage.

Cajander (1913), who considers both the geological and biological sides, says concisely "Geologisch sind die Moore natürliche Lagerstätten von Torf. Biologisch stellen die Moore torfbildende Pflanzenformationen dar" (op. cit. p. 7). Later in the same paper he adds to this definition with a comment about the forest biology: "Ein gutgewachsener Wald ist forstlich wie biologisch Wald und nicht Moor, die Torfschicht mag mächtig sein, wie sie will, und ein Moor, dass nur mit Krüppelföhren bestanden ist und das auch sonst alle biologischen Eigenschaften des Moores zeigt, ist forstlich wie biologisch ein Moor, wie dünn die Torfschicht auch sein mag" (op. cit. p. 8). This definition is satisfactory and is also generally comprehensive in the context of forestry.

Sjörs (1948, p. 46, and in his textbook, 1956, p. 163) points out that the term mire refers both to the plant community and to the substratum and thereby also covers the geographical viewpoint (see also Faegri 1935).

In a paper by Du Rietz (1954, p. 571) is written: "Das Moor umfasst somit nicht nur das von seiner heutigen Organismenwelt und dessen leblosen Jetztzeitumwelt zusammengesetzte Gleichgewichtsystem oder Ökosystem, sondern auch die subfossilen Rückstände der früheren Entwicklungsstadien dieses Ökosystems."

It is obvious that for a practical definition of peat land or mire the thickness of the peat layer has been of great importance (see Weber 1908). Lende-Njaa (1917, p. 12) stated that mire is the name given to a soil layer at least 20 cm in depth which consists mainly of more or less humified plant remains. Løddesøl and Lid (1943) say that the least thickness of the peat layer—apart from the plant cover—is 20 cm in a drained state or 30 cm in undrained state for an area to be characterized as mire.

Granlund, who was concerned with the practical requirements relevant to the peat land survey in south Sweden (von Post and Granlund 1926) considered that peat land ('torvmark') is a mire ('myrmark') with a peat layer of at least 40 cm (Granlund 1932, p. 8). Mire is in turn distinguished by vegetation adapted to high soil water content, etc.

From the above account it is apparent that only to a very limited extent is there a terminology which is suitable also for drained and forested peat land. Only Cajander (op.cit.; see also Faegri 1935, p. 3) gives recommendations about its use under these special conditions. In recent Finnish research, however, most types of mires have been classified according to various classes of potential forest growth (Heikurainen, Huikari, Sarasto). This classification is in the main based on Cajander's fundamental work.

However, in order to attain the consistency in presentation, which was considered in the introduction to this chapter to be desirable, there will be an attempt to use the term mire mainly in the plant sociological sense. The mire is (or was) characterized by a certain combination of species of plants distinguishing the environment. In the present context the topographical meaning is of secondary significance. The term peat land, on the other hand, is applicable to a peat-covered area as a geological site and also, more generally to a geographical phenomenon. This means that, in principle, Jägarmossen is today a peat land and the term mire is not applicable to it, except for a very small area. However, when the condition before drainage is considered the term mire, as well as peat land, can be applied to the whole of the investigated area.

Chapter 3. General description of the area

A. Geography and geology

Jägarmossen consists of 45 hectares (110 acres) of afforested peat land drained a good 40 years ago. It is situated in the eastern part of Uppland, about 60 km (37 miles) NNE of Stockholm and 50 km (31 miles) ESE of Uppsala. In the new series of maps 'Topographical map of Sweden', scale 1: 50 000, sheet 11 I Uppsala NE, it is shown 3.5 km (2.2 miles) NE of Rimbo church. The peat land is bounded here by the 35 m (115 ft.) contour and by main road no. 280.

This part of Uppland (Roslagen) is only slightly hilly with low forested morainic slopes, between which lie some lakes and clay plains used for arable cultivation. The highest point in the area is ca. 50 m (165 ft.) above sea level and most of the lakes are at 15—25 m (50—80 ft.). There is little variation in height; in 'Atlas över Sverige' (AöS) it is classified among the landscapes with least relative relief of land surface, i.e. ≦ 25 m (82 ft.). As a rule such a landscape has only few lakes but in Roslagen lakes are fairly numerous (see AöS), and the number was formerly even larger (von Post and Granlund 1926).

The geological substratum is made up of granite of the Stockholm granite type, but Archaean granites and Svionian veined gneisses are found in the immediate vicinity. With regard to the fertility characteristics of these rock types, they are classified in quality group Bc in J. Eklund's scheme of classification (AöS), i.e., the second poorest group in capacity to provide plant nutrients. However, in clay-rich areas the fertility is in general hardly affected by the bed rock, although in those moraines which are poor in clay it has a considerable significance.

In the forested area the layers above the bed rock are formed to a large extent of large- and rich-blocked glacial drift, which at least on and near the highest parts is very tightly packed. The glacial till is mostly gravelly to sandy, but in small areas distinctly finer-grained fractions can dominate, as is the case in the area directly south of Jägarmossen where silty to clayey till occurs (Table 1).

The relief of the landscape is somewhat sharpened by two eskers which cut through it in a north-south direction. The easternmost, Lohärad's esker, stretches for a considerable length, whereas the other, on which part of the main road runs, is rather flattened and indistinct in form. There are also a number of terminal moraines,

Table 1. Mechanical analysis and various chemical properties of the glacial till sampled at five points in the neighbourhood of Jägarmossen

Particle size mm	Name	Percentage composition				
		1	2	3	4	5
<0.002	Clay	2.5	4.8	4.7	4.9	20.2
0.002— 0.006	Fine silt	0.9	0.7	2.1	1.8	8.0
0.006— 0.02	Coarse silt	4.6	2.8	4.5	4.0	11.1
0.02 — 0.06	Very fine sand	9.6	6.9	11.4	9.0	16.1
0.06 — 0.2	Fine sand	14.5	16.1	17.9	9.9	11.6
0.2 — 0.6	Medium sand	18.8	16.3	15.1	15.0	12.3
0.6 — 2.0	Coarse sand	14.7	15.1	11.2	18.3	6.8
2.0 — 6.0	Fine gravel	14.6	15.0	15.7	15.6	9.2
6.0 —20.0	Coarse gravel	19.8	22.3	17.4	21.5	4.7
Loss on ignition %		0.9	1.7	1.1	1.3	2.6
pH		5.3	5.3	5.1	6.0	5.6
P %		0.07	0.03	0.04	0.03	0.02
K %		0.16	0.16	0.19	0.16	0.41
Ca %		0.34	0.28	0.38	0.42	0.44

arising from small oscillations during the retreat of the ice cover, collected in the area directly north and northeast of Jägarmossen. Geo-chronological investigations have shown that the retreating inland ice left the area about 7700 B.C. (AöS).

According to Lundqvist's (AöS 1953; 1958) classification of the soil type regions of Sweden, the area lies in Uppland's clayey till region (see Lundqvist 1958, p. 72), which implies that clayey tills occur extensively. From his description it can be seen that the finest-grained material in these clays comes from the Cambro-Silurian rocks in the Gulf of Bothnia, the dispersed products of disintegration of which are known to cover large areas of east central Sweden. However, the lowest investigated layer of the till soil profile shows, at the most, only moderate values for calcium content (Table 1). The samples were taken at 65—75 cm below soil surface; very likely the leaching of Ca which has taken place since the land rose above sea level has reached a greater depth. The pH lowering which has accompanied this leaching of calcium has been estimated for the surface, as 1—2 units (Sjörs 1956, p. 70). However, the comparatively short time (4 000—5 000 years) since the emergence of the area from the sea and the fairly low precipitation, imply that leaching and acidification are likely to be relatively moderate. In the marine glacial clay, the 'glacialmergel' (marl), the calcium content is constantly high at a certain depth, as shown by a number of old analyses (Svedmark 1887, p. 59). His sample from arable land about 1.5 km south of the area contained 9.13 per cent calcium carbonate, and another taken directly west of the area at 1 m depth contained 6.13 per cent. These contents in the clay are 5—10 times higher than those which were now found for the moraine slopes adjacent to Jägarmossen, but which were derived from a somewhat shallower level (Table 1). Post-glacial clay is 'lime-free' (op. cit. p. 60).

Troedsson's (1955) analyses of surface water and ground water from the lowlying Grenholmen region (ca. 30 km in an ENE direction) show high Ca contents in the ground water as compared with the surface water. In addition, there are determinations from the same area of the position of the 'lime limit' in the soil profile at heights up to 20 m above sea level, i. e. in areas considerably younger than Jägarmossen (33 m). The 'lime limit' is said to vary between 1 and 10 dm below surface (unpublished data by Almberger and Mattson Mårn 1946, and Eriksson and Haglund 1948).

B. Climate

In spite of its fundamental importance in the development of mires only some of the more general features of the climate—mainly from AöS—will be mentioned here. The area is too small to show any macro-climatic difference, and except for micro-climatic effects of the forest cover, etc., climate can be considered to be constant as a set of ecological factors. However, detailed information on the surplus of precipitation over evapo-transpiration, expressed in terms of annual run-off of water, would be of great value. Because of the extensive technical installations needed, it has not been possible to make such determinations. The map recently worked out by O. Tamm (1959) gives general information in this respect. The 'humidity value', i.e. the difference between the mean annual precipitation and the mean annual evapo-transpiration, the latter computed from a formula derived from all available relevant run-off measurements, is somewhat less than 200 mm (op. cit. p. 37). However, conditions on the drained mire may deviate considerable from average figures (Heikurainen, verbal communication).

The mean annual temperature is given as + 5 to + 6° C. In the coldest month, February, the temperature is — 3 to — 4° C; and in the warmest, July, about + 16° C. Spring (0 to + 10° C) lasts about 65 days; summer (> + 10° C) 115 days; autumn (+ 10 to 0° C) 65 days; and winter (< 0° C) 120 days. The number of frost days is about 140. Annual precipitation reaches somewhat more than 500 mm, of which less than a quarter falls as snow. The duration of the snow cover is about 110 days. The driest months are February and March, with monthly precipitation 20 mm, and the wettest is August, with monthly precipitation somewhat more than 80 mm. During the "vegetation period" (≧ 3° C, according to AöS) of about 200 days, there is about 250—300 mm precipitation.

C. The main features of the origin and development of Jägarmossen

The factors which to a large degree determined the development of the peat lands of the region, as well as those of east central Sweden as a whole, are a comparatively low precipitation, a fairly high temperature during the vegetation period, and not least, the considerable original lime content of the soil.

In the large peat land inventory which was made in the 1920s in south and central Sweden, part of the results of which are given by von Post and Granlund (1926), Jägarmossen is placed in Svealand's low-lying former lake area. In this area the main part of the peat land has arisen through filling-in of shallow lakes by sediments and vegetation. In the system of classification which was developed at the same time, the area is a topogenous peat land type (op. cit. p. 63), i.e., a type which is completely dependent for its formation and development on its position in the terrain.

The type of formation of these peat lands means that they have a schematic pattern of development, the details of which are modified mainly by nutrient availability in the peat-building plant communities and by fluctuations in waterlevel (Ingmar 1963). The main features of a vertical profile in such an area show how the different layers of lake sediments and peat succeed one another, and the changing water and nutrient availability can be deduced from the type of vegetation from which the peat layers were formed. The peat which is poorest in nutrients is nearest the surface; in the central parts of some mires it may even be ombrogenous (Weber 1909, p. 8), i.e., formed from vegetation whose only source of nutrients is the atmosphere. Under this are successive layers formed from fen type vegetation, and under these are the sediments (mainly various sorts of gyttja soils) which were originally deposited in the lake, resting on the lake bottom made up of mineral deposits (clay, sand, glacial till, etc.) or occasionally rock. Instructive examples of stratigraphical types can be found in Weber (1908) and, in particular, in von Post and Granlund (1926). The profiles found in Jägarmossen are of the type just described and will be dealt with in more detail in Ch. 7.

Topographically, Jägarmossen consists of the lower parts of a spoon-shaped depression with the outflow towards the east. The passage out of the depression lies at about 33 m above sea level.

Granlund (1931, p. 21) has given curves for the land uplift in the Uppsala region. However, he (op. cit. p. 48) has shown that the salt water boundary for Uppsala lies about 25 per cent higher than for Stockholm and about 20 per cent higher than for the parish of Skederid in Roslagen, not far from Jägarmossen. Provided the rate of land rise after the Litorina maximum was proportional at Uppsala and central Roslagen, then the time of cut off from the sea would have occurred about 4 500—5 000 years ago.

The catchment area of the peat land is comparatively small because the topography is only slightly hilly. Its extent can be estimated from the topographical map as 220 hectares (544 acres), so that the approximate ratio between peat land and catchment area is 1: 5. Available aerial photographs do not allow greater precision.

D. The recent developmental history of Jägarmossen

In practice, the only way to find out more about the recent history of the area has been the study of the maps available.

1. Old land survey maps from 1705 and 1732
2. Ordnance map, sheet 85 Norrtelge from 1879, revised 1936
3. Sweden's geological survey, sheet Norrtelge from 1884—85
4. Topographical map of Sweden, sheet 11 I Uppsala NE from 1957
5. Aerial photographs from 1945, 1950 and 1959
6. Forest maps from 1912—13, 1921, 1924 and 1958
7. Work-map from 1927

On the oldest examined document about the Ekebyholm property, the land survey maps, Jägarmossen is very summarily shown, but under the more expressive name 'Hägermåssen' (Heron bog). 'Kåhlbylemåssen', situated ca. 1 km to the north, has been given with more details of its physiognomy. Since this area of peat land is in principle formed in the same way as Jägarmossen and in addition was mapped by the same man in the same year, it is permissible to make a comparison between the two areas. It is said of the part of Kolbylemossen which corresponds to Jägarmossen in the way it is drawn, in descriptive notes with the 1705 map, that "the open fen is very wet and has pine, birch and willow growing there. It gives 27 loads (of hay)"/transl./. Of the immediately surrounding parts it is said that "the meadow has trees and willow growing there" and finally of the central part that this consists of "an open, wet bog". It is probable that a hay harvest has also been obtained from parts of Jägarmossen, but if this is the case one wonders why it was not mapped more carefully, with the hay-producing fen communities shown specially. Information about its capacity for production of cattle fodder would also have been expected.

The scale of the Ordnance map naturally does not allow the comparatively small units concerned to be shown in any detail. Jägarmossen and Kolbylemossen are shown only by the sign for low-lying, wet ground in general, together with signs for scattered coniferous trees.

The geological map has the interesting information that bog peat occurs mainly in only two localities on the whole of the Norrtelge sheet, one of which is in an area west of Sadelmakarekrogen (the Saddlemaker Inn) in the parish of Rimbo; this is Jägarmossen.

Neither the economic map of 1907 nor a revision of the Ordnance map sheet in 1936 contribute anything further to the picture of the development. The new topographical map of 1957 shows only the final stages of the disappearing mire. Only the courses of the ditches, in an area of forest otherwise shown as homogeneous indicate the character of the land.

The aerial photographs available for the area have to some extent been utilized in field reconnaissance. However, the period in which aerial photographs of this area have been taken is only ca. 20 years, so that the possibility of making comparative studies of the course of plant colonization is limited, although structural changes in the density of the tree stand show up very clearly. It can be seen how the network of ditches becomes more and more hidden by the growing forest which gets progressively denser. An evident shift in the proportion of different tree species now takes place in Mjölnar fen, i.e., the south and west edge of the area.

Much better evidence is obtained from the forest maps. On the forest map of 1912—13 separate details in the appearance of the mire begin to be apparent. Only a very small part of the peat land at this time consisted of productive forest land (the part corresponding closely to that now called Långholmen, between Mjölnar fen and the central *Ledum*-pine wood). There had been no ditching at this time. On the map the main part of the peat land had the sign for marshy ground, but the central pine bog and the peripheral fen communities were well distinguished. This map was later used as a basis to show the new condition which had developed by 1921. The ditching important for the development of the mire had then been going on for three years, and the still sparse network began to be apparent.

In 1924 a completely new forest management map of Ekebyholm's common forest land was made. The ditch network had been completed in 1922 and the whole of it is shown on this map. The power line, used for orientation subsequently, had also been erected. The trees had been classified into different stands according to productivity, age and species composition; however, only Långholmen had such a high volume of timber that a figure is quoted (30 m³/hectare). Thus, at this time other stands had a content of timber less than this, which is interesting in comparison with the present situation. In Mjölnar fen (Mjölnarkärret, Fig. 2), named for the first time, production was then at an incipient stage, since its age class was given as 1—5 years and the only tree species were black alder and birch.

The most recent forest map, from 1958, shows the intense development undergone by the tree stand in the intervening period. All parts of Jägarmossen are now classified as productive forest land, with a timber content varying between 130 and 255 m³/hectare for the various stands.

Finally, the map which has been most important and most used for the field work must be mentioned. This is the work-map, scale 1: 4 000, of peat land only, made in 1927, and intended to serve as a basis for a broad investigation of the conditions for production in the drained area. This is a good map and together with the descriptions of habitat and vegetation made a few years later it gives an excellent picture of the conditions which obtained at that time.

As far as one can judge, from this examined map material the area has undergone lasting changes only in the last 40 years. Before this, grazing and to some extent hay-harvesting had probably taken place, but in general these had no great effect on development. In contrast, the drainage carried out in 1918—22 abruptly and profoundly changed ecological conditions, vegetation and potential of forest production toward a state, in many respects similar to, although not identical with that of a forest on mineral soil.

Chapter 4. The vegetation

A. The aims and methods of the investigation

In descriptions of Swedish vegetation, the vegetation of drained mires and the changes in connection with drainage have attracted little attention as a subject for detailed analytical study. This type of vegetation is therefore generally little-known in many respects. A critical survey of published work in this field shows that there has hardly been a single publication in the last 25 years. However, in foreign forestry literature there have been some more recent authors. In Finland Lukkala (1937, 1951) and Sarasto (1951, 1952, 1957 and 1961) and many more, in Switzerland Grünig (1955). It is, however, characteristic of these works, with the exception of Lukkala (1951), that the vegetational studies have commenced a long time after the draining; so that, at the best, only the main features of the original plant communities can be reconstructed (see further Ch. 5).

One of the purposes of the present investigation is to give a detailed description of the vegetation characteristics of a piece of forested peat land in east central Sweden, which has been drained for at least 40 years. The description includes a classification of the present vegetation, with special treatment of certain elements of the flora (the woody species), together with an attempt to analyse the vegetational succession after drainage.

There are now many different well-developed methods available for the detailed study of vegetation. In numerous plant sociological publications in recent decades, the same principle has been applied, in the main, to the studies of the composition of the vegetation, viz., a floristic survey of a number of small squares within the frame of a larger area, in a homogeneous plant community. Work of Arnborg (1943), Albertson (1946), v. Krusenstjerna (1945), Julin (1948), Sjörs (1954, etc.), Steen (1954) may be cited. Du Rietz (1921, 1930 etc.) discusses the fundamental principles.

For choosing the sample area and the size of the sampling quadrats, the structure of the community to be studied must be taken into account. For example, a lichen community on a rock substratum requires a much smaller area than a forest plant community (Du Rietz 1921; Ellenberg 1956).

The vegetation analyses presented here have been made using 10—20 (1 m^2) quadrats within sample areas (numbered Jm 1—Jm 12) of 800—1 700 m^2 (Fig. 2), with the aim that the quadrats should represent "the whole of the range of variation of the community in the locality". Some of the species-rich communities are very difficult to describe with only a few small quadrats. In the tree layer there may be a high degree of homogeneity, while the vegetation of the field layer is very uneven. Thus species which have escaped analysis, and are given as "other species" in the tables, may constitute a large share of the total number of species in the sample area. But when only just over 50 per cent of the total number of species in the area is represented in the quadrat analysis (as for sample area Jm 5) this indicates an unusually wide scatter of the species in the community. According to Dahl (1956, p. 29) this may be explained by ecological differences within the area: "If ecological conditions over an area are uniform we would also expect that the vegetation would be uniform or homogeneous." The ecological factor which may operate in this special case is time (see below; grass-rich birch-spruce wood). The significance of the time factor for soil formation has been pointed out by Jenny (1941) in a factorial equation which has later been developed by Major (1951) to be applicable to vegetation.

The results of the vegetation analysis are usually given in tabular form, with each species occuring in the sample area recorded, followed by a symbol for the degree of cover and by the quadrat frequency of the species within the sample area. This is a presentation which in practice is only a repetition of the notes made in the field, but which gives an illuminating picture of the vegetation in the locality. Sjörs (1954, p. 35) has indicated a simple method for analysis of the data, by putting together in a single expression the species' frequency and the "average degree of cover" for the sample areas investigated or—if desired—for the plant community as a whole. In later papers this method of presentation has been used consistently, in a somewhat modified form (Persson 1961; Malmer 1962 a, b), and it undoubtedly has advantages if it is desired to obtain the maximum information about the characteristics of the community in a concise form. However its disadvantage, as pointed out by Sjörs (1954), is that the picture of the distribution of the species is naturally partly lost in this quantitative summary. That is why only primary vegetation analysis data are presented here.

In this paper the vegetation analyses are given in table form, according to current Swedish practice. The contents of the tables have been arranged in terms of the different layers in the vegetation; however the shrubs in the field layer have been given separately. Information about the composition of the tree layer is presented later, in the account of the production study. In cases where tree seedlings have been observed in the quadrats, the number is given under a special table heading. To express the degree of cover of the various plant species the 5-grade scale of Hult—Sernander—Du Rietz, which is now used as a pure cover scale in Scandinavia but originally referred to density or frequency in its lower degrees, has been adopted (see Du Rietz 1921, p. 223).

Scale of degree of cover (after Du Rietz 1921)

5 dominant	(at least half the surface area)
4 abundant	1/4 —1/2 — " —
3 scattered	1/8 —1/4 — " —
2 occasional	1/16—1/8 — " —
1 rare	less than 1/16

However, this scale, otherwise very convenient, has not always been completely satisfactory mainly because of its low sensitivity at each end. In some communities with *Oxalis* or *Maianthemum* in the field layer, and with *Lastrea dryopteris* in some places, and *Hylocomium splendens* or *Pleurozium schreberi* in the bottom layer, it is not uncommon that one of these species covers the ground completely. On the other hand, in *Oxalis* communities there are sometimes relicts of some of those species which formed part of the vegetation before or directly after drainage, e.g., *Carex elongata* and *Calamagrostis canescens,* but which are now represented by only one or two shoots per m^2. With the 5-grade scale, the first case is classified as grade 5, equivalent to complete cover of $^1/_2$—1 m^2 (instead of $^3/_4$— 1 m^2 in the Braun-Blanquet, 1951, p. 60, system, for example); and this is acceptable. But for the latter case grade 1 is appropriate, and this corresponds to a cover of up to 625 cm^2, although the species may actually cover 5—10 cm^2 at the most; and this is of more doubtful value. That more divisions of the cover grade scale are needed is shown by all the analysis data in which the figures for the degree of cover are supplemented with a + or —, in order to point out more closely the characteristics of the species (see Du Rietz 1921, p. 225; Dahl 1956, p. 45). In some cases the absolute cover values for the symbols (+ or —) have been intimated (Albertson and Larsson 1960, p. 357). In the present paper "+" is used in Ellenberg's sense (1956, p. 27) "spärlich und nur wenig Fläche bedeckend".

The plant sociological unit which has been found most suitable for the classification of the vegetation is the association, i.e., a community of moderately high rank, with several layers and based mainly on the qualitative species composition. The next smaller unit, the sociation, which is distinguished within the frame of an association only on the basis of quantitative differences (Du Rietz 1942, 1949), will also be used.

The divisions between the plant communities of Jägarmossen are far from being sharp; the transitions from one to another are often gradual and even, and of various widths. The boundaries are distinct between the dwarf shrub communities of the central peat land, but between the peripheral, herb-rich communities they are sometimes difficult to define.

One element of the work has been the estimation of the forest production in the various plant communities. Because of this it was occasionally difficult, in laying out the sample areas, to reconcile the plant sociological requirement for homogeneity in all the layers of vegetation (with the units now used) and the requirement for sufficiently large areas for an estimate of forest production. The principle for selection of the areas was that they should be representative both for various tree stands and for various lower-growing communities. It was originally desired that pure stands of pine and spruce

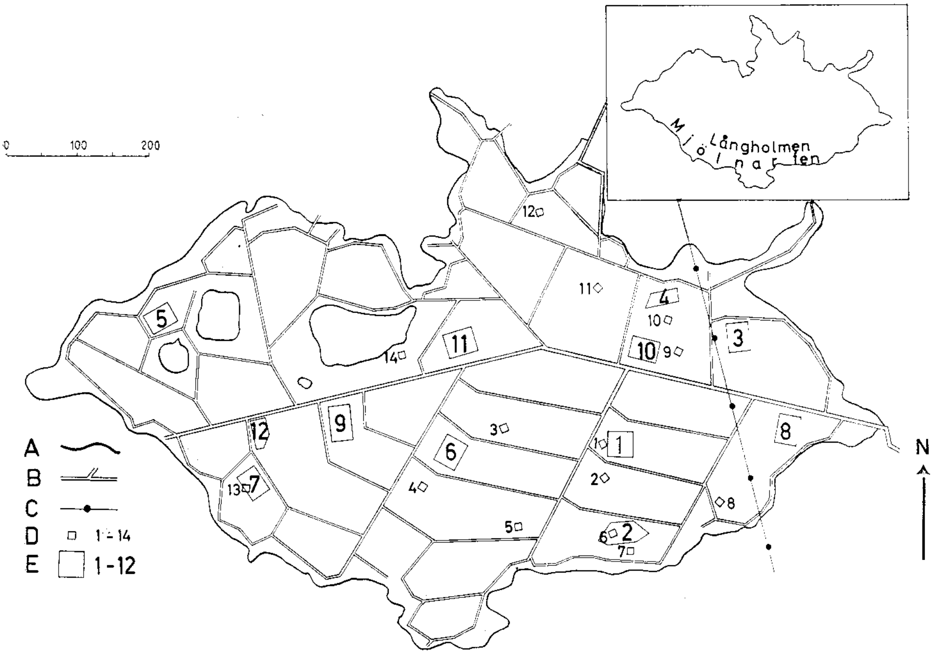

Fig. 2. Jägarmossen. Plan of the drainage system and sample areas.—A. Limits of the peat land. B. Ditches. C. Power line. D. Former sample quadrats (1—14). E. Present samples areas (Jm 1—12).

should be sought so that disturbing effects of other tree species would be avoided in the comparison of the amount of production in the different communities. However, it soon became clear that pure stands of only one tree species were exceptional in the vegetation of Jägarmossen, as has later also proved to be the case on the other drained peat lands which have been examined. The main subordinate tree is birch (*Betula pubescens*), or alder (*Alnus glutinosa*) in some places where spruce is the main tree species. The field layer and bottom layer of the vegetation are naturally affected by this, and the proportions of the various tree species have a significant influence on the composition of these layers. In the majority of the areas it has nevertheless been possible to reach an acceptable degree of homogeneity in all the layers of the vegetation.

The vegetation map has been based on the above-described method for the analysis of the plant communities together with a simple form of line survey (by compass measurements and pacing out) for drawing the plant community boundaries on the basic map. At the same time, information was obtained for the study of the distribution pattern of the woody species, etc. (Ch. 4.C.).

A special chapter will be devoted to the effect of drainage on the vegetational development, as deduced from the present vegetation and other known qualities. This chapter will include an attempt to describe the character of the vegetation of drained mires and the direction in which change takes place after drainage. There are no contemporary records to assist in the study of vegetational changes, but the main basis has been an old manuscript including a description of the vegetation conditions directly after the ditching. Since this chapter will be concerned with development up to the present time a certain amount of repetition of the vegetation description will be unavoidable.

Higher plant nomenclature follows Hylander (1955); moss nomenclature follows in the main Jensen (1939) and Nyholm (1954—1960).

B. The plant communities

Heath-forest communities

Pinus – Ledum – Pleurozium association (I. *Ledum*-pine wood)

One of the characteristic features of the vegetation of Jägarmossen is that the plant communities are concentrically arranged around the *Ledum*-pine wood situated in the middle of the area (Fig. 3). This community covers ca. 2 hectares (5 acres) of surface. It is easily distinguishable in its typical form, and well separated from adjacent communities. The maximum thickness of the peat there is 3 m. Down to a depth of 2 m it consists of low to moderately humified (H_2—H_5 by von Post's scale; von Post and Granlund 1926) *Sphagnum*- and *Sphagnum*-cyperaceous peat with *Scheuchzeria* increasing in amount downwards.

The permanent water table in the peat is 25—35 cm under the surface during the vegetation period, and it therefore hinders the downward penetration of the roots. (For other information about the water conditions, see part II.)

The association, from the point of view of forestry, has the least productive tree stand, with pine (Fig. 4) as the main tree species. The development of the pines from seedlings to the trees now about 10 m high has been virtually wholly confined to the period since drainage. In spite of the rather poor conditions they have grown relatively well (25 cm per year, on average) and have healthy green though comparatively sparse crowns. However, the two other tree species, spruce and birch (*B. pubescens*), show marked signs of sub-optimum conditions. The birches have a bushlike habit and during the vegetation period

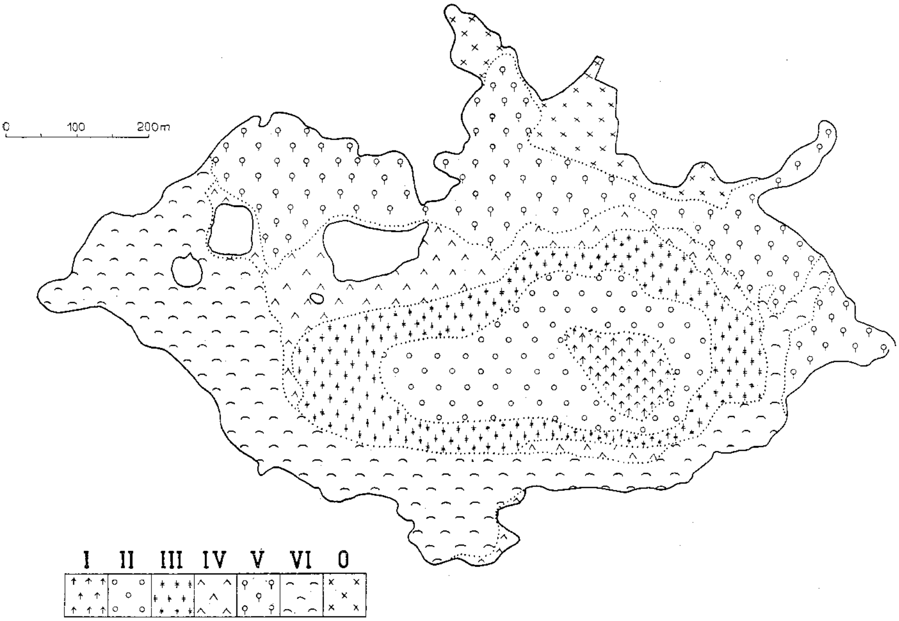

Fig. 3. Jägarmossen. Map of the vegetation.—I. *Pinus – Ledum – Pleurozium* ass (Type I. *Ledum*-pine wood). II. *Pinus – Vaccinium myrtillus – Pleurozium* ass (Type II. Bilberry-pine wood). III. *Picea – Maianthemum – Vaccinium myrtillus – Pleurozium* ass (Type III. Bilberry-spruce wood). IV. *Picea – Oxalis – Maianthemum – Brachythecium rutabulum* ass (Type IV. *Maianthemum*-spruce wood). V. *Picea – Oxalis – – Brachythecium rutabulum* ass (Type V. *Oxalis*-spruce wood). VI. *Picea – Betula pubescens – Calamagrostis canescens – Melica nutans – Brachythecium rutabulum* ass (Type VI. Grass-rich birch-spruce wood). O. A community with a very poorly developed field layer. This type is not phytosociologically investigated. See Ch. 5. "Others".

they have only small leaves which are often light green. Only exceptionally do they grow taller than 1½ m. The spruce are usually overgrown with lichens and sluggishly grown (annual increment in length 2—5 cm) and have short, yellow-green needles. They are seldom more than 1 m high. Their occurrence is exceptionally scattered; it was thus not possible to find a sufficient number (10) of individuals within the boundaries of the sample area (Jm 1) of 35 × 35 m for collection of needle samples for nutrient determinations.

The field layer (Table 2) is dominated almost completely by the shrubs *Ledum palustre* and *Vaccinium uliginosum*. In the spring, before *V. uliginosum* has leaves, *Eriophorum vaginatum* is an easily visible feature. *Ledum* usually occurs in small groups; it is luxuriant along the ditches. Of the other shrubs, *Vaccinium vitis-idaea* is important, but *V. myrtillus* is a recent arrival and is the only shrub not

Fig. 4. *Ledum*-pine wood (sample area Jm 1). Only pine in the tree layer; stand age ca. 40 years. The largest pine in the centre is about 12 m tall.—June 1960.

yet seen in flower. The abundance of *Lycopodium annotinum* is worthy of note. It can be seen in several places along the ditches. The absence of *Empetrum nigrum* is remarkable. Among other field layer species, *Luzula pilosa* may be classified as occasional in the community, but *Melampyrum pratense* belongs to the regularly occurring species. Because its diaspores are dispered by ants (see Sernander 1906), it can doubtless be expected to appear anywhere in the peat land, as the ant, *Formica rufa,* is very common.

The most important species of the bottom layer are *Pleurozium schreberi* and *Dicranum polysetum,* which both occur everywhere in the community.

The two commonest *Sphagnum* species are *S. magellanicum* and

Table 2. Vegetational analyses from the *Pinus* - *Ledum* - *Pleurozium* ass (Type I. *Ledum*-pine wood) and the *Pinus* - *Vaccinium myrtillus* - *Pleurozium* ass (Type II. Bilberry-pine wood). 20—21 July, 1959

Trees (number of seedlings)	Jm 1		F-%	Jm 6	F-%
Betula pubescens	- - - - -	- - - - - - 1 - - 1 1 -	18	- - - - - - - - - - - - - - - - -	0
Picea abies	- - - - -	- - - - - - - - - - - -	0	- - - - - - 1 - - - - - - - - - -	6
Pinus silvestris	- - - - -	- - - - - - - - - - 1 -	6	- - - - - - - - - - - - - - - - -	0
Dwarf shrubs					
Andromeda polifolia	- 1 1 1 1	1 1 1 - 1 1 1 1 - 1 1 1	82	- - - - - - + - - - - - - - - - -	6
Ledum palustre	1 - 1 2 3	- - 1 1 1 - - - - - 4 -	47	- - - - - - - - - - - - - - - - -	0
Vaccinium myrtillus	- 1 - - 2	- - - - - - - - - - 1 -	18	5 1 2 1 2 4 5 2 3 + 3 5 1 1 3 5 5	100
oxycoccus	1 - 1 1 1	1 - - 1 1 1 - - 1 + 1 2	71	- - - - - - - - - - - - - - - - -	0
uliginosum	1 2 3 5 2	4 3 3 4 4 5 2 4 4 5 4 1	100	- 1 - - - - 1 5 - 2 - - - - 1 1 -	35
vitis-idaea	1 2 3 3 2	3 2 3 3 2 3 1 2 1 2 1 5	100	1 5 1 1 1 1 1 2 1 5 3 2 5 - 4 1 3	94
Grasses and herbs					
Dryopteris spinulosa	- - - - -	- - - - - - - - - - - -	0	- - - - 1 - - - - - - - - - - - -	6
Eriophorum vaginatum	3 4 1 1 3	1 2 1 2 4 1 - - 1 2 1 1	88	- - - - - - - - - - - - - - - - -	0
Luzula pilosa	- - - - -	- - - - - - - - - - - +	6	- + - - + - + - - 1 - - - - - - -	24
Melampyrum pratense	- - 1 - -	- - - - - - - - - - - -	6	- - - - - - 1 - - - - 1 - - - - 1	18
Rubus chamaemorus	1 1 3 2 1	2 4 1 1 1 1 1 1 2 2 2 2	100	- - - - - - 1 1 - - - 1 1 - - - 1	29
Mosses and lichens					
Aulacomnium palustre	1 1 1 1 -	- - - - - 1 - - - - 1 -	35	- - - - - - - 1 - 1 - - 1 2 - - -	24
Brachythecium rutabulum	- - - - -	- - - - - - - - - - - -	0	- + - - - - 1 - - - - - - - - - 1	18
Dicranum polysetum	1 1 2 3 1	2 2 1 4 1 3 4 2 3 3 3 2	100	1 - 2 5 3 1 3 2 3 1 2 1 2 1 1 3 1	94
scoparium	- 1 - 1 -	1 - - - - - 1 - - - - -	24	+ - - - 1 - - 1 2 + 1 - 1 3 1 1 1	65
Hylocomium splendens	- - - - -	- - - - - - - - - - - -	0	- - 1 1 1 - - - - + 1 2 - 1 1 - -	47
Plagiothecium denticulatum	- - - - -	- - - - - - - - - - - -	0	+ - - - - - - - - - - - 1 1 - 1 -	24
Pleurozium schreberi	1 3 1 2 1	3 5 1 3 5 4 2 3 5 4 1 2	100	3 3 5 3 5 1 3 5 3 3 5 3 5 5 5 4 4	100
Polytrichum strictum	2 - 1 1 -	- 1 4 - 1 - - - 1 1 2 -	53	- - - - - - - - - - - - - - - - -	0
Ptilium crista-castrensis	- - - - -	- - - - - - - - - - - -	0	- - - + - - - - - - - - - 1 - - -	12
Sphagnum magellanicum	3 - - - 2	- - - - - - - - - + 3 1	29	- - - - - - - - - - - - - - - - -	0
parvifolium	4 5 5 5 5	2 2 1 1 1 1 - - 1 1 2 -	82	- - 1 - - - - - - - - - - - - - -	6
Cladonia cornuta	- 1 - - 1	1 - 1 - - - - - - + - -	29	- - - - - - - - - - - - - - - - -	0
deformis	- - - - -	- 1 - - - - - - - + - -	12	- - - - - - - - - - - - - - - - -	0
rangiferina	1 - 1 - 3	2 - 3 - - 1 1 1 + 1 + 1	71	- - - - - - - - - - - - - - - - -	0
silvatica	1 - - 1 1	2 1 1 - 1 - 1 + + + - 1	71	- - - - - - - - - - - - - - - - -	0

F = Frequency   Jm 1. the first group represents a Sphagnum parvifolium-rich variant.

Additional species (degree of cover 1 or +): Jm 1: Picea abies, Sphagnum fuscum. Jm 6: Betula pubescens, Deschampsia flexuosa, Eriophorum vaginatum, Ledum palustre, Quercus robur, Rubus idaeus, Trientalis europaea and Orthodicranum montanum, Sphagnum centrale, Cladonia silvatica.

S. parvifolium, whereas *S. fuscum* covers only a very small area (Table 2).

Ledum-pine wood is a community very poor in species of higher plants, and it is also characterized by a conspicuously constant species composition. Almquist (1929, pp. 274, 306) reported that the species occurring occasionally are very few, and that the number of species in the field layer is limited to 10±2 (see also Du Rietz and Nannfeldt 1925). On the basis of this information it is of interest to mention something about the very divergent vegetation which grows in and by the ditches in the area. Quite a large number of different higher plant species have come in here. These species have nothing in common with *Ledum*-pine wood in the limited sense, but belong to communities of another character altogether, which in all environments within Jägarmossen are very much more nutrient-rich than the *Ledum*-pine wood.

Alnus glutinosa	*Luzula multiflora*
Calamagrostis purpurea	*Milium effusum*

Carex appropinquata
elata
pseudocyperus
Filipendula ulmaria
Glyceria fluitans
Parnassia palustris
Potentilla palustris
Ranunculus repens
Salix pentandra
Viola epipsila

and about 20 other higher plant species which are "foreign" to the community.

Since neither the ditches nor the plant roots reach down to more nutrient-rich layers of the peat, the cause can only be the addition of nutrient-rich water from the mineral soil at the periphery of the area. This supposition is supported by the observation that ditches which lead directly from there are considerably richer in species than those which are at an angle to these, i.e., the ditches which link the main run-off ditches.

Put in its regional context, the association has a distribution which coincides with the occurrence of *Ledum,* at least up to south Norrland. It is common in Finland (Cajander 1913, p. 155), but is partly replaced by *Chamaedaphne*-rich types in the eastern parts of the country. The main distribution is in the more continental parts of Europe, such as Poland and Russia, and it has its equivalent in regions with a similar climate on the north American continent (Osvald 1937, p. 97; Sjörs 1963, p. 87 f.), although with black spruce replacing the pine. See also Harnisch's regional survey (1929, p. 22, 25) and Kulczinski's (1949, p. 77) treatment of the bogs of the Polesie basin.

The community has in Sweden been given various names, most of which have been quoted by Almquist (1929). In Osvald's book (1937) "skogshögmosse" (wood on raised bog) is used, a direct translation of the earlier used term "Waldhochmoor" (Osvald 1925, p. 711). Malmström (1928, p. 288) writes of slightly raised bogs, i.e. forest-covered bogs, of east Swedish type, in the same way as Tolf (1903, p. 99). In more recent work there is Du Rietz's *Ledo-Parvifolion* alliance (1949, etc.), a name used by v. Krusenstjerna (1945, p. 148) and others. Sjörs (1948), who came into contact with the association in the eastern parts of the area he was studying, used the term "*Pinus–Ledum–Vaccinium* moss ass."

These names show that the community has been distinguished and described on several occasions. This is of interest because the *Ledum*-pine wood is the only one of the plant communities of Jägarmossen with fully equivalent communities described from other localities. For the other Jägarmossen communities there are in general no complete equivalents in the literature, as will be shown later.

Ledum-pine wood lacks any connection with the communities on the mineral soil and may thus be regarded as a type specific for peat land, which however changes towards a heath type of pinewood with dwarf shrubs (see Ch. 5), when drainage has been very intensive.

Pinus – Vaccinium myrtillus – Pleurozium association (II. Bilberry-pine wood)

Bilberry-pine wood (Fig. 3) is characterized by pine as the main tree species, by a field layer which consists almost exclusively of various shrub species (but with *Ledum* only in very small amounts), and by a bottom layer exclusively of mosses, mainly *Pleurozium schreberi* (Table 2, Jm 6). Living *Sphagnum* occurs only in scattered patches, but as in *Ledum*-pine wood the peat is formed of *Sphagnum* species. The constituent species are the same as in the *Ledum*-pine wood, but in the bilberry-pine wood *Eriophorum vaginatum* was important in peat formation. Identification of the peat-building vegetation is, however, made difficult by the fact that there has been more humification in the surface layers than in the *Ledum*-pine community. As a rule it is $\geqq H_5$ in the von Post scale.

The surface layers of the peat are dark brown in colour and its consistency when dry rapidly becomes granular to powdery.

The thickness of the peat is 2 to 3 m in the bilberry-pine wood area. In this community the permanent water table in the peat would not be expected to be important in determining the depth of root penetration, since it is seldom as high as 40—45 cm below the surface during the vegetation period (see part II).

A good diagnostic species between *Ledum*-pine wood and bilberry-pine wood is spruce, which regularly occurs in the latter and even grows to trees. Towards the outer limits of the bilberry-pine wood, nearest the edge of the peat land, spruce may even form stands. *Vaccinium myrtillus* is also well-developed in the community and is usually dominant in the field layer.

This area of pine wood is closely parallel with Almquist's (1929, p. 307) *Vaccinium vitis-idaea* pine wood. However, *V. myrtillus* is at present so dominant an element that the name must reflect this. Besides, *V. myrtillus* shows many features characteristic of expansion, while *V. vitis-idaea* is clearly decreasing in the bilberry-pine wood. This doubtless depends to a large extent on the increasing occurrence of small spruces, with a shading effect. The inhibiting effect of a closed tree canopy on the field layer, particularly the shrubs, can best be shown by an example. The vegetation analysis in Table 3 is for an

Table 3. The influence of different degrees of cover in the tree layer on development of the vegetation in the field and bottom layer

	(1)											(2)									
Tree seedlings (number)																					
Picea abies	-	1	1	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	1	-	-
Dwarf shrubs																					
Vaccinium myrtillus	-	1	-	-	-	1	-	1	-	-	-	-	-	-	1	-	1	-	1	1	-
uliginosum	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	1	2	-	-	2
vitis-idaea	-	-	-	-	-	-	-	-	-	-	-	5	4	5	5	5	5	5	5	2	5
Grasses and herbs																					
Luzula pilosa	-	+	+	+	1	1	-	-	+	1	+	1	1	+	+	-	-	-	-	1	-
Maianthemum bifolium	1	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Melampyrum pratense	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Mosses																					
Brachythecium rutabulum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+	-
velutinum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dicranum polysetum	2	2	1	+	1	2	2	1	-	2	1	-	-	1	-	1	-	-	2	1	1
scoparium	-	-	-	-	-	1	1	1	-	1	+	1	-	-	-	-	-	-	-	-	-
Hylocomium splendens	2	2	2	4	1	1	3	1	4	1	2	-	-	-	-	-	-	-	-	-	-
Pleurozium schreberi	5	5	5	3	5	5	5	5	4	5	5	4	1	1	-	2	3	+	5	2	-
Pohlia nutans	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	1	-	-	-
Ptilium crista-castrensis	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	1	-	-
Rhytidiadelphus triquetrus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-
Sphagnum parvifolium	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
Lophocolea heterophylla	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-

Additions (degree of cover 1 or +): Eriophorum vaginatum, Ledum palustre, Quercus robur (seedling), Solidago virgaurea. (1) and (2) are sample areas 5 by 5 m^2, inside which quadrats 1 by 1 m^2 have been analyzed; distance between sample areas less than 10 m.

area not far from the boundary with the next association, and this explains the presence of *Maianthemum*.

The main difference between the analyses is that the first (1) is for a fairly closed stand where spruce is the main tree species and has a marked shading effect, while the second (2) is for a stand where pine is the main tree species. The light penetration is clearly greater in the latter, partly because of the somewhat sparser tree stand, partly because of the nature of the pine crowns, which allow more light through. The effect of this difference in conditions is remarkable. In the first case the field layer is almost non-existent, represented by single individuals of the species present. However, the bottom layer is well developed, with complete cover.

In the lighter part (2) there are luxuriant dwarf-shrubs which in turn seem to inhibit the development of the bottom layer. The presence of *Brachythecium rutabulum* and *Rhytidiadelphus triquetrus* in this heathy wood vegetation should be noticed.

However, it must be added that other causes may also contribute to the differences between the vegetation, although the light climate in this case is doubtless of great significance.

Because of the boundaries which have been drawn between the associations, the bilberry-pine wood is unavoidably of a somewhat heterogeneous nature. The unevenness is shown, for example, by the fact that the following sociations have been distinguished preliminarily during the field work.

a. *Pinus – Vaccinium myrtillus – Pleurozium* soc
b. *Pinus – Vaccinium uliginosum – Pleurozium* soc
c. *Pinus – Vaccinium vitis-idaea – Pleurozium* soc
d. *Pinus – Picea – Vaccinium myrtillus – Pleurozium* soc
e. *Picea – Vaccinium myrtillus – Pleurozium* (possibly *Hylocomium splendens*) soc

The last of these sociations (e.) occupies a small area on the boundary of the bilberry-spruce wood, but this has not been taken as a reason to include it there, since its connection with bilberry-pine wood is still obvious. Only a short time ago the tree stand was dominated by pine, but through the effect of felling the present spruce-rich stand has come about. As a result, the community has an indeterminate, intermediate sociological position, until it eventually progresses to a bilberry-spruce wood, probably with *Maianthemum* as a final stage.

The association is characterized by a clear relationship with the *Ledum*-pine wood. The similarity was probably even greater before drainage, when the whole of the bilberry-pine wood and the *Ledum*-pine wood was made up of *Ledum*-pine bog. The two communities are the only ones in which *Ledum palustre, Rubus chamaemorus* and *Eriophorum vaginatum* occur in noteworthy quantities (see Fig. 5) and, in addition, it is only in these communities that pine forms stands on the peat land (Fig. 14).

Almquist (1929, p. 307) has described a vegetation type which agrees quite well with that described here. He also pointed out that it developed from dried out or drained "tallmossar" (pine bogs), and he cites Melin's (1917) observations from the Gimo area in Uppland. A somewhat different form of the community occurs on a mineral soil substratum, and according to Almquist (1929), it is the province's most important pine wood type.

The dominants in the field layer vary, according to the composition of the tree layer. Under a sparse tree layer of pine the field layer is made up of *Vaccinium vitis-idaea* and *V. uliginosum;* whereas a more closed tree layer of pine and spruce is combined with *V. myrtillus* and *V. vitis-idaea;* and a closed tree layer mainly of spruce with *V. myrtillus* dominant. In this ring-shaped zone pine is dominant towards

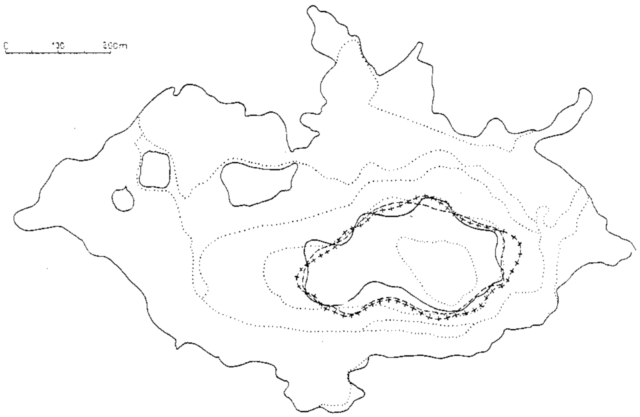

Fig. 5. *Eriophorum vaginatum* (— — — — —), *Ledum palustre* (————————) and *Rubus chamaemorus* (+ + + + +). These species occur within the indicated areas. Note how well the limits of distribution coincide with the pine wood area (Fig. 14).

the centre and spruce more peripherally. In the same way there is a gradient in tree height—low near the centre and increasing towards the periphery. In number of stems per unit surface area spruce is clearly predominant (sample area Jm 6), but in unit volume of timber pine is predominant, and less than $^1/_4$ of the total volume of the stand is due to spruce.

Birch (*Betula pubescens*) is also present in the tree layer (Fig. 6). Here and there, for example, birch branches touch pine crowns of 10—12 m height. There is a clear difference between birch growth in the *Ledum*-pine wood and the bilberry-pine wood, in that the boundary between the two is also the boundary between thin-stemmed or bush-forming birch and tree-forming birch.

Seedlings of spruce occur here and there, but most sparsely nearest to the *Ledum*-pine wood, except on the narrow lines of disturbed peat turves along the ditches. As a rule, there is a really good supply of seedlings where the peat has for some reason been bared through disturbance of the surface layer, i.e. on the peat turned up along the ditches and along roads and paths. Good seed beds are also formed in places with intensive deer trampling. The restricted supply of seedlings inside the stand is illustrated to some extent by the fact that seedlings occurred in only one of 16 sample areas of 1 m^2.

As in *Ledum*-pine wood, the field layer is characterized by quite extreme poverty in species. Within the community the dwarf-shrubs have a luxuriant, often tall, growth habit but fertility seems to be low throughout.

Fig. 6. Bilberry-pine wood (sample area Jm 6). Pine, spruce and birch in the tree layer, stand age ca. 40 years.—June 1960.

When spruce increases in frequency and in degree of cover a number of field layer species come in, first as scattered individuals, then more and more richly, e.g. *Deschampsia flexuosa* and *Dryopteris spinulosa*. *Calamagrostis canescens* begins to come in along the ditches. *Dactylorchis maculata, Trientalis europaea* and *Carex pilulifera* occur occasionally in the stand.

The increase in spruce also means that a number of species are no longer present in the species lists, e.g. *Vaccinium oxycoccus* and *Cladonia* spp. But it is not only a question of small qualitative and quantitative changes in the vegetation at the "spruce boundary". The main significance of the spruce dominance in the tree layer is perhaps that the impression given by the peat land vegetation as a whole is radically changed. In the *Ledum*-pine wood and the nearest parts of the bilberry-pine wood the vegetation has a clear mire-wood character, but nearly all the area lying outside this, i.e., the main part of the peat land, gives an undoubted impression of forest on dry land.

The constant species of the community, in 1 m^2 quadrats, are for higher plants only *Vaccinium myrtillus* and *V. vitis-idaea,* and for mosses—as in the *Ledum*-pine wood—*Dicranum polysetum* and *Pleurozium schreberi.* All other species have only a moderate or small quadrat frequency. It is possible that the frequency of *Hylocomium splendens* has been somewhat underestimated. However, its degree of cover only exceptionally attains high values in this association (see Table 2).

Certain species in the community are of an obvious relict type. In its peripheral parts the good tree growth and scattered occurrence of broad-leaved herb species gives a general impression of greater luxuriance, which indicates the occurrence of an environment considerably richer in nutrients than that in which the following species are normally found, here regarded as relict bog species: *Andromeda polifolia, Ledum palustre, Eriophorum vaginatum, Sphagnum parvifolium* and possibly *Vaccinium uliginosum* and *Rubus chamaemorus.*

In the field layer half the species are herbs and half are dwarf shrubs, while in the *Ledum*-pine wood the herb species amount to two thirds of the number of dwarf shrubs.

Picea – Maianthemum – Vaccinium myrtillus – Pleurozium association (III. Bilberry-spruce wood)

Between the dwarf shrub-rich pine communities in the centre and the herb-rich spruce wood communities at the periphery of the peat land there is a community with intermediate qualities (Fig. 3). This is characterized by several features that it has in common with the pine wood, and at the same time by several new features which are characteristic of the herb-rich meadow spruce forest.

The main tree species is spruce (e.g. Jm 2; Fig. 7) with some pine in places (Jm 9, and Jm 10). Birch may occur in considerable amount (Jm 10), and *Alnus glutinosa* begins to be a constant feature, though it is still only occasional even towards the meadow-spruce forest. There is no well-developed bush layer, and the bushes that occur are distributed sparsely. The field layer shows quite a large variability, but *Maianthemum* and *Vaccinium myrtillus* are found throughout. The larger ferns begin to be present in increased quantity, mainly *Dryopteris spinulosa. D. filix-mas* and *Athyrium filix-femina* have been

Fig. 7. Bilberry-spruce wood (sample area Jm 9). Stand age ca. 65 years. Weakly developed field layer.—June 1960.

observed growing at the edges of ditches, but they are scarcely part of the community. *Brachythecium rutabulum* is more and more significant in the bottom layer. As a consequence of differences at the time of drainage (changing water conditions, possible clear felling in connection with the draining, etc.) the tree stands are very different in age and development in different parts of the community. These conditions have also affected the composition of the field layer and the bottom layer.

The following sociations have been distinguished:

a. *Picea – Vaccinium vitis-idaea – Hylocomium splendens* soc

b. *Picea – Deschampsia flexuosa – Pleurozium schreberi* soc

c. *Picea – Maianthemum – Vaccinium myrtillus – Pleurozium schreberi* soc

d. *Picea – Vaccinium myrtillus – Hylocomium splendens* soc
e. *Picea – Vaccinium myrtillus – Pleurozium schreberi* soc

a. The *Picea – Vaccinium vitis-idaea – Hylocomium splendens* soc includes only a small area in the eastern part of the peat land. At the time of ditching this was clear-felled completely (felled in 1917), and this is the reason for the present very even and close spruce stand. Measurements of some of the qualities of the stand, made in 1927, i.e. 5 years after the completion of the ditching, show that the spruce had then only reached a mean height of 1.5 m (stems ≧ 1.0 cm at breast height). The mean diameter was 1.9 cm, volume of stems was 1.12 m^3 per hectare, and number of stems was 1 553 per hectare. In 1931 the stem number was already 3 895 per hectare, the mean height had increased to 2.1 m and the volume of stems to 5.9 m^3 per hectare. The number of spruce seedlings was estimated as about 1 000 per hectare in 1927, and the number of birch seedlings as about 13 000 per hectare

The equilibrium in the field layer and the bottom layer is very labile, but it would be expected to become stabilized in the main part of the area as a *Picea – Maianthemum* soc after a natural or possibly a man-made thinning-out and maturation of the stand. The remainder, the parts nearest the periphery of the peat land, probably changes in the direction of *Oxalis*-spruce wood, i.e. a transition to meadow-spruce forest.

As a consequence of the very closed tree layer and the limited light penetration, the field layer is often very sparse or may even be absent. Because of the large fall of needles the bottom layer may also be absent.

Representatives of heath- and meadow-series occur in the community in an apparently random mixture. The type has been observed by Almquist (1929, p. 299) who considered that he could only doubtfully assign it to a place in the sociological system. Almquist pointed out its intermediate character (moss-herb-dwarf-shrub-rich coniferous wood) "between proper heath- and meadow-woods, connected to the heath series because of a more or less rich occurrence of bilberry and cowberry in a mixture with herbs (and grass)"—transl. He further pointed out that it is characteristic for the community that "the boundary is fluid, in both directions". He eventually includes the type in the heath series, and this is certainly correct. But likely some parts will later pass into purely meadow-wood communities.

The following is a common species composition. The left column comprises typical species for the heath series, the right those which are common within the meadow series:

Examples of species occurring in the field layer:

Deschampsia flexuosa
Luzula pilosa
Lycopodium annotinum
Melampyrum pratense
Ramischia secunda
Solidago virgaurea
Trientalis europaea
Vaccinium myrtillus
vitis-idaea
Calamagrostis canescens
Fragaria vesca
Lastrea dryopteris
Melica nutans
Milium effusum
Oxalis acetosella
Rubus idaeus
Veronica officinalis
Viola riviniana

Examples of species occurring in the bottom layer:

Dicranum polysetum
scoparium
Hylocomium splendens
Pleurozium schreberi
Ptilium crista-castrensis
Brachythecium rutabulum
salebrosum
Mnium cuspidatum
Rhodobryum roseum
Rhytidiadelphus triquetrus

The intermediate place which has here been allotted to *Rhodobryum* and *Rhytidiadelphus* has also been pointed out by v. Krusenstjerna (1945, p. 114) who considers that the two species "are a meadow element which in a typical heath-forest — — — clearly bring about the transition to meadow communities" (transl.).

b. The *Picea – Deschampsia flexuosa – Pleurozium schreberi* soc also has a very closed tree stand, where a field layer is developed only on small, open patches. In these patches, *Deschampsia flexuosa* is quantitatively the most important element. It is seldom fertile. The *D. flexuosa*-rich sociation is distinguished from the preceding in that, for example, the meadow herbs are absent. The typical species are restricted to *Vaccinium myrtillus* and *V. vitis-idaea*—which are co-dominant with *D. flexuosa* in several other places—together with *Lycopodium annotinum, Melampyrum pratense, Luzula pilosa* and single examples of *Dryopteris spinulosa.* In addition, the sociation is an "outpost" area for *Rubus chamaemorus* (Fig. 5).

The most important bottom layer species are *Pleurozium, Hylocomium splendens, Ptilium crista-castrensis* and *Dicranum* species. On moister patches *Sphagnum girgensohnii* is also observed.

This wood community is very close to the type which Malmström (1949, 1956) named "mossrika barrskogar med ris" (moss-rich coniferous woods with dwarf shrubs) and is, as far as it is possible to judge, a more peaty variant of Almquist's (1929, p. 302) "*Picea – Myrtillus – Hylocomium*" wood. In Arnborg's system (1943) its field layer

Table 4. Vegetational analyses from the *Picea* - *Maianthemum* – *Vaccinium myrtillus* - *Pleurozium* ass (Type III. Bilberry-spruce wood). 14 July, 1959

Trees (number of seedlings)	Jm 2	Jm 9	Jm 10	F-%
Betula pubescens	- - - - - - - 12- -	- - - - - - - - - - - - - - - - -	- - - - - - - - - - - - - - - - -	
Picea abies	- - 1 2 2 - - - - 1	- - - - - - - - - - - - - - - - -	- - - - - - - - - - - - - - - - -	
Sorbus aucuparia	- - - 1 - - 1 - - -	- - - - - - - - 1 - 1 - - - - - -	- - - - - - - - - - - - - - - - -	
Bushes				
Rubus idaeus	- - - - - - - - - -	- - - - - - - - - - - - - - - - -	- - - - - - - - - - - - - - - - -	
Dwarf shrubs				
Lycopodium annotinum	- - - 1 3 4 - - - -	1 - - - - - - - - - - 1 - - - - -	2 - 2 - - - 1 - - - - - - - - - -	18
Vaccinium myrtillus	1 1 5 2 2 2 - 4 3 1	- + - 1 1 1 + - - + + - 1 1 - 1 -	- 1 1 1 1 1 1 1 1 1 - - 1 1 1 1 1	75
vitis-idaea	- - 1 - - + - - - -	+ - - - - - - - - - - - - - - - -	- - - - - - - - - - - - - - - - -	7
Grasses and herbs				
Carex digitata	1 - - - - - - - - -	- - - - - - - - - - - - - - - - -	- - - - - - - - - - - - - - - - -	2
Chamaenerion angustifolium	- - - - - - 1 - - -	- - - - - - - - - - - - - - - - -	- - - - - - - - - - - - - - - - -	2
Dryopteris spinulosa	- - - - - - - - - -	- - - - - - - - - - - - - - - - -	- 1 1 - - - - - - - - - - - - - -	5
Galeopsis tetrahit	- - - + - - - - - -	- - - - - - - - - - - - - - - - -	- + - - - - - - - - - - - - - - -	5
Luzula pilosa	1 3 1 1 1 1 1 1 3 2	1 1 + 1 1 1 + 2 2 + + 1 2 1 2 1 1	1 1 - + - + + + + - + - 1 1 1 - -	86
Maianthemum bifolium	5 3 3 4 3 2 4 - - -	1 2 - - - - - - - - - 1 - 1 - - 1	2 4 3 - - 1 1 - - - - - - - 4 - 1	43
Melampyrum pratense	1 - 1 - - - - 3 - 1	- - - - - - - - - 1 - - - - - - -	- - - - - - - - - - - - - - - - -	11
Melica nutans	- 1 - - - - - - - -	- + - - - - - - - + - - - - - - -	- - - - - - - - - - - - - - - - -	7
Moehringia trinervia	1 - - + - - - - - -	- - - - - - - - - - - - - - - - -	- - - - - - - - - - - - - - - - -	5
Oxalis acetosella	1 - - - 1 - 1 1 - -	- - - - - - - - - - - - - - - - -	- - - - - - - - - - - - - - - - -	9
Taraxacum sp.	- - - + - - - - - -	- - - - - - - - - - - - - - - - -	- - - - - - - - - - - - - - - - -	2
Trientalis europaea	- - + 1 1 1 - 1 - -	- - - - - - - - - - - - - - - - -	- 1 1 + - - - - - - - - - - - - -	18
Mosses				
Brachythecium rutabulum	- - - + 1 1 - 1 - -	3 - 1 3 + - 1 1 + 1 1 3 3 1 5 3 1	+ 1 1 - - 1 + - - - - - - 1 - 1 1	61
salebrosum	- - - - - - - - - -	1 - + - - - - - - - - - - - 1 1 -	- - - - - - + - - - - - - - - - 1	14
Cirriphyllum piliferum	- - - - - - - - - -	1 - - - - - - - - - - 1 - - - - -	- - - - - - - - - - - - - - - - -	5
Dicranum fuscescens	- - - - - - - - - -	- - - - - - - - - - - - - - - - -	1 + 1 - - + - - - - 1 - - - - - -	11
polysetum	- 1 1 1 - 1 1 1 1 +	+ 1 + 1 + + + - - + + - 1 - - 1 1	1 3 2 1 + + - + 1 + 1 - 1 3 1 1 1	80
scoparium	1 1 1 1 1 - 1 1 1 1	1 1 1 + + + 2 + 1 2 1 1 - 2 1 2 -	1 - 1 1 1 1 - + 2 - + - 1 1 1 1 2	84
Hylocomium splendens	2 4 5 3 2 5 4 4 3 2	3 4 3 4 5 5 5 2 4 5 1 3 3 5 2 5 3	5 5 3 6 4 3 4 2 2 5 2 4 5 1 5 5 2	100
Plagiothecium denticulatum	- - + + - - - 1 - -	- - - - - - - - - - - - - - - - -	+ + - - - - - - - - - - 1 1 - 1 1	20
Pleurozium schreberi	5 5 3 5 5 1 4 2 5 5	3 4 5 4 1 1 2 3 4 3 5 5 5 2 1 4 5	3 2 4 1 1 5 2 5 5 2 4 5 4 5 1 1 5	100
Ptilium crista-castrensis	1 1 - 1 1 1 1 + 1 1	1 1 - - - - - 1 - - + 1 - - 1 1 1	1 - 1 - - - 2 - - 1 2 - 1 1 - - -	55
Rhodobryum roseum	- - - - - 1 + + - -	- - - - - - - + - - - - - - - - -	- - - - - - - - - - - - - - - - -	4
Rhytidiadelphus triquetrus	1 1 - 1 1 1 1 + 1 1	2 - - + 1 1 1 - + - - 1 1 4 - - -	- - 1 - 4 + 2 - - - - - - - - 1 -	52
Sphagnum parvifolium	- - - - - - - - - -	- - + + - - - - - - - - - - - - -	- - - - - - - - - - - - - - - - -	4
Lophocolea heterophylla	- - - - + + - 1 - -	- - + - - - - - + - - - 1 - - 1 -	- - - - - - - - - - - - - - - - -	16
Ptilidium ciliare	- - - - - - - + - -	- - - - - - - - - - - - - - - - -	- - - - - - - - - - - - - - - - -	2

F = Frequency

Additional species (degree of cover 1 or +): Jm 2: See table . - Jm 9: Carex digitata, Cerastium holosteoides, Chamaenerion angustifolium, Chelidonium majus, Cirsium vulgare, Dryopteris spinulosa, Equisetum palustre, Lactuca muralis, Milium effusum, Moehringia trinervia, Oxalis acetosella, Rhamnus frangula, Rubus idaeus, Taraxacum sp., Trientalis europaea. - Jm 10: Dryopteris cristata, Melampyrum pratense, Rhamnus frangula, Sorbus aucuparia, Vaccinium vitis-idaea; Rhodobryum roseum.

would be classified as "*Deschampsia flexuosa* society", which comes under the "*Vaccinium myrtillus* union", and, as at Jägarmossen, occurs in open areas such as gaps in the tree canopy, felled areas etc.

The next three sociations are more typical parts of the association and make up the major proportion of the area of the bilberry-spruce wood.

c. *Picea* – *Maianthemum* – *Vaccinium myrtillus* – *Pleurozium* soc. In large parts of the sociation, shading and needle-fall from the trees is less severe than in the previous sociations. Hence as a rule there are well-developed field and bottom layers. Sample area Jm 2 (Table 4) is an example of the species combination within the association which is nearest to the meadow-spruce wood. Grasses and herbs transitional to the meadow-wood communities are *Lactuca muralis, Melica nutans, Moehringia trinervia* and *Oxalis acetosella,* which are however very sporadic in occurrence. The dominants in the sociation, *Maianthemum* and *Vaccinium myrtillus,* are usually constant in 1 m² quadrats and may alternate in dominance. A constant species of no diagnostic value is *Luzula pilosa,* which occurs in every 1 m² quadrat. This species is found in lichen-, shrub- and low-herb-woods (Malmström 1949). The woodland mosses, *Hylocomium splendens* and *Pleurozium schreberi,* are also always present here, with a high degree of cover, in the bottom layer. *Dicranum polysetum* has a high frequency. *Brachythecium rutabulum* and *B. salebrosum* occur in the species-poor bilberry-pine wood (Table 2, Jm 6) as well as in all meadow-wood communities. In ecological range these species seem therefore to be similar to *Lastrea dryopteris,* which, although uncommon, has been observed in bilberry-pine wood but has its maximum frequency in the herb-rich communities. The same sort of trend is shown by *Rhytidiadelphus triquetrus,* but this may make less demand on the substrate than the previous species as it has a wider area of distribution and fairly high frequency even in the transition zone between the pine- and spruce-wood communities (Table 8, quadrat 4). It is apparent from Table 4 that it is fairly common in the different variants of bilberry-spruce wood (about 50 per cent frequency in the vegetation analysis). v. Krusenstjerna (1945, p. 122) is also of the opinion that it can be dominant in the meadow- as well as the heath-series, even though he points out (p. 211) that it is an indicator for dry to medium moist meadow-woods. However, it occurs at least as often in moist or even wet meadow-wood communities (Sjörs, personal communication).

Two of the sample areas in Jm 2 (Table 4) are exceptional in that the field layer is comparatively poorly developed, with *Luzula pilosa* in place of *Maianthemum.*

In the western part of the area of the association the tree layer is closed so that the projections of the crowns cover 90 per cent, or in patches 100 per cent, of the ground. The light intensity is permanently low under the trees and only when the sun is high in the sky are some patches on the ground illuminated directly for a short time. A good example of the result of this condition is sample area Jm 9, which has however been thinned somewhat. The most obvious feature is that the field layer—both quantitatively and qualitatively—is usually very poorly developed. The sociation's dominants, *Vaccinium myrtillus* and *Maianthemum bifolium,* fail to achieve degrees of cover higher than 2 (Table 4). The bottom layer is clearly favoured by the lack of competition from the field layer and luxuriant carpets are formed.

In some large gaps in the canopy, luxuriant *Maianthemum* gives an impression of clearing vegetation. *Dryopteris spinulosa, Chelidonium majus, Rubus idaeus, Melica nutans, Galeopsis tetrahit, Milium effusum, Luzula pilosa* (sometimes abundant), *Deschampsia flexuosa, Rhamnus frangula,* etc., are present in varying amounts.

d. The *Picea – Vaccinium myrtillus – Hylocomium splendens* soc occurs in two small areas in the south and south-west parts of Långholmen. The presence of a number of old trees shows that there was a stand of trees even before drainage (see Ch. 3.D.). There is a wide age range of spruce from first year seedlings to trees ready for felling. In patches in the stand are small groups of birch. Where the tree layer is sparse a clearing flora has developed, but in contrast to the previous sociation the bottom layer dominant is *Hylocomium splendens.* The species suggestive of a clearing are in the main the same, but with the following additional ones: *Calamagrostis arundinacea, Carex digitata, Lactuca muralis, Angelica silvestris, Fragaria vesca, Cirsium vulgare,* etc.

e. The *Picea – Vaccinium myrtillus – Pleurozium schreberi* soc. The combination *Vaccinium myrtillus – Pleurozium* is mainly found in the parts of the bilberry-spruce wood which are nearest the dwarf-shrub-pine wood, but the sociation has other scattered occurrences within the association.

It is common that *Pleurozium* and *Hylocomium* are co-dominants in the bottom layer. Since there are large numbers of pine in some places and few herbs, the community may superficially appear to be more related to a spruce-rich variant of dwarf-shrub-pine wood. However, *Maianthemum* shows that the sociation really belongs to the bilberry-spruce wood association.

A comparison of the analysis data from the three sample areas (Table 4, Jm 2, Jm 9 and Jm 10) gives some interesting information about the association. Of all the species recorded there are only two, the mosses *Hylocomium splendens* and *Pleurozium schreberi,* which have 100 per cent frequency, i.e. which are in all the 44 quadrats analysed.

Only two of the 15 field layer species, *Vaccinium myrtillus* and *Luzula pilosa,* have more than 50 per cent frequency; and as many as 9 have less than 10 per cent frequency. Of these, 5 are represented only in Jm 2, which is somewhat atypical because it is in a boundary area.

The bottom layer species are distributed much more evenly within the association, with 7 of 13 species with frequency from 100 to 50 per cent, and only 2 with a frequency of less than 10 per cent. (It should be remembered that the frequency values quoted are relevant only for communities in this particular area of drained peat land when studied with quadrats of one sq.m size.)

Communities similar to the bilberry-spruce wood have been described by Cajander (1921), Malmström (1925, etc.), Almquist (1929), Arnborg (1943), and others. The nearest equivalent in Almquist (1929, p. 229) is "*Picea – Anemone – Myrtillus – Hylocomium*" wood. However *Anemone nemorosa* is not so important that it can with advantage give its name to an association, although it occurs in the community. Malmström's (1925, etc.) *Dryopteris* type seems to be nearly comparable, qualitatively. In Cajander's (1921) *Oxalis – Myrtillus* type several of the constituent species are much too demanding to do well in the bilberry-spruce wood environment. This type is nearest the association to be described next. In Malmström's later papers (e.g. 1949, p. 60) the equivalent to the community is found in the collective term 'low-herb woods'; later (1956, p. 7) also in "low-herb-coniferous woods". In this latter group the *Maianthemum* type has been given the same rank as the *Dryopteris* type named above. The nearest equivalent in Arnborg (1943) is *Thelypteris dryopteris – Vaccinium myrtillus* union (1943, p. 172), but with the modifications imposed by the more northerly site.

Bottom layer communities of the same character are termed *Ptilio-Hylocomietum* by v. Krusenstjerna (1945, p. 112), a union which comes under the very widely-occurring *Pleurozium–Hylocomium–Dicranum* alliance.

Meadow-forest communities

The three associations distinguished as meadow-forest communities are in the peripheral parts of the peat land (Fig. 3).

The peat is of moderate thickness (Fig. 34) with greatest depth exceptionally more than 2 m.

The humification of the peat is good throughout, from the surface down to the underlying sediments, especially for associations IV and V (see below) where the surface is usually crumbly or granular ('peat mull'). In several places the uppermost 10–20 cm has a mull-like appearance. Because of compression and high water content the peat under this level is more compact in structure. When dug it tends to fall apart in large pieces which can in turn be broken up along clearly formed planes of weakness. In the grass-rich association VI (see below) the peat is held together as a blanket of dead and living plant parts in the surface layer, because of the thorough root penetration. Under this, it is similar in appearance and qualities to the deeper layers in the other two meadow-wood communities.

Good indicator species distinguishing the meadow-series vegetation from the heath-series occur in the field layer as well as in the bush and tree layer. In the field layer the most obvious are *Filipendula ulmaria, Paris quadrifolia* and *Urtica dioeca.* In the bush layer the most reliable are *Daphne, Lonicera xylosteum* and *Viburnum opulus* (Fig. 26, 28); and in the tree layer *Fraxinus* is the most important meadow-wood species. *Tilia cordata* and *Ulmus glabra* (Fig. 20) are also present, but are so rare that they are of no diagnostic value. It has not been possible to distinguish any exclusive meadow-wood mosses. Both *Brachythecium* species and *Mnium* species, which are the only ones which occur generally, also grow in heath-wood communities. It is better to say merely that these mosses have a preference for meadow-series communities. It should be pointed out that the *Mnium* species probably are more demanding in their requirements than the *Brachythecium* species.

Picea – Oxalis – Maianthemum – Brachythecium rutabulum association (IV. *Maianthemum*-spruce wood)

Maianthemum-spruce wood (Table 5; Fig. 8) has the major part of its area of distribution north of the main run-off channel. The parts south of this are restricted to a wedgeshaped offshoot in the western part of the area and an isolated outpost at sample area Jm 2. In addition, it is the most important community in the transition area to the non-peaty land. However, this does not show in the vegetation map (Fig. 3).

In the transition area to the non-peaty land the association diverges somewhat from the type-community on deep peat, but the differences are not large. They comprise only minor shifts in the dominance pattern.

The boundary zone is of varying width, depending on the slope of the surrounding land towards the peat land. The main feature of the boundary region is that the grasses, especially *Calamagrostis arundinacea* and *Deschampsia flexuosa,* increase noticeably on the non-peaty side. Both species are found on the peat land, but the former in particular is rare on a peat substratum. However, on the surrounding non-peaty land it is dominant in the field layer under pine. In this it is opposite to *C. canescens* which tends to grow densely on the peat land (see section "Grass-rich birch-spruce wood" below). *Pteridium aquilinum* is another species that seems to avoid a purely peaty

Table 5. Vegetational analyses from the *Picea* - *Oxalis* - *Maianthemum* - *Brachythecium rutabulum* ass (Type IV. *Maianthemum*-spruce wood). 20 July, 1959

Bushes	Jm 2				Jm 11																					F-%
Rubus idaeus	3	3	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12
Dwarf shrubs																										
Lycopodium annotinum	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4
Vaccinium myrtillus	-	-	+	-	1	-	-	-	1	-	-	+	1	-	-	1	1	-	1	-	-	1	-	-	-	36
vitis-idaea	-	-	-	-	-	-	-	-	+	+	+	1	1	-	+	-	-	-	1	1	1	-	-	-	-	36
Grasses and herbs																										
Anemone nemorosa	-	-	-	-	-	-	1	-	1	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	12
Carex digitata	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	4
Chamaenerion angustifolium	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4
Dryopteris spinulosa	-	-	-	-	-	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8
Epilobium palustre	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4
Fragaria vesca	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4
Galeopsis tetrahit	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8
Lastrea dryopteris	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4
Luzula pilosa	+	+	1	-	+	-	+	1	+	+	1	-	-	+	+	1	1	1	1	-	1	1	1	1	1	80
Lysimachia thyrsiflora	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	4
Maianthemum bifolium	-	1	3	2	1	1	1	1	-	1	2	2	-	+	1	1	-	-	-	1	-	-	-	-	-	64
Melampyrum pratense	-	-	-	-	+	1	-	+	1	1	-	+	1	-	1	-	1	-	-	-	-	-	-	-	-	36
Moehringia trinervia	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4
Oxalis acetosella	5	5	5	5	5	5	5	5	5	5	5	4	5	5	5	3	3	4	4	4	3	2	3	3	2	100
Potentilla erecta	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	4
Pyrola minor	-	-	-	-	-	-	-	-	+	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	8
Ramischia secunda	-	-	-	-	-	-	-	-	-	1	-	+	-	-	-	-	-	-	-	-	1	-	-	-	-	12
Rubus saxatilis	-	-	-	-	1	-	-	-	1	-	-	+	1	-	-	-	-	1	-	1	1	-	-	1	-	32
Taraxacum sp.	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8
Trientalis europaea	-	-	-	-	1	-	+	-	-	+	+	+	-	-	1	-	-	-	-	-	-	-	-	-	-	24
Urtica dioeca	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4
Mosses																										
Brachythecium rutabulum	4	3	1	1	1	3	2	3	2	4	3	1	3	1	1	1	1	5	5	2	5	5	3	3	5	100
Cirriphyllum piliferum	-	-	-	-	-	1	-	-	-	+	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	12
Dicranum polysetum	-	-	-	-	-	1	-	+	-	+	-	-	-	-	1	1	-	-	-	-	-	-	1	1	-	28
scoparium	-	+	+	+	3	1	1	1	-	2	1	-	-	-	1	1	1	1	-	-	1	1	-	1	-	64
Hylocomium splendens	-	1	2	1	2	2	2	2	3	1	2	-	1	1	1	2	3	2	2	2	1	2	5	2	3	92
Mnium cuspidatum	-	-	-	-	-	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8
Plagiothecium denticulatum	-	-	-	1	1	+	+	-	-	1	-	-	+	-	+	1	1	-	-	-	1	-	-	1	1	48
Pleurozium schreberi	-	1	4	1	2	2	+	+	-	1	1	-	-	+	2	5	4	1	1	1	1	1	1	1	1	84
Ptilium crista-castrensis	-	-	1	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	16
Rhodobryum roseum	-	+	+	-	1	1	1	-	-	-	-	-	-	-	-	1	1	-	-	-	-	1	-	1	1	40
Rhytidiadelphus triquetrus	1	1	+	-	-	-	1	1	1	-	3	1	1	-	1	1	-	-	1	2	-	2	-	1	1	64
Lophocolea heterophylla	1	1	-	+	1	1	-	1	1	1	1	1	1	1	-	1	-	-	-	-	-	-	-	1	1	64

F = Frequency

Additional species (degree of cover 1 or +): Jm 2: Anemone nemorosa, Chelidonium majus, Cirsium vulgare, Deschampsia flexuosa, Dryopteris filix-mas, D.spinulosa, Epilobium montanum, Galium palustre, Lysimachia vulgaris, Melampyrum silvaticum, Poa nemoralis, Populus tremula (seedlings), Prunus padus, Rhamnus frangula, Ribes alpinum, R.spicatum, Solanum dulcamara; Brachythecium salebrosum, B.velutinum, Calliergonella cuspidata, Dicranum majus. - Jm 11: Acer platanoides (seedlings), Calmagrostis canescens, Carex elongata, Dryopteris cristata, Filipendula ulmaria, Deschampsia caespitosa, Fraxinus excelsior (seedlings), Galeopsis tetrahit, Lactuca muralis, Lastrea dryopteris, Lonicera xylosteum, Lycopodium annotinum, Paris quadrifolia, Quercus robur (seedlings), Rhamnus frangula, Ribes alpinum, Rubus idaeus, Solidago virgaurea, Sorbus aucuparia.

substratum and therefore is first met with in the transition area between non-peaty and peat land where the substratum is peat mixed with large amounts of sand.

The majority of the characteristic species of the bilberry-spruce wood (Table 4) are also found in *Maianthemum*-spruce wood, but the dominance as well as the frequency relations have shifted in the

Fig. 8. *Maianthemum*-spruce wood. *Maianthemum bifolium* grows luxuriantly in openings or where the trees are scattered. Peat depth 1.5—2.0 m.—July 1960.

direction of the meadow series species. Thus *Oxalis* is important in the field layer, where it is as a rule dominant and has 100 per cent frequency in the quadrats, whereas the dwarf shrubs, mainly *Vaccinium myrtillus,* have a very low degree of cover and do not occur in all the quadrats of the sample area. *V. vitis-idaea* is restricted almost completely to old tussocks or stumps. Meadow-wood mosses, mainly *Brachythecium rutabulum,* have become dominant in the bottom layer, while the heath series mosses, *Hylocomium splendens* and *Pleurozium schreberi,* may still occur as sub-dominants. *Rhytidiadelphus triquetrus* and *Rhodobryum roseum* were discussed in the previous section, but it should be pointed out that both these species show a marked preference for meadow-spruce wood communities. Arnborg (1950, p. 11) regards them as not exclusive for meadow-woods but also as elements of the heath series, where *R. triquetrus* is diagnostic for the *Triquetrum* union, occurring in nutrient-rich areas. In contrast, *Brachythecium* species come in the *Brachythecium* union, a part of the meadow-spruce wood community.

Of the 29 field layer species coming in the quadrat analysis, only

3, *Luzula pilosa, Maianthemum bifolium* and *Oxalis acetosella,* have a quadrat frequency of more than 50 per cent, and as many as 18 do not reach 10 per cent. The bottom layer is much more even in composition, as in the preceding association. *Brachythecium rutabulum, Hylocomium* and *Pleurozium* occur in all the quadrats, and 6 of the 12 species have more than 50 per cent frequency, while only one has less than 10 per cent.

The share of the dwarf shrubs in the vegetation is further decreased as compared with that in the previous community and makes up about 1/10 of the total number of field layer species.

The association is in general so homogeneous that there has been no necessity to separate vegetation units of lower rank on the basis of their dominants. Because of its relationship with the type described by Almquist, mentioned below, one unit which diverges from the normal within the community can be named. Directly east of sample area Jm 2 there is a small area with a tree layer which consists mainly of scattered birches. The under-vegetation is therefore better illuminated, and this is reflected in the development of the bush and field layers. There is an extensive bush layer with *Prunus padus, Rhamnus frangula, Rubus idaeus, Sorbus aucuparia* and *Viburnum opulus* as the most important species. In spring, *Anemone nemorosa* makes a noticeable and decorative contribution to the field layer. *A. nemorosa* is followed by *Filipendula ulmaria* which has a high degree of cover over large parts of the area. The main species with these two are *Oxalis* and *Maianthemum.* A high frequency, although only a low degree of cover, is reached by *Milium effusum, Viola riviniana* and *Convallaria majalis.*

The number of tree seedlings within the association is variable, despite the evenness of the tree layer; however, it may be, to a large degree, the development of the field layer which determines the seedling frequency. Parts of the field layer are unfavourable to tree seedlings' early development, e.g. the *A. nemorosa* community mentioned above, or parts with luxuriant large ferns.

In respect of field layer species the type most related to the *Maianthemum*-spruce wood is that with a similar name, viz., the *Oxalis*—*Maianthemum* type (OMaT) of Cajander (1921, p. 31). However, Cajander does not state any occurrence on peat land. Almquist's (1929, p. 287) *Picea – Anemone – Hylocomium* wood, a low-herb-spruce wood, is somewhat different from the Jägarmossen type, in that *Anemone hepatica* and *A. nemorosa* are more important on non-peaty land. On Jägarmossen, *A. hepatica* has only a few known localities and *A. ne-*

morosa is only occasionally one of the foremost constituents of the community (see above).

In Malmström's survey of forest communities (1956, p. 7) the type, like the foregoing and the following association ("III" and "V"), is placed among the low-herb-coniferous woods (see below, *Oxalis*-spruce-wood). The term low herb-woods (Malmström 1949, p. 60) has also been used by Sjörs (1956, p. 120) and by Samuelsson (1960, p. 85). In Arnborg's (1943) woodland communities there are no good equivalents to the *Oxalis* – *Maianthemum* association. With regard to the importance of dwarf-shrubs, it is intermediate between the unions of the *Aconitum septentrionale* group and the *Geranium silvaticum* – *Vaccinium myrtillus* union.

Picea – *Oxalis* – *Brachythecium rutabulum* association (V. *Oxalis*-spruce wood)

With the exception of a minor section in the eastern part of the peat land, this community is restricted to the area north of the main run off channel (Fig. 3). The peat thickness within the area of the association is comparatively small. The maximum thickness is up to 1$^1/_2$ m, but it is usually $\leqq$ 1 m (Fig. 34). The effect of the mineral layers underneath could therefore be greater in this community than in any of those described previously. Before the ditches cut off the direct link, the surrounding non-peaty land exerted a certain effect through the water which seeped in from it over the peat land. These conditions are responsible to a large extent for the differences in nutrient conditions which now occur in different parts of the area. The nutrient analyses from the sample areas in the *Oxalis*-spruce wood thus show marked differences from the other communities in, for example, nitrogen, phosphorus and calcium contents. As a consequence of the fairly high density of the soil in the community the differences in the reserve of plant nutrients are still more obvious.

The distinguishing characteristic of the vegetation as opposed to the preceding association is the almost complete absence of dwarf shrubs. In addition, there is regularly a large number of exclusive meadow-wood species such as *Paris quadrifolia* and *Urtica dioeca*, and *Fraxinus excelsior* is always present. The constant occurrence of the ferns *Dryopteris spinulosa*, *Athyrium filix-femina* and *Lastrea dryopteris* is also conspicuous, and *Dryopteris filix-mas* and *Lastrea phegopteris* occur somewhat less commonly. The number of species of bushes and trees is also larger than in the other communities. There is, for example, scattered occurrence of *Ulmus glabra* and *Tilia cordata*.

Table 6. Vegetational analyses from the *Picea - Oxalis - Brachythecium rutabulum ass (Type V. Oxalis*-spruce wood). 15 July, 1959

Trees (number of seedlings)	Jm 3	F-%	Jm 4	F-%	Jm 8	F-%	Average F-%
Fraxinus excelsior	- -	0	- -	0	- 1 - - 1 - 1 - - 2 - - - - - - -	24	7
Picea abies	- -	0	- - - 1 - - - - - - - - - - - - - - - - -	5	- - - - - - - - - - - - - - - - -	0	2
Sorbus aucuparia	- 1 - - - - - - - - - - - - - - - - - - -	5	- -	0	- - - 2 - - - - - - - - - - - - -	6	3
Bushes							
Prunus padus	- -	0	- -	0	- - - - - - 1 1 1 2 - - - - - - -	24	7
Ribes alpinum	- -	0	- -	0	1 - - 1 - - - - - - - - - - - - -	12	3
Rubus idaeus	- -	0	- 1 1 - 1 - 1 3 2 1 - - - - - 2 - - 2 - -	43	- - - 1 1 - - - - - 1 - - - - 3 -	24	22
Grasses and herbs							
Anemone nemorosa	- -	0	- - - - - - - 1 - - - - - - - - - - - - -	5	- - - 1 - - - - - - - - - - 1 1 -	18	7
Athyrium filix-femina	- -	0	- - 3 5 4 - 4 - 3 - 3 - - - - - - - - - -	29	- - - - - - - - - - - - - - - - -	0	10
Calamagrostis canescens	- - - - - - - - + - - - - - - - - - - - -	5	- -	0	- - - - - - - - - - - - - - - - -	0	2
Carex digitata	- -	0	- + - - - - - - - - - - - - - - - - - - -	5	- - - - - - - - - - - - - - - - -	0	2
elongata	1 - + - - - - - + - - - - - - - - - - - -	14	- - - 1 - - - - - - - - - - - - - - - - -	5	- - - - - - - - - - 1 - - - - - -	6	8
Chamaenerion angustifolium	+ - - - - - - - - - - - - - 1 - - - - - -	10	- - - - - 1 - - + - - - - - - - - - - - -	10	- - - - - - - - - - - - - - - - -	0	7
Chelidonium majus	- -	0	- -	0	2 1 + 1 1 2 4 3 4 - 1 - - 2 - 2 -	71	20
Dryopteris spinulosa	- - 2 - 1 3 2 - - - - - - - - 1 - 3 1 - 1	38	1 - - - 2 4 - 3 - 1 4 - - 3 5 5 5 2 4 2 5	67	+ - - - - - - - - 1 - - - - - 2 -	18	42
Filipendula ulmaria	- - 1 - - - - - - - - - - 1 1 - - - 1 - -	19	- 1 1 - 1 - - - 1 1 - - - - - - - - - - -	24	- - - - 1 - - + 1 2 4 1 1 - - 4 -	47	29
Fragaria vesca	- -	0	- -	0	+ - - - - - - - - - 1 - - - - - -	12	3
Galeopsis tetrahit	- -	0	- -	0	- + + - - + - + - - - - - - 1 1 -	35	10
Geranium robertianum	- -	0	- -	0	- - - - - - - - - - + - - - - - -	6	2
Lactuca muralis	- -	0	- 1 - - - - - - - - - - 1 - - - - - - - -	10	2 - 1 + - - - - - 1 2 1 - - - - -	35	14
Lastrea dryopteris	- 1 1 - - - - - - - - - - - - - - 2 - - -	14	1 4 4 - 5 - - 4 - 4 2 - - - - - - - - - -	33	- - - - - 4 - - - - 2 - 3 - - - -	18	22
Luzula pilosa	- - 1 - - - - - - - - - - - - - - - - 1 -	10	- -	0	- - - - - - - - - - - - - - - - -	0	3
Maianthemum bifolium	1 - 1 - - - - - - - 1 1 - 1 - - - 1 1 1 1	43	- - - 1 - 1 - - - - 1 - 1 - - - - - - - -	19	1 1 - - 1 1 - - 1 - 1 2 - - 1 1 -	53	37
Milium effusum	- -	0	- - - - - - - - + - - - - - - - - - - - -	5	- - - - - - - - - - - - - - - - -	0	2
Moehringia trinervia	- -	0	- -	0	- 1 - - 1 - - - - - - - - - - - -	12	3
Oxalis acetosella	5 5 5 5 5 5 5 5 4 5 4 5 5 5 5 5 5 4 5 4 5	100	5 5 4 4 1 5 4 3 5 5 2 5 5 4 1 3 2 4 2 5 3	100	5 5 5 5 5 5 2 4 5 5 4 5 5 3 5 3 5	100	100
Paris quadrifolia	- -	0	- -	0	- - - 2 - - 2 - 2 - - - 1 - - - 3	29	8
Ranunculus repens	- -	0	- -	0	- - - - - - 2 - - - - - - - - - -	6	2
Rubus saxatilis	- - - - - + 1 - - 1 - - 1 - - - - - 1 - 1	29	- 1 1 1 - 1 1 1 1 1 - - - - - - 2 - - - -	43	- 2 1 - 1 - - - 1 - 1 1 2 - 1 - 1	53	41
Solidago virgaurea	- -	0	- - - - - - - 1 - - - - - - - - - - 1 - -	10	- - - - - - - - - - - - - - - - -	0	3
Trientalis europaea	- -	0	- -	0	- - - - - - - - - + - - - - - 1 -	12	3
Urtica dioeca	- -	0	- 1 - - - - - - 2 - 3 - - - - - - - - 3 -	19	3 3 - - 5 - 5 5 1 1 3 2 2 5 2 4 1	82	31
Viola palustris	- -	0	- -	0	1 - - - - - - - - - - - - - - - -	6	2
riviniana	- -	0	- - - - - - - - - + - - - - - - - - - - -	5	- - - - - - - - - - - - - - - - -	0	2
Mosses							
Brachythecium reflexum	- -	0	- -	0	- - - - - - - + - - - - - - - - -	6	2
rutabulum	5 3 5 1 + 2 4 3 3 3 4 2 1 4 4 1 1 1 5 5 5	100	1 1 1 3 1 2 1 1 1 1 1 - 4 1 1 - 1 1 1 4 1	90	1 - 3 2 1 1 1 3 2 2 2 2 1 3 5 1 3	94	95
salebrosum	- - - - - + - - 1 - - - 1 1 1 - 1 1 1 1 -	43	- - - 2 - - - + - - - - - - - - - - - 1 1	19	- - - - - - - - 1 - + - - - - - 1	18	27
velutinum	- + - - - - - - + - - 1 - - - - - 1 - - -	19	- - - 1 - - - - - - - - - - - - - - - - -	5	- - - - - - - - - - - - - - - - -	0	8
Cirriphyllum piliferum	- - - + - - - - - - - - - - - - - - - - -	5	- 1 - - - - - - - - - - - - - - - - - - 1	10	- - - - - - - - - - - - - - - - -	0	5
Climacium dendroides	- -	0	- -	0	- - - - - - - - + - - - - - - - -	6	2
Dicranum scoparium	- + + - - - - - - + - - - - - 1 - - - - -	19	- -	0	- - - - - - - - - - - - - - - - -	0	7
Eurynchium zetterstedtii	- - - - - - - - - - 3 - - - - - - - - - -	5	- -	0	- - - - - - - - - - - - - - - - -	0	2
Hylocomium splendens	1 - 1 + + 1 1 - 1 1 1 - - 1 4 1 - - 1 1 2	71	- - - 1 - + - - - - - - 1 - - - - - - - -	14	- - - - - - - - - - + - - - - - -	6	33
Mnium cuspidatum	1 + + - - + - - - - - - - - - - - - - - -	19	- -	0	- - - - - - - - - 1 - - - 4 - - -	12	10
rugicum	- -	0	- -	0	- - - - - - - - + - - - - - - - -	6	2
Plagiothecium denticulatum	- - - - - - - - + - - - - - - - - - 1 1 -	14	- -	0	- - - - - - - + + - - - - - - - 1	18	10
Pleurozium schreberi	- - 1 - - + - - + + + - - 1 1 1 - - - 1 1	48	- -	0	- - - - - - - - - - - - - - - - -	0	17
Rhytidiadelphus squarrosus	- -	0	- -	0	+ - - - - - - - - - - - - - - - -	6	2
triquetrus	1 + + + + + 1 + 1 - 1 1 - - 1 1 - - 1 1 -	71	1 1 - 1 - - 1 1 + 1 + - 3 1 2 - - 1 1 2 -	67	1 - 1 1 - + - - 1 - 1 - 1 - - 1 -	47	63
Lophocolea heterophylla	1 1 1 + + 1 1 1 + 1 1 1 1 1 1 1 1 1 1 1 1	100	- - 1 + - - - + - 1 - 1 1 - 1 - 1 1 1 1 1	57	1 1 1 1 - - - - 1 - 1 - 1 - - - 1	47	70
Ptilidium ciliare	- -	0	+ -	5	- - - - - - - - - - - - - - - - -	0	2

F = Frequency

Additional species (degree of cover 1 or +): Jm 3. Anemone nemorosa, Angelica silvestris, Athyrium filix-femina, Equisetum silvaticum, Fragaria vesca, Lactuca muralis, Melampyrum pratense, Milium effusum, Paris quadrifolia, Prunus padus, Rhamnus frangula, Lastrea phegopteris, Ribes alpinum, Rubus idaeus, Solanum dulcamara, Solidago virgaurea, Trientalis europaea, Vaccinium myrtillus, Viola palustris, Urtica dioeca; Brachythecium reflexum, Mnium seligeri, Ptilium crista-castrensis.

Jm 4. Carex loliacea, Dryopteris filix-mas, Fragaria vesca, Galeopsis tetrahit, Geum rivale, Luzula pilosa, Moehringia trinervia, Paris quadrifolia, Ribes alpinum, Sorbus aucuparia, Trientalis europaea, Vaccinium myrtillus, Veronica chamaedrys; Drepanocladus uncinatus, Fissidens adianthoides.

Jm 8. Angelica silvestris, Anthriscus silvestris, Chamaenerion angustifolium, Athyrium filix-femina, Cirsium palustre, Geum rivale, Iris pseudacorus, Lysimachia vulgaris, Melica nutans, Milium effusum, Rhamnus frangula, Ribes spicatum, Scutellaria galericulata, Solanum dulcamara, Solidago virgaurea.

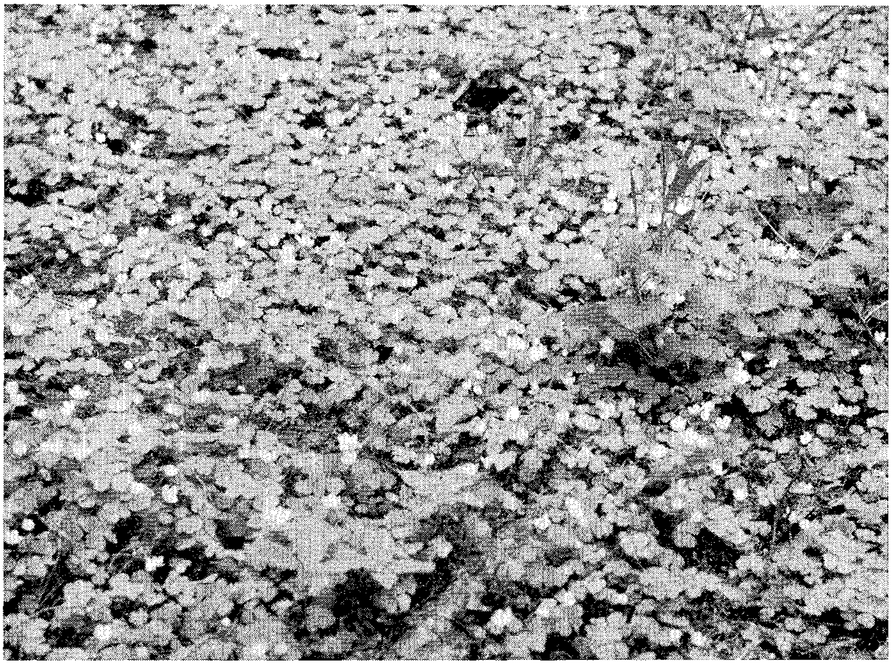

Fig. 9. *Oxalis*-spruce wood. The field layer is often dominated by *Oxalis acetosella* which here is seen together with its commonest associates: *Urtica dioeca, Paris quadrifolia* and *Milium effusum.*— June 1960.

Within the association there are only the following sociations to be distinguished:

a. *Picea – Oxalis – Brachythecium rutabulum* soc

b. *Picea – Oxalis – Dryopteris spinulosa – Brachythecium rutabulum* soc

c. *Picea – Oxalis – Urtica dioeca – Brachythecium rutabulum* soc

Hylocomium splendens and *Rhytidiadelphus triquetrus* occur more or less richly in the bottom layer, the former however with uneven frequency.

The *Picea – Oxalis* and *Picea – Oxalis – Dryopteris* sociations cover the greater part of the area of the association, whereas the *Picea – Oxalis – Urtica* sociation is mainly localized to sample area Jm 8 and nearby. Minor patches of the sociation are also seen as ditch-edge vegetation in some places in the north part of the peat land.

a. The *Picea – Oxalis – Brachythecium* soc is exemplified by sample area Jm 3 (Table 6). It is usually most clearly developed in the densest, most luxuriant spruce stands where there are only a few broad-leaved trees. There is usually no complete bush layer, and this

Fig. 10. *Oxalis*-spruce wood. In the most eutrophic parts of Mjölnar fen, now invaded of spruce, *Paris quadrifolia* dominated patches, here with additions of *Oxalis acetosella*, *Urtica dioeca* and *Filipendula ulmaria*, can be encountered.—June 1960.

layer is represented only by scattered occurrences, mainly of *Lonicera xylosteum, Prunus padus, Ribes alpinum, Sorbus aucuparia* and *Viburnum opulus*. In the bush layer low individuals of tree species occur sporadically and also single examples of *Corylus avellana* and *Ribes spicatum*. The comparatively species-poor field layer has most species in common with the preceding association, but the shrubs, as far as they occur at all, are restricted to old, crumbly, moss-covered stumps. *Oxalis* is dominant (Fig. 9) and usually has almost complete cover in large areas. Table 6 shows that it may sometimes be the only field layer species within the quadrats. But even in these very closed stands scattered ferns may spread at the expence of the *Oxalis*. In the same way, the bottom layer dominant, *Brachythecium rutabulum,* forms mats with complete cover over large areas, though these are broken up in patches by litter. The other mosses grow intermingled in the carpets of *Brachythecium*. *Hylocomium splendens* and *Pleurozium schreberi* do not often grow directly on the ground, but usually occur on stumps and fallen trees, root bases etc., where other species have decreased competitive ability. The occurrence of *Eurhynchium zetterstedtii* is worthy of note. In sample area Jm 3 (Table 6) it occurs only in one place, and it has otherwise been seen in only two places in the area. The constant occurrence of the very slender liverwort, *Lophocolea heterophylla,* which is in all quadrats, is unique. It is mainly found as a bright light-green cover on twigs, small branches and cones lying on the ground.

b. The *Picea – Oxalis – Dryopteris – Brachythecium* soc differs from the preceding one in having a well-developed field layer of large ferns, *Dryopteris spinulosa, Athyrium filix-femina* and sometimes also *D. filix-mas.* The sociation is most luxuriant in more open tree stands, but is also well-developed even under a fairly close canopy of spruce. Other species in the field layer are *Geum rivale, Filipendula ulmaria, Lactuca muralis, Lastrea dryopteris, Milium effusum, Paris quadrifolia* (Fig. 10), *Solanum dulcamara* and *Stachys silvatica* (abundant in places, but usually rare). *Actaea spicata* is also characteristic, although relatively uncommon.

c. The *Picea – Oxalis – Urtica – Brachythecium* soc is clearly favoured by tree stands which are open in places, or at least rather sparse. An obvious distinguishing feature of the community is the high content of species favoured by man's activity (hemerophilous species); these account for a large part of the species additional to those in the two foregoing sociations. Thus besides *Urtica dioeca* (dominant), there are *Anthriscus silvestris, Chelidonium majus, Galeopsis tetrahit, Geranium robertianum. Ranunculus repens, Scrophularia nodosa,* etc. The bottom layer is to some extent affected by the development of the field layer, and so it may be quite sparse where herbs are most abundant. The sociation is richer in species than any of those hitherto described, and it has no equivalent among the other communities of the peat land, in luxuriance and productivity in the field layer.

The number of coniferous tree seedlings in the *Oxalis*-spruce wood is particulary small. In the densest tree stands there are in many places no spruce seedlings within an area of 100 m^2 or even more, and in the parts rich in ferns and herbs it is not uncommon to find no seeedlings within an area of 500 m^2.

The three sociations of the *Picea – Oxalis* association can each be considered to belong to one of the variants into which Almquist (1929) divides the corresponding woodland community, *Picea – Anemone – Hylocomium* wood. However, the association is clearly different from Almquist's low herb-spruce wood in that *Brachythecium rutabulum* is dominant in the bottom layer and not *Rhytidiadelphus triquetrus.*

In Malmström's grouping, made on a purely physiognomical basis, this association as well as the two preceding ones falls into the low-herb-wood group (Malmström 1949, p. 60), which is less satisfactory for the peat land communities. The low-herb-woods have points in common with both the heath and meadow series of communities and are thereby linked to several of the units of middle rank (associations) distinguished here. These associations are also easily distinguishable from one another on a nutrient-ecology basis (as will be shown later). The reason that the herb-rich communities of the peat land do not fit directly into Malmström's system may lie in the fact that the "low-herb-woods" are distinguished for non-peaty land conditions, and mainly based on north Swedish forest communities.

Nor is there a type in Cajander (1921, p. 31) which alone covers those distinguished here—a parallel may be found in his *Oxalis – Maianthemum* type (OMaT) and better still in the fern type (FT). This partly depends on the tree layer, which for OMaT is usually made up of spruce (although a mixture with broad-leaved trees is common). FT also has spruce as the main tree species, but here the broad-leaved tree element is larger, and *Alnus glutinosa* is a constant and very common species. Moreover, besides birch there are other species recorded as rare here: *Ulmus glabra, Tilia cordata* and *Acer platanoides*. By their presence only, these last three species give a definite impression of Cajander's fern type.

v. Krusenstjerna (1945, p. 137) has described communities from the Uppsala region which are similar in respect to the bottom layer. Points in common are found in the *Eurhynchium* federation and in the *Mnium – Climacium* federation, the former in good habitats of medium moistness and the latter in wetter habitats.

Picea – Betula pubescens – Calamagrostis canescens – Melica nutans – Brachythecium rutabulum association. (VI. Grass-rich birch-spruce wood)

The main area of distribution of this association is a broad U-shaped region along the edge of the peat land in the west and south, forming the outermost fringe of Jägarmossen on that side. The other end bends off towards the north-east and north and cuts through the *Oxalis*-spruce wood in that part of the area (Fig. 3).

From the area south of the "islands" of non-peaty land in the north-west, and along the main part of the southern boundary of the peat land, the type community is developed. In other parts of its area of distribution the community is more divergent. As has been pointed out, the depth of peat is not large (maximum depth measured 1.3 m, and see Fig. 34). The transition of the community to the surrounding non-peaty land is not usually direct, but there is a border of varying width mainly consisting of a community similar to *Maianthemum*-spruce wood. However, in small stretches the grass community may reach right up to the edge of the non-peaty land.

The ground is generally quite even, with little left of the pronounced tussocky nature which was characteristic of the area at the time of drainage. To a certain extent, the remaining tussocks are hidden by trees or bushes now growing on them. Because the older trees are often localized on tussocks, the stand has gaps in the canopy throughout, with large open areas (up to several hundred m²) between the groups of trees in many places.

The tree stand consists mainly of birch (*Betula pubescens*) and spruce. At present, birch is the dominant tree species in volume, while there are more individuals of spruce. There is a large number of *Alnus glutinosa,* usually in a band towards the edge of the non-peaty land (Fig. 15), as evidence of the previously wetter environment, whereas the single pines which occur (Fig. 14) are a relict of the previous tussock vegetation.

This association is distinguished from the others by the large number of species in the field layer. Thus there may be 50—70 vascular plant species in a sample area, but it is seldom that any of the others have as many as 40 or more in the same surface area. Another characteristic of the association is the heterogeneity in the composition of the field layer. Thus of the 67 species of higher plants, excluding the trees but including tree seedlings, in sample area Jm 5 (Table 7), only 28 (42 per cent) are included in the ten 1 m² quadrats used in the vegetation analysis. In contrast, sample area Jm 1 (*Ledum*-pine wood) may be mentioned. In this 11 species (85 per cent of total) were included in the 11 quadrats.

The labile state of the vegetation is the background to this. The gaps in the stand which have never had trees growing in them, where the plant community is part of a rapidly progressing succession, continuosly afford new opportunities for colonization by plants whose ecological requirements are fulfilled by the changing conditions. A large number of plants have been favoured in this way during the development, including some which were once pioneer species (see, e.g. Tansley 1939, p. 217; Ellenberg 1956, p. 89) and now have a more or less relict character, and others which are now pioneers again. Some

Table 7. Vegetational analyses from the *Picea - Betula pubescens - Calamagrostis canescens - Melica nutans - Brachythecium rutabulum* ass (Type VI. Grass-rich birch-spruce wood). 17 and 20 July, 1959

Bushes	Jm 5	F-%	Jm 7	F-%	Jm 12	F-%	Average F-%
Rhamnus frangula	- - - - - - - - - -	0	1 1 - - - - - - - - -	18	1 - - - - - - - - - - - - - - -	6	8
Ribes alpinum	- - - - - - - - - -	0	- - - - - - - - - - -	0	2 - - - - - - - - - - - - - - -	6	3
Rubus idaeus	1 2 - 2 - - - 1 1 -	50	- - - 1 - - - - - - 1	18	1 - 1 1 - 1 2 - - - 2 1 1 - 1 2	63	46
Salix aurita	- - - - - - - - - -	0	- - - - - - - - 1 - -	9	- - - - - - - - - - - - - - - -	0	3
Sorbus aucuparia	- - - - - - - - - -	0	- - - - 1 - - - - - -	9	- - - - - - - - - - - - - - - -	0	3
Dwarf shrubs							
Vaccinium vitis-idaea	- - - - - - - - - -	0	- - + - - - - - - - -	9	- - - - - - - - - - - - - - - -	0	3
Grasses and herbs							
Agrostis canina	- - - - - - - - - -	0	- - - 1 + - - - - - -	18	- - - - - - - - - - - - - - - -	0	5
Anemone nemorosa	- - - - - - - - - -	0	- - - - - - - - - - -	0	- 1 - - - - 1 - - - - - - - - -	13	5
Angelica silvestris	- - 1 - - - - - - -	10	- - - - - - - - - - -	0	- - - - - - - - - - - - - 1 - -	6	5
Calamagrostis canescens	5 5 5 4 3 4 - - - 1	70	1 2 1 1 1 1 1 3 4 1 1	100	2 1 - 3 1 2 4 5 4 5 4 5 5 5 5 4	94	86
purpurea	- - - - - - - - - -	0	- - - - - - - - - - -	0	- - 2 - - - - - - - - - - - 2 -	13	5
Campanula trachelium	- - - - - - - - - -	0	- - - - - - + - - - -	9	- - - - - - - - - - - - - - - -	0	3
Cerastium holosteoides	- - - - 1 - - 1 - -	20	- - - - - - - - - - -	0	- - - - - - - - - - - - - - - -	0	5
Chamaenerion angustifolium	- - - - - - - - - -	0	- - - - - - - - - - -	0	- + - - - - + - - - - 1 - - - -	19	8
Dryopteris cristata	- - - - - - - - - -	0	- - - - - 1 - - - - -	9	2 - - - - - - - - - - - - - - -	6	5
spinulosa	1 - - - 1 - - - - -	20	- - - - - - - - 2 - -	9	- - - - - - - - - - - - - - - -	0	8
Epilobium montanum	- - - - - - - 1 - -	10	- - - - - - - - - - -	0	- - - - - - - - - - - - - - - -	0	3
Equisetum palustre	- - - - - - - - - -	0	2 2 2 1 2 1 3 3 3 1 2	100	- 1 1 - - - - - 1 1 1 1 - - 1 1	50	51
pratense	1 - - - 1 1 1 1 - 1	60	- - - - - - - - - - -	0	- - - - - - - - - - - - - - - -	0	16
Filipendula ulmaria	- - 1 - 3 3 - 1 1 3	60	+ - - - 1 + - - 1 - 1	45	1 - - 1 - 1 - 2 1 2 1 1 1 1 - -	63	57
Fragaria vesca	1 1 - - 4 2 4 4 - -	60	- 1 - - - - - - - - -	9	- - - - - - - - - - - - - - - -	0	19
Galeopsis tetrahit	- - - 1 - 1 - - - -	20	- - + - + - - - - - -	18	- - - - - - - 1 - - - - - - - -	6	14
Galium mollugo	- - - - - - - - - -	0	- - - - - - - - - - -	0	- - - - - - 2 - - - - - - - - -	6	3
palustre	- - 1 - - - - - 1 -	20	- - - - - + - - - - -	9	- - - - - - - - - - - 1 - - - -	6	11
uliginosum	- - - - - - - - - -	0	- - - - - - - - - + -	9	- - - - - - - - - - - - - - - -	0	3
Geum rivale	- - 1 1 - - - - - -	20	- 1 - - - - - - - - -	9	- - - - - - - - - 1 - - - - - -	6	11
Lactuca muralis	- - - - - - - - - -	0	- - - - - - - - - - -	0	1 - - - - - - - - - 1 - - - - -	13	5
Luzula pilosa	1 - 1 1 - - - - - -	30	- + - - 1 - + - - - -	27	2 - - + - - - 2 1 - 1 - - - - -	31	30
Lysimachia thyrsiflora	- - - - - - - - - -	0	1 1 1 - + - - 1 1 + +	73	- - 1 - 1 1 - - - - - - - - - -	19	30
Maianthemum bifolium	- - - - - - - 1 - -	10	1 2 4 4 2 - - 1 - - 1	64	- 1 2 1 1 - 1 1 - - - - - - - -	38	38
Melampyrum pratense	- - - - - - - - - -	0	1 1 1 1 1 1 1 1 1 1 1	100	- 1 - 1 1 1 1 - - - - - - - - -	31	43
Melica nutans	- - 1 - 3 1 - 1 - -	40	4 2 2 1 3 4 1 2 3 4 4	100	1 2 3 3 3 4 2 1 - 1 3 1 2 2 2 1	94	81
Milium effusum	1 2 1 3 2 1 1 1 - -	80	- 1 1 - 1 - - 2 - + -	45	2 3 2 1 3 1 1 1 2 2 1 1 1 2 1 1	100	78
Moehringia trinervia	- - 1 - - - - - - -	10	+ - + 1 - - - - - - +	36	1 + - + - + 1 1 - - - - - - - -	38	30
Oxalis acetosella	1 - 2 2 1 3 4 1 - -	70	- - - - - - - - - - -	0	2 1 - - + - - 3 2 1 - - - - - -	38	35
Paris quadrifolia	- - - - - - - - - -	0	- - - - - - - - - - -	0	- - - - - - + - - - - - - - - -	6	3
Poa nemoralis	1 - 1 1 2 1 1 - - -	60	- - - - - - - - - - -	0	- - - - - - - - - - - - - - - -	0	16
Potentilla erecta	- - - - - - - - - -	0	+ + - 1 1 1 - 1 - - -	55	- - - - - - - - - - - - - - - -	0	16
Pyrola minor	- - 1 - 1 - 1 - - -	30	+ - - - - - - - - - 1	18	- - - - - - - - - - - - - - - -	0	14
rotundifolia	- - - - - - - - - -	0	1 - - - - - - 1 - - -	18	- - 1 - - - - - - - - - - 1 - -	13	11
Ranunculus repens	- - - - - - - - - -	0	- - - - - - - - - - -	0	- - - - 1 - - - - - - - - - - -	6	3
Ramischia secunda	2 - - - - - - - - -	10	- - 1 - + - 1 - - - -	27	- - - - - - - - - - - - - - - -	0	11
Rubus saxatilis	- - - - - - 1 - - 1	20	3 3 1 3 1 - 1 2 1 2 -	82	- 2 - 1 2 2 1 - - 1 - - - - - -	38	46
Scutellaria galericulata	1 1 1 1 1 - - - - -	50	- - - - - - - - + + -	18	- - - - - - - - - - - - - - - -	0	19
Trientalis europaea	- 1 - - 1 1 1 1 - 1	60	- 1 1 1 1 - 1 1 1 1 1	82	- 1 - 1 1 1 1 - - - - - - - - -	31	54
Tussilago farfara	- - - - 1 - - - - -	10	- - - - - - - - - - -	0	- - - - - - - - - - - - - - 1 -	6	5
Veronica chamaedrys	- - - - - - - - - -	0	- - - - 1 + - - - - -	18	- - - - - - - - - - - 1 - - - -	6	8
officinalis	- - - - - - 1 - - -	10	- - - - - - - - - - -	0	- - - 1 1 - - - - - - - - - - -	13	8
Vicia sepium	- - - - - - - - - -	0	- - - - - - - - - - -	0	- - - - - - - - - - - - 1 - 1 -	13	5
Viola epipsila	2 1 2 - 1 - - - - -	40	2 2 1 2 1 3 2 2 2 2 1	100	- 1 1 2 1 1 2 - - - - - - - - -	38	57
palustris	- - - - - - - - - -	0	- - - - - - - - - - +	9	- 2 1 1 1 1 + - - - - 1 1 - 1 -	56	28
riviniana	- - - - - 1 1 - - 2	30	2 1 1 - 1 - - - - 1 1	55	- - - - - - - - - - - - - - - -	0	24
Mosses							
Brachythecium reflexum	- - - - - - - 1 - -	10	- - - - - - - - - - -	0	- - - - - - - - - - - - - - - -	0	3
rutabulum	- 4 4 1 4 2 4 4 4 -	80	1 + 2 2 2 2 1 1 + 3 1	100	4 1 1 1 + 1 1 4 5 1 - 2 2 1 2 2	94	92
salebrosum	1 1 1 - 2 - 1 1 1 1	80	- - - - 1 - - - 1 1 -	27	1 1 2 + - - + 1 1 - 3 1 1 - - -	63	57
velutinum	- - - - - - - - - -	0	- - + - - - - - - - -	9	1 - - - - - - - - - + + - - - 1	25	14
Dicranum scoparium	1 - - - 1 - - - - -	20	- - - - - - - - - - -	0	- - - - - - - - 1 - - - - - - -	6	8
Eurynchium zetterstedtii	- - - - - - - - - -	0	- - - - - - - - - 1 -	9	- - - - - - - - - - - - - - - -	0	3
Hylocomium splendens	- - - - - - 1 - - -	10	- - + - - - - - - - -	9	- - - - - - - - 2 - - - - - - -	6	8
Mnium affine	- - - - - - - - - -	0	- - - - - - - + - - -	9	- - + - - - - - - - - - - - - -	6	5
cuspidatum	- - - - 1 - 2 - - -	20	- - - - - - - - - - -	0	- - - - - - - - - - - - - - - -	0	5
rugicum	- - - - - - - - - -	0	- - - + + - - - - + -	27	- - - - - - - - - - - - - - - -	0	8
seligeri	2 - - - - - - - - -	10	- - - - - - - - - - -	0	- - - - - - - - - - - - - - - -	0	3
Plagiothecium denticulatum	2 - - - 1 - - 1 1 -	40	- - - + - - - - - - -	9	- - - - - - - - - - - 1 - - - -	6	16
Pleurozium schreberi	- - - - - - - - - -	0	- - 2 1 - - - - - - -	18	- + - - - - - - 1 - - - - - - -	13	11
Rhytidiadelphus triquetrus	- - - - - - 1 - - -	10	- - - - - - - - - - -	0	- - - - - - - - - - - - - - - -	0	3
Rhodobryum roseum	- - - - - - - - - -	0	- - - - + - - - - - -	9	- - - - - - - - - - - - - - - -	0	3
Cephalozia bicuspidata	1 - - - - - - - - -	10	- - - - - - - - - - -	0	- - - - - - - - - - - - - - - -	0	3
Lophocolea heterophylla	4 1 - - 4 - 1 1 - -	50	- + + 1 - - - - - - +	36	1 1 - - - - - - - 2 1 - - - - -	25	35

F = Frequency

Additional species (degree of cover 1 or +): Jm 5. Acer platanoides (seedlings), Anemone nemorosa, Anthriscus silvestris, Athyrium filix-femina, Calamagrostis arundinacea, Carex digitata, C.elata, C.nigra, Cirsium arvense, C.vulgare, Daphne mezereum, Deschampsia caespitosa, Dryopteris cristata, D.filix-mas, Galium uliginosum, Juniperus communis, Lastrea dryopteris, Lonicera xylosteum, Lysimachia thyrsiflora, Melampyrum silvaticum, Paris quadrifolia, Pinus silvestris (seedlings), Poa remota, Potentilla erecta, Ranunculus auricomus, Rhamnus frangula, Lathyrus pratensis, Roegneria canina, Salix myrsinifolia x aurita, S. cinerea x aurita, Solidago virgaurea, Sorbus aucuparia, Stachys silvatica, Taraxacum sp., Urtica dioeca, Vaccinium myrtillus, Valeriana officinalis, Veronica chamaedrys, Viola palustris. - Ptilidium ciliare.

Jm 7: Agrostis tenuis, Angelica silvestris, Carex elata, Chamaenerion angustifolium, Cirsium vulgare, Dryopteris filix-mas, Fraxinus excelsior (seedlings), Paris quadrifolia, Populus tremula (seedlings), Salix myrsinifolia, Vaccinium uliginosum, Viburnum opulus. - Bryum sp., Dicranum scoparium, Pohlia nutans, Rhytidiadelphus triquetrus, Ptilium crista-castrensis.

Jm 12: Agrostis canina, Anemone hepatica, Athyrium filix-femina, Cirsium vulgare, Deschampsia flexuosa, Dryopteris spinulosa, Epilobium montanum, Fragaria vesca, Lastrea dryopteris, Lysimachia vulgaris, Poa nemoralis, Potentilla erecta, Stellaria graminea, Vaccinium vitis-idaea, Viburnum opulus, Viola riviniana. - Mnium rugicum.

of the species may be expected to remain when the tree stand becomes closed, others will probably disappear from the community.

The following are regarded as relicts:

Carex elata
nigra
Equisetum palustre
Iris pseudacorus
Lysimachia thyrsiflora
vulgaris
Pinus silvestris
Scutellaria galericulata

The following are regarded as pioneers:

Angelica silvestris
Anthriscus silvestris
Taraxacum spp.
Campanula trachelium
Calamagrostis spp.
Dryopteris cristata
Lathyrus pratensis
Potentilla erecta
Ranunculus auricomus
Cirsium spp.
Tussilago farfara
Valeriana sambucifolia
Viola epipsila
palustris

Most of the species in this latter group are seldom found in the closed stand of the spruce wood—towards which the community is developing—as evidenced by analyses from such areas (sample areas Jm 3 and Jm 4, Table 6).

Finally, there is a group of species which has apparently not been affected very much by the change in water condition brought about by the drainage. A part of the earlier tussock vegetation was affected only to a small extent by the high water table before drainage and was adapted to the moderately moist environment which prevailed in the upper parts of the tussocks. The lowering of the water table by drainage has not therefore caused any radical change in the habitat conditions for this group of species and they therefore continue to grow fairly undisturbed. *Vaccinium* spp., *Salix* spp. and other bushes, *Fragaria vesca, Geum rivale, Oxalis acetosella, Paris quadrifolia* and *Trientalis europaea* belong to this group.

It is mainly the two grass species, *Calamagrostis canescens* and *Melica nutans,* which distinguish the field layer of this community from the others. In patches, practically always in more open stands or under gaps in the canopy (Fig. 11), these grasses, either alone or together, form pure stands. Untypical conditions obtain under a dense tree canopy or on thin peat with a fairly impermeable layer under it (in the north-west part of the area). However, it has not generally been difficult to determine the boundaries of the community since even when it is least typically developed it retains conspicuous features of the type community. The characteristic species *Calamagrostis* and *Me-*

Fig. 11. The formerly very wet fen areas in Mjölnar fen are still, in several parts, free from trees. The field layer is dominated by *Melica nutans*, *Milium effusum* and *Calamagrostis canescens*.—June 1960.

lica are found as a rule even in small areas. In addition, the particularly sharp distinctions between the tree stands help in drawing the boundary between the community and the neightbouring ones. Thus in comparison with the surrounding community the grass-rich birch-spruce wood has a considerably lower average age and is less closed. In addition, it has different proportions of the various tree species. These factors, as mentioned above, also have a marked effect on the field layer.

As far as it is possible to judge, there are at least three different communities of lower rank within the association. However, the analysis material is at present too sparse to allow a close examination of these, but some observations will be put forward.

In the north-west part of the community, under the thin peat layer (Fig. 34) there is a layer of almost impermeable clay, which greatly limits vertical water movement. Because of the slightness of slope of the surface, horizontal run-off is also reduced. This condition was more pronounced when and immediately after the ditches were laid down, but during periods of snow melt it is still obvious. This part serves also as a catchment area for melt water from the surrounding areas of non-peaty land, which here slopes fairly steeply in towards the peat land. These factors have probably considerably hindered the trees to grow up the same extent as in the other drained areas (Ch. 6).

The main feature of the field layer in this part is its content of large-leaved herbs, which may be dominant in many places. In shady and moist places *Filipendula ulmaria* and *Tussilago farfara* sometimes cover the ground completely and only a few slender grass-leaved plants like *Roegneria canina, Milium effusum* and *Calamagrostis canescens* can grow with them. In this mixed community *Urtica dioeca* and *Rubus idaeus* may also grow densely, mainly in the better illuminated patches under the gaps in the canopy.

Where the tree stand is very sparse or in glades with a high light intensity the composition by species is variable. The most common are *Roegneria canina* (dominant), *Scrophularia nodosa, Valeriana sambucifolia, Filipendula ulmaria, Cirsium heterophyllum* and *Milium effusum.* Of the more interesting species found in this environment, the rare occurrence of *Ulmus glabra* is worth mentioning.

The easternmost part of the area of the association has a field layer which is a transition between the type just described and the grass-dominated main part of the community. Thus there is a considerable number of broad-leaved plants but the grass element is conspicuous too. However, the field layer is very variable in composition, because the boundaries with several of the other communities occur here. *Calamagrostis* and *Melica* are always present, as a common feature of the different variants of the community. They are often in combination with *Fragaria vesca, Rubus saxatilis* or *Oxalis acetosella,* but may also be together with *Vaccinium vitis-idaea* on the sides of tussocks or near the non-peaty land. However, the most characteristic feature of this part is the particularly delightful-looking *Anemone nemorosa* community in spring and early summer. Only here in the whole of the area of peat land is there a well-developed *A. nemorosa* community (however, see also above, *Maianthemum*-spruce wood). The tree layer is comparatively even, with well-grown spruce in a stand which is very closed in parts. *Betula pubescens* and *Alnus glutinosa* are less important.

In its typical form the association is represented by sample areas Jm 7 and Jm 12 (Table 7; Fig. 12), which show immediately that the species of the heath series are very sparsely represented. The constant species of the field layer of the community are conspicuous physiognomically, but it should be pointed out that not always either *Calama-*

Fig. 12. Grass-rich birch-spruce wood. Within some areas there was at the time of drainage a fairly even bush layer of birch, which now has given rise to a comparatively thin birch stand. It can be seen how spruce begins to invade. Scattered alders from the wet period are also seen.—October 1960.

grostis canescens or *Melica nutans* alone reaches complete dominance. However, the two together often form a completely closed stand, which after the pressure of the winter snow covers the ground with a tight, thick blanket. In several places *Milium* is important in the grass vegetation. *Calamagrostis purpurea* is found in the community, but seldom plays an important part.

It should now be apparent that one of the characteristic features of the community is the large quantity of narrow-leaved grass-like plants. The broad-leaved herbs which grow in the main part of the association are of secondary importance to the physiognomy, although they may form an understorey of the field layer well-developed in patches and may have a high degree of cover. *Viola* species, *Maianthemum bifolium, Rubus saxatilis, Fragaria vesca* and the sterile *Filipendula ulmaria* stands, for example, may form part of this layer.

The grass-rich birch-spruce wood has its equivalent, in Uppland, in Almquist's (1929, p. 324) *Calamagrostis lanceolata (purpurea)* – rich deciduous wood. He characterized this type as a stage of development mostly on drained peat, and this fits the situation described above.

Besides the vegetation types named above (I—VI), there are many others too on drained peat lands, as found on a survey of other sites in Uppland in particular. However, most of them seem to be variations of the communities described. Thus, the main types met with may be characterized as dominated by dwarf-shrubs, herbs, or grasses as on Jägarmossen. A conspicuous type, only weakly developed on Jägarmossen, is a community characterized by high degree of cover for *Lycopodium annotinum*. It has been observed in typical form on well-drained sites poor in phosphorus and potassium but fairly high in nitrogen (seen e.g., on Prästgårdsängen and Måsmossen, E Uppland, and Tärnmossen, W Uppland).

The tree layer varies depending on water table, successional stage and nutrient conditions. Early developmental stages with either pine or birch are seen in many places (e.g. Kerstinbo mire, W Uppland). Spruce is seen as pioneer only as admixture to birch under which it gets shelter from frosts in late spring, e.g. on Gisselås mire in Jämtland (poorly drained). Generally the "climax" wood is spruce, except for very wet and nutrient deficient sites, where pine is the only tree species.

C. The woody species

One of the main objects of this paper is to attempt to define the habitat conditions prevailing on an area of drained peat land. Thus in the two next parts, a group of habitat conditions, viz., those measured by soil analysis, will be discussed. In addition, there follows below a general examination made indirectly, i.e., by seeing how such properties have contributed to the distribution and success of certain species. Points about the habitat requirements and the apparent vigour of the species will also be included in this autecological section, but there is no detailed study of any particular factor.

It may seem arbitrary which species or group of species are chosen in such a context. But since it has not been practically possible, nor desirable, to treat all the species of Jägarmossen in this way, it was most suitable to chose a group of plants with some feature in common. The woody plants make up a group with a fairly large number of species, and several of them have a number of known general qualities of habitat preference (though not as a rule known precisely).

It is known, for example, that certain species have a relatively small requirement for nutrient availability, if other conditions for growth are favourable. Such species have a wide ecological range in respect to nutrient factors and can grow on good or on less good soil. But on better soil they fail to compete with species which have a greater demand, either generally or specifically, on the plant environment. The distribution of pine and spruce, which are opposites in this respect, can be compared (below).

There are also species which have a wide habitat range and are relatively insensitive to competition, e.g., *Rhamnus frangula* and *Sorbus aucuparia*. Both these species have a very even distribution throughout Jägarmossen with the exception of the poorest part, where they are absent.

Because of the unevenness of the substrate and also its change with time in some parts, there is a rapid selection of species which get the opportunity to colonize new areas. A study of the distribution also gives valuable information to help in understanding these circumstances. With the data on the distribution of plant nutrients (to be presented in part II) it is possible to study the relation between the distribution of the plants and the plant nutrient conditions.

Distribution maps for the majority of tree and bush species are included, with a simplified vegetation map as a base, so that the distribution can be seen clearly.

The data below have been arranged so that the main tree species (spruce, pine, birch and alder) come first; the others follow in systematic order.

Spruce *(Picea abies)* is quantitatively far and away the most important of Jägarmossen's tree species. From the descriptions above it is apparent that it is a member of all the different plant communities, although it does no always form stands. Thus in the centre of the peat land (*Ledum*-pine wood) and in the nearest parts of the adjacent community (bilberry-pine wood) it is represented only by scattered dwarf trees. But in the middle parts of the bilberry-pine wood it is already an important element in the understorey and towards the outer boundary the upper tree layer has spruce with increasingly higher frequency. Its more important continuous area of distribution lies north of the main run-off channel where a spruce stand of very uniform appearance covers practically the whole area in the east-west direction. The occurrence of spruce south of the main run-off channel is less continuous. The most important but at the same time the most dissimilar sites in this part are Långholmen, with Jägarmossen's most impressive and even spruce stand, and Mjölnar fen where spruce still does not make up more than 30—40 per cent of the volume of timber of the stand.

It is clear that, except for the parts dominated by pine, the present distribution of spruce coincides in its main features with that which existed before drainage, since spruces which are older than the time since drainage have been found in all the other communities. But even the area now under pine was not completely lacking in spruce before drainage. Within the sample areas examined in these communities no spruces have been examined which date with certainty from the pre-drainage time, but on the other hand there are spruces which are at least 60 years old (at stump height), i.e., date from before drainage, in some places in the bilberry-pine wood close to the *Ledum*-pine wood.

Tree age at breast height is usually less than the time since drainage, which indicates that the distribution even of young spruce trees was very much restricted before the ditching took place.

A clear feature in the picture of spruce distribution is that the species has certainly not yet reached its definitive limit in the pine communities, but is in a stage of rapid colonization of land previously without spruce. It is hardly possible to say more exactly how fast it is spreading, but it is clear that the area of distribution is increasing fairly rapidly. It is not now possible to determine where the final boundary will lie during the next tree generation. The most important factor limiting continued advance will undoubtedly be the low availability of the most important nutrient elements in the central part. In this connection the importance of the effect of a high water table in the peat during a large part of the vegetation period may be mentioned. This is limiting to a certain extent, and since it determines the depth of root penetration it also determines access to nutrient supply. This is not so important for potassium and phosphorus since these are mostly in the surface parts of the peat. However, the position of the water table is very important for nitrogen supply, perhaps not primarily, but through the secondary effect of bad aeration and the consequent slow or sometimes non-existent breakdown of the organic material in the surface layer of the peat.

The age of the spruce in the sample areas studied is particularly variable, and this shows the unevenness of the sparse stands which were present at the time of drainage. The average age of the trees examined is in general greater than the time since drainage, in spruce-dominated stands. Older trees are found in the peripheral parts, where the peat is comparatively thin, and also in more central parts on much thicker layers of peat. The maximum known age is from the southeast periphery where a spruce more than 130 years old has been found, but in the Långholmen stand there are also spruce trees more than 100 years old. It is also worth mentioning that in the grass-rich lagg areas in the south and west there are fairly old trees, e.g., in sample area Jm 5 there are spruce trees about 100 years old. In all these cases the trees have grown on tussocks, now shrunken.

Maximum diameter and height have also been measured within the areas. Thus in sample area Jm 8 there is a spruce with a diameter of 44 cm (height 22.9 m), and in Jm 2 one of height 25.9 m (diameter at breast height 24 cm).

In the more favourable localities the diameter growth of spruce has been good after drainage and on average the highest value has been achieved 10—15 years after. However, in other localities maximum diameter growth has not been reached until nearly 30 years after drainage (see Ch. 6).

For single trees in some years the growth in diameter has been as much as 15—20 mm, while an average of 10 mm in the measured trees is not uncommon even over long periods.

Branch abcission is mostly not very active. The only stand where there is satisfactory saw-timber quality is in Långholmen. The crown boundary—i.e., the lowest green parts of the crown—which is here taken as a relative measure of the occurrence of branch abcission, is an average of 5.1 m above the ground (1.6—10.0 m) in sample area Jm 2, and 5.9 m (2.5—9.0 m) in Jm 9. The ratio of length of crown to total tree height, the crown ratio, is hence as high as about 75 per cent. In Mjölnar fen, where the trees often form groups, the crown ratio is highest ($\geqq 90$ per cent). This stand is also comparatively young. The crown boundary for the three sample areas here is 1.2, 0.8 and 0.6 m (0.1—2.7 m) above the ground, which means that the lower whorl of branches is often entangled in the luxuriant grass field layer. There are dead branches remaining on the trees practically always right down the trunk, in all stands. As a consequence, timber quality is rather variable, but as a rule considerably reduced, and this reduction in quality is mainly in the valuable main trunk.

It should be pointed out that the degree of closure of the stand does not seem to have been of much significance for the amount of branch abcission (see Stålfelt 1932). Judging from observations made on other similar peat lands, e.g., Bjurfors district in Västmanland (see figs. in Lundberg, 1952), relatively little branch abcission seems to be a fairly characteristic feature at least for the first generation of spruce on drained peat land (see Börjeson 1937). The newly-formed stand begins from individuals of very varying age, but all the trees from the time before drainage are characterized by very slow growth up until drainage, and have very short distances between the whorls of branches as compared with those afterwards. These older branches are very resistent to rotting, and have a tendency to remain on the trunks until a late stage in the life of the tree. It is thus not unusual to find dead branches more than 60 years old left on a tree which is itself not more than 10 years older.

Observations have been made of the tree root distribution at different depths in the soil and of the maximum root depth. These observations are only of a general nature. These features of the roots are of particular interest in respect to the later discussion of the size of the tree's nutrient supply in the soil.

Since the previously described plant communities contain spruce stands with very great variation in age, it is not possible to make a comparison between the plant community and the tree root depth. The general features of spruce root distribution at the various localities will, however, be mentioned.

The deepest spruce roots have been observed in sample areas Jm 2 and Jm 4, where they reach down to 60 cm under the soil surface. The maximum depth here is usually between 45 and 55 cm. On the other hand, the least maximum depth is in the grass-rich communities (Mjölnar fen). In sample area Jm 7 no roots deeper than 30 cm have been found. The average age of the spruce here is also generally considerably lower than in the other places.

For two of the investigated sample areas (Jm 3, Jm 5) the maximum root depth is determined by the sediment layers (clay gyttja, clay) which lie under the peat. Spruce roots have a marked tendency not to penetrate the dense sediments. However, they often run in the boundary between sediment and peat.

The levels at which roots are most frequent are considerably shallower than those just quoted. For the great majority of sample areas there is a zone richly woven through by roots from 1 or 2 to about 25 cm below the surface. It is mainly fine roots which are found at greater depths. Coarse ones (> 15 mm in diameter) are only exceptionally deeper than 20 cm. Sample area Jm 9 was exceptional in that there was even and abundant root distribution down to 35 cm.

A common phenomenon on peat land where the peat cover has shrunk considerably and where some of the trees originated on old tussocks or stumps is the appearance of thick stilt roots, which give

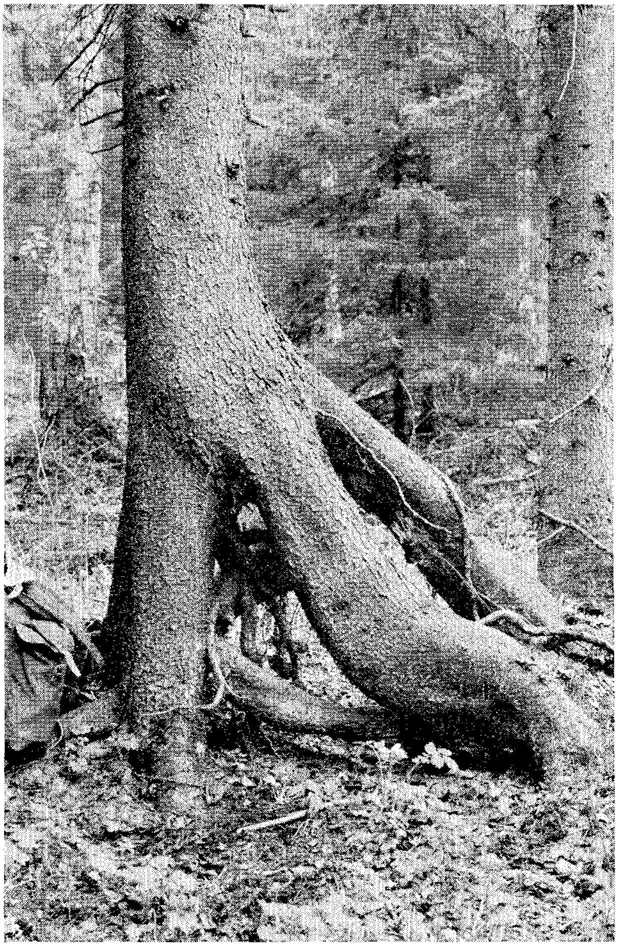

Fig. 13. *Oxalis*-spruce wood (sample area Jm 8). Trees are encountered, especially at the margin of the peat land, which have grown on old, more or less shrunken peat tussocks.—May 1960.

the vegetation a mangrove-like look (Fig. 13; see also Lundberg 1952, p. 37). When these roots were first laid down they followed the contours of the tussock or stump, directly under the soil surface; and then when it rotted and fell away they were exposed like legs of a tripod. This feature occurs particularly in the peripheral zones of the peat land where the distance to the mineral layers underneath is fairly short.

Pine ***(Pinus silvestris)***. A picture of the main area of pine distribution has already emerged incidentally from the description of the occurrence of spruce. Thus pine is the characteristic tree of the central

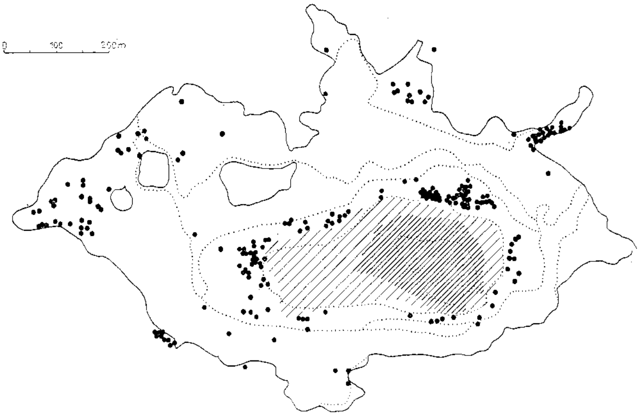

Fig. 14. *Pinus silvestris*. Dense shading: pine dominant in the tree layer; thin shading: pine with an understorey of spruce and birch; points: isolated occurrences.

parts of the peat land, where it is ubiquitous in the parts with peat which is least humified and poorest in nutrients. When the quality of the peat improves out towards the edges, spruce is more common but at the same time the pines have greater diameter and height. This means that right up to the boundary of its general distribution pine always makes up the largest proportion of the volume of the stand.

As well as in the central section, pine is found as isolated examples in all the plant communities which have been distinguished. In these cases it certainly constitutes remains of the earlier mire vegetation. Except in the present-day pine communities, spontaneous establishment of pine after drainage has occurred only to a very small extent; and the conditions in the stands would hardly be expected to be such as to favour extensive establishment of pine. Pine seedlings' requirement for high light intensity excludes them from the well-closed spruce stands. An obvious feature in the picture of distribution (Fig. 14) is thus the very few occurrences of pine in the luxuriantly-grown, herb-rich stands north of the main run-off channel. However, scattered examples have been found on this side, even from after ditching, as is shown both by field notes and by some quite well-preserved stumps. Where the trees still remain, a late stage of the uneven competition for light with spruce can now be seen. This is particularly so in the northern part of the peat land (the unnamed area on the vegetation map, Fig. 3). The pine crowns are shaded by spruce to such an extent that it probably will not be many years before the pines are completely dead. The pines in the western part of the peat land are also relicts, but here there is still not sufficient competition from other trees to inhibit pine growth. However, the very few pines in the main part of Mjölnar fen belong to the category that will not survive much longer.

The growth conditions have previously been partly mentioned Some supplementary observations will be made here. In the middle part of the *Ledum*-pine wood (sample area Jm 1) the dominant trees reach 12—14 m in height. Out towards the edges of this association and in the next, the tree height rises continuously to 15—17 m in the outer part of the bilberry-pine wood (sample area Jm 6). The tallest are single pines in sample areas Jm 9 and Jm 10, which are 19.4 and 18.6 m. The present difference between different areas will certainly persist for a considerable time, because of the marked difference in conditions of production between the central and edge parts of the pine wood area. In addition, the outpost trees will eventually disappear, because of competition from spruce or interference by man.

The diameter of pine is fairly small, 18—25 cm at 1.3 m above ground (breast height). The lowest values are for the *Ledum*-pine wood and the highest for the bilberry-pine wood. Since the trees in the two habitats are about even-aged, this is an illustration of the effect of habitat on the growth of the trees.

The growth-form of the pines is somewhat variable, depending on the locality, but it is in general such that good quality saw-timber will not be produced by the present stand generation. Broad crowns with coarse, spaced-out branches are the normal developmental type in the *Ledum*-pine wood and bilberry-pine wood, and are otherwise a common feature of pine growing on a peat substratum (see Sylvén 1916, p. 205). The solitary pines in the peripheral parts of the peat land are of a rather different type charcterized by a long branch-free trunk and a more or less tuft-like crown. But even here there are pines with thick dead branches extending a long way down the trunk. The large number of pines on the bay projecting out towards the north-east (Fig. 14) and also others in the immediate neighbourhood of the non-peaty land have a growth-form which is identical with that which prevails on the non-peaty land. Thus the trees all reach a height of 20 m or more, and have quite a straight stem, branchless until fairly high up.

On the majority of favourable mineral soils pine has a fairly extensive and deep root system (Sylvén 1916). However, its extent is affected by the conditions of the habitat, in particular by the water table. Arnborg (1953, p. 63) considers that in general no roots go deeper than 50—60 cm in good soils. In a young pine stand Arnborg (1951) has found pine roots at a depth of 65 cm; in the same place grass roots extended to more than 1 m deep. Heikurainen (1955) points out that there is little reason to look for pine roots deeper than 20 cm on peat lands, even if drained. He found that the uppermost 5 cm of the soil contains 70 per cent of all roots; and the uppermost 10 cm contains 90 per cent. Root length per unit of surface, in a fully-grown vigorous stand, was estimated at 1 km per m^2. The root maximum is already attained in a young stand and there is afterwards little increase, although the roots go deeper as the age of the stand increases (Heikurainen 1955, p. 79). Laitakari (1927) carried out investigations on the same lines.

Nowhere on Jägarmossen is the pine especially deep-rooted, and the root system is usually quite horizontal. The high water table has doubtless previously been the main factor determining the depth of root penetration (see water table measurements given in part II). Thus, as expected, the shallowest root development is in the *Ledum*-pine wood, where the bulk of roots is between 1 and 10 cm and where the greatest recorded root depth is 20 cm. In the neighbouring communities the pine root depth is somewhat more and the "relict" pines in the bilberry-spruce wood often have roots between 1 and 30 cm, with the deepest observed roots at 80 cm.

Birch *(Betula pubescens)* is quantitatively the most important deciduous tree. In spite of careful searching it has not been possible to find any large tree-formed example of *B. verrucosa* on the drained peat land, although this species is common on the surrounding non-peaty land. It is generally known, and confirmed by all who have worked on the ecology of these two birches, that *B. pubescens* occurs in moister habitats and *B. verrucosa* on drier (see, for example, Arnborg 1943, 1946, 1953; Lagerberg 1950; Lindquist 1953; Malmström 1949, among more recent authors).

Within the boundaries of the peat land, *B. pubescens* has the widest range of habitats. It occurs in all the plant communities, in the poor *Ledum*-pine wood as well as in the luxuriant herb-rich *Oxalis*-spruce wood, but in very variable quantities. This can probably be attributed only to a very limited extent to soil properties. Competition from spruce and interference by man have probably been more important in determining the distribution and amount of birch.

Birch is now most common in Mjölnar fen where it dominates the stand with respect to volume. In the three sample areas sited here it comprises between 39 and 75 per cent of the number of stems, and 58—94 per cent of the stem volume. Historical factors have been an important cause of this. At the time of drainage there was a copious sowing of birch in Mjölnar fen, as in other parts near the non-peaty land (see bilberry-spruce wood), at the same time as the dwarfed birches in this part of the peat land began to grow rapidly (see diagram of annual rings, Ch. 6). Subsequent development proceeded in different directions, as reflected by the different proportions of the various tree species in the stands at the present time. For example, the area around sample area Jm 12 has to a large extent retained its original character (94 per cent birch, 6 per cent spruce). Spruce first became established very recently and forms only a very weak understorey. In contrast, sample area Jm 5 is an example of an area with a relatively weak birch dominance (58 per cent birch, 42 per cent spruce).

Apart from these places, birch alone is not an important stand-building species, but contributes quite a moderate amount of the volume of the stand ($\leqq$ 20 per cent).

On Jägarmossen, the growth of *B. pubescens* persists for a considerably shorter period than that of the other tree species studied (spruce, pine and alder). This is a generally known phenomenon but it is not usual for growth to decrease sharply at as early an age as 30 years, as happens for the birch in Mjölnar fen. The reason for this is not known and cannot be explained by data available.

As a rule, birch has a root system which is more extensive and deeper than either spruce or pine in the places where the trees grow together. This has been shown, generally, in an extensive study by Laitakari (1935, p. 200).

Birch does not generally show the same tendency as spruce to avoid root growth down into the mineral sediments, when these lie at a moderate depth. In sample areas Jm 3 and Jm 5, where peat thickness is 40—50 cm, there are fine birch roots in the clay-gyttja and the clay, but not more than 10 cm down in this material. The maximum recorded root depth was in Jm 10 and Jm 12, where single roots reach nearly 80 cm deep. In Jm 7, where spruce roots are not seen below 30 cm, birch roots go down to 60—65 cm. But birch, like pine and spruce, has the major proportion of the roots much nearer the surface than this. The layer 2—30 cm below surface is an average depth for abundant and even occurrence of roots.

In many places birch has considerable dimensions, scarcely less than those of spruce and much greater than those of pine. However, like spruce, it cannot develop to large trees within the *Ledum*-pine wood, but there forms sluggishly-growing dwarf trees.

The tallest birches are in the closed, rapid-growing spruce stand along the north and east edge of the area, where their tops are 1.5—2.5 m under those of the spruce, i.e., 18—20 m high. The tallest measured tree is 23.8 m (diameter at breast height 43 cm). In sample area Jm 10, where the stand consists of pine, spruce and birch in the proportions by volume 10: 70: 20, birch is a little (0.4 m) taller than spruce, whereas pine is about 3 m shorter. In Mjölnar fen, as has been mentioned, birch is still more important. However, the evening-out which is going on is exemplified by sample area Jm 5, where the highest layer (birch) is now only 1.4 m over the tops of the spruce (16.8 m as opposed to 15.4 m). The major part of Mjölnar fen is represented by Jm 7 where birch is 4.7 m taller than spruce (17.1 m as against 12.4 m); whereas in Jm 12, with complete birch dominance, the maximum height of birch is 17.0 m as against 7.6 m of spruce.

Birch has approximately similar diameter dimensions to spruce. In Jm 3 and Jm 4, birch maximum diameter at breast height is 40—43 cm, but it is usually not more than 25—30 cm throughout the whole extent of the stand north of the main run-off channel. The same diameter is attained in Mjölnar fen. In Jm 5, spruce has a larger diameter than birch at breast height (22.4 cm as compared with 21.1 cm) although its height still remains less (see above).

There is a large probability that within a very limited time *B. pubescens* will no longer be one of the more important tree species on Jägarmossen. As a pioneer tree it rapidly widened its area of distribution at the time of drainage but gradually the coniferous trees, and spruce in particular, grew up and competition from them became more and more difficult to withstand. In addition, forest management is directed towards eliminating birch from the stands.

Alder ***(Alnus glutinosa)*** is the remaining tree species which has been included in the production study. This implies that in some of the sample areas alder was present in such quantities that it was necessary to take its contribution to production into account. However, this is generally quite small, a few per cent of the total volume, although in one case (Jm 8) it is rather above 20 %.

Like the preceding species, alder occurs in all the plant communities, but it has a very characteristic pattern of distribution with highest frequency in the marginal zone of the peat land (Fig. 15). Hence the distribution coincides almost completely with that of plant communities containing *Oxalis* and also gives an indication of the direction of development of the wet alder-birch fen after drainage (Ch. 5). The following species are the most characteristic of those occurring to-

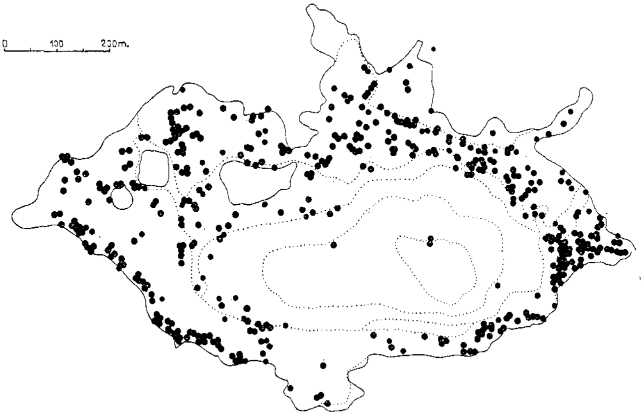

Fig. 15. *Alnus glutinosa.* The map includes mainly tree-forming alders.

gether with *Alnus glutinosa.* The majority of these have high demands on the substratum.

Anemone nemorosa
Anthriscus silvestris
Chamaenerion angustifolium (ster.)
Chelidonium majus
Filipendula ulmaria
Galeopsis tetrahit
Geranium robertianum
Geum rivale
Iris pseudacorus
Lactuca muralis
Lysimachia vulgaris
Paris quadrifolia
Ranunculus repens
Solanum dulcamara
Urtica dioeca

The group includes also *Actaea spicata* and *Stachys silvatica,* which are rather rare. Many of these are regarded as "nitrate species" (Hesselman 1917; see also Romell 1939a). Bushes characteristic of the environment are *Lonicera xylosteum, Rhamnus frangula* (common in most of the peat land communities, but typical of the old alder fen), *Ribes alpinum* and *Viburnum opulus.*

It is interesting that communities which correspond almost exactly with this combination of species, in different geographical regions, have been described by several authors, e.g., Eriksson (1912), Hesselman (1917), Halden (1928), in Sweden; Bornebusch (1914) in Denmark; Kujala (1924), Hildén (1929), in Finland; Lorenz (1858), but a type which is not so clearly defined, Paul (1907), Tüxen (1937) with *Alnetum glutinosae typicum,* Erlenbruchwald, Knapp (1949) with Schwarzerlen-Bruchwälder (*Alnetalia glutinosae*) in Germany; etc. These descriptions are usually of areas unaffected by drainage. The flora which occurs together with *Alnus glutinosa* thus shows a clear tendency to persist, even when the habitat has undergone such a drastic change as that imposed by drainage. In addition, on several occasions alder has been thinned out after so that in patches there is only the field layer flora of the alder-birch fen remaining. The bottom layer has usually lost the moist habitat mosses which it contained and hence lost its fen character.

Pettersson (1958, p. 258) has published similar observations of stability in the vegetation, based partly upon an older study of mire vegetation on Gotland (Mästermyr). Thus he states that almost all the higher plant species from the undrained mire were still present after drainage, while the mosses and algae had disappeared.

Apart from the peripheral areas, with their meadow-wood type of plant community, there are some occurrences of alder, but only as single trees, in the characteristic heath-wood communities (bilberry-pine wood and bilberry-spruce wood). It would be expected that on mineral soils *Alnus glutinosa* would occur occasionally in heath-wood communities or in drier habitats (see for example Kujala 1924; Tschermak 1950). There is an outpost locality for alder in the "poor" *Ledum*-pine wood just NW of sample area Jm 1 (Fig. 2), where there are two trees, 4 m in height, which have grown from seed at the edge of a ditch. See also Ch. 4. B. for further information about the divergent ditch edge vegetation which occurs within the *Ledum*-pine wood. The occurrence of *Alnus* in bilberry-pine wood should also be regarded as an example of a fairly extreme locality. None the less, there is a tree of about 12 m in height in a luxuriant and fairly closed stand of pine.

Alnus glutinosa is usually regarded as a tree with a high light requirement (Lagerberg 1950, 1953) which does best in a fairly open stand. But even in the comparatively closed spruce stand at Jägarmossen it develops well. There is no obvious difference in its growth in the different localities where it occurs in large quantities. Its relatively high requirement for moisture and good soil nutrient content is well known and is reflected in the pattern of distribution in the studied area.

Some details about the nutrition ecology of *Alnus glutinosa* have been given by Björkman (1942, p. 105). In experiments in which he cultivated the plants with humus of various types as the substrate, he found that neither root nor shoot production was affected by additions of ammonium nitrate, but that the formation of root nodules (*Actinomyces alni*) decreased with increasing nitrogen additions, as compared with the controls grown on a substrate to which only distilled water had been added. In contrast, addition of phosphorus gave increased root and shoot production and stimulated root nodule formation. Simultaneous addition of nitrogen and phosphorus gave further increase in root and shoot production, compared with phosphorus alone, but there was decrease in nodule formation, down to zero at high levels of nitrogen and phosphorus.

It appears from this that in these conditions *Alnus glutinosa* is comparatively independent of the nitrogen content of the substrate for its dry matter production (there is of course a certain basic amount of nitrogen in the humus substrate), and that an increase in nitrogen content of the substrate leads to a change in the type of nutrient economy of the tree. Addition of phosphorus has a double effect; it affects the nutrient economy of the tree itself, and it favours the microorganism responsible for alder root nodule formation. The same effect would be expected for other mineral nutrients.

In this way some light is thrown on the general significance of mineral nutrient status on the distribution of alder. In a eutrophic environment it will have increased competitive ability. At the periphery of the peat land—where alder is most frequent—the phosphorus content of the peat is approximately double that in the centre and the calcium content is 5—10 times higher.

The characteristic formation of shoots from alder stumps (but not from roots) has, in a few places where there are fresh stumps, given rise to luxuriant groups of shoots at the base of the old trees. However, in present conditions this sucker formation does not lead to the growth of trees, but the shoots die back successively, probably as a consequence of heavy shading.

Where investigated, alder has proved to be very deep-rooted. However, more detailed information in the literature about the root distribution at various depths, and the maximum root depth, is particularly sparse. There is usually only a general statement that the roots penetrate deep into the soil (Paul 1907, p. 56). However, in a paper by Bornebusch (1914), some results are given showing the approximate maximum root depth for alder in its normal environment. He wrote that "the roots go down to a water-containing layer just below the peat at a depth of 105 cm" (transl.). It is apparent from the figures in the paper that root penetration can be down to 120—130 cm below soil surface.

In places where careful observations of alder roots have been made it is clear that a root depth of ca. 100 cm is quite common. The maximum root depth measured is in sample area Jm 8 where the roots penetrate right through the peat layer of 60 cm and down into the clay-gyttja where there are still 10 mm thick roots at 105 cm. The finer roots are no longer seen below a depth of 120 cm. Thus it may be assumed that an important part of the root zone is in an environment very poor in oxygen where water movement through the dense clay gyttja is very probably extremely slow. Tüxen (1937, p. 138) has also pointed out that "Das typische Alnetum wächst offenbar auf sauerstoffärmeren Boden bzw. Grundwasser . . .", which had earlier been noted for *Alnus glutinosa* by Bornebusch (1914, p. 85): "...the soil water must have a certain oxygen content, though the black alder has a low requirement in this respect" (transl.).

In age, height and diameter growth, *Alnus* has approximately similar characteristics to birch, on Jägarmossen. Thus its age is up to 60—70 years in the eastern part of the peat land, where the age of a few trees was measured. In sample area Jm 8 the height of the tallest tree is 25.8 m and the mean height of the 10 tallest is 20.4 m. For comparison it may be mentioned that Tschermak (1950, p. 418) records stands of black alder 30 m in height in East Prussia and the Baltic states.

Diameter at breast height, excluding the bark, is a maximum of 31 cm, and the mean for the 10 trees with thickest trunks is 26.7 cm.

The trunks are often fairly straight and well-grown with few branches in the lower part. No rot disease has been encountered. Lagerberg (1950, p. 138) is of different opinion; he considers that the fairly short life of a single trunk is due to damage by rot.

Others

Juniperus communis occurs in only a few places on the peat land (Fig. 16) and there as bushes less than 1 m in height. Its localities are in the *Ledum*-pine wood, the bilberry-pine wood, the bilberry-spruce wood, and the grass-rich birch-spruce wood. In Mjölnar fen it probably grew on tussocks before drainage and now survives as a relict.

***Salix* species.** *S. aurita* is the most common willow, and like *S. myrsinifolia, S. cinerea* and hybrids between them, is found mostly in open sites, for example in Mjölnar fen or along the main run-off channel. *S. caprea* has been observed only in two places, in the peripheral area. The occurrence of *S. pentandra* and *S. repens* in the *Ledum*-pine wood is unique. They both grow there in the ditch bank vegetation (Ch. 4. B). *S. repens* has also been observed in Mjölnar fen.

Aspen *(Populus tremula)* is rare on the peat land, as seen in Fig. 17. Several of the localities there are in the transitional zone to the non-peaty land, where the peat layer is insignificant. Aspen grows fairly well there, with tall, straight and branch-free trunks. It also occurs on deep peat which is only moderately nutrient-rich within a large part of the rhizosphere. This shows that it has a fairly modest demand for soil nutrients. However, it avoids the poorest parts of the area. The occurrences in the bilberry-pine wood are of a few individuals with thin trunks, only ca. 2 m in height. In the bilberry-spruce wood, aspen is on 1.5—2.0 m thick peat and may grow to trees 15 m in height. These two localities are of interest because of aspen's difficulty in reproducing from seed, due to the rapid decrease of viability after seed dispersal and to the sensitivity of the seedlings to drying out in their first year (Lagerberg 1950). The localities are so far from the nearest possible parent tree that the plants cannot have originated from root sucker formation but must have grown from seed. In no place does aspen form large stands, but occurs as groups of up to 10 to 12 trees (see Fig. 17). The largest aspen on Jägarmossen is in the west part of Mjölnar fen, with a height of ca. 20 m and diameter at breast height 42 cm.

Hazel ***(Corylus avellana)*** has natural habitats in the more fertile part of Jägarmossen situated near the non-peaty land (Fig. 18). It grows well there, tending to form luxuriant bushes with several trunks. Its fertility is low and fruiting individuals are found only exceptionally. Its occurrences in the central part (bilberry-spruce and bilberry-pine woods) are of such a type that they may be supposed to be only temporary. In these places hazel plants grow up to $^1/_2$ m high, but usually considerably less, before fairly rapidly succumbing to the unfavourable environment. Dispersal of the nuts in the area is, as far as one can judge, by squirrels and, perhaps mainly, by jays, which are particularly common at times (see also section on oak, below).

Oak ***(Quercus robur)*** has a distribution pattern (Fig. 19) which is quite striking at first sight, with a large number of localities on the peat land. There is a clear tendency to grouping of the occurrences round the central part, with remarkably high frequency in the heath-wood communities, but it is absent from the *Ledum*-pine wood.

Oak has high requirements from the habitat, for good growth, and it develops best on clay-containing, good mull soil (Lagerberg 1947, 1950). It also occurs on raw humus soils where it has greater competitive ability than on the better soils (Weimarck 1947, 1953). To a certain extent this is a parallel to the peat land occurrences.

However, the environment available to oak on Jägarmossen does not seem to be especially favourable, as it has difficulty in succeeding in competition with the dominant tree species. The seedlings apparently live only a few years after germination. In the great majority of

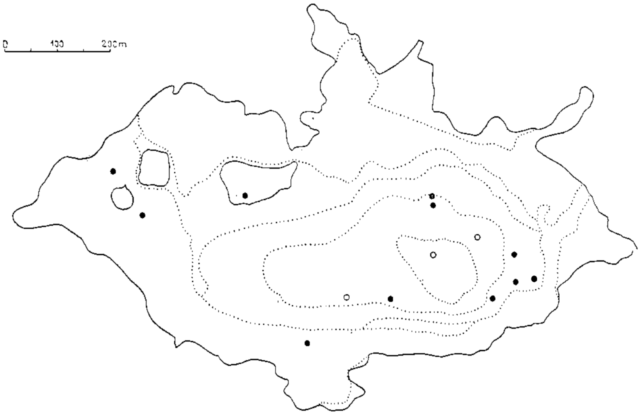

Fig. 16. *Juniperus communis* (●) and *Calluna vulgaris* (○). See text.

cases, only thin stems a few cm thick and less than ½ m high are seen. It grows like this both in heath- and meadow-wood communities. In two cases only considerably larger oaks have been recorded. These are 7—8 m in height, but they are strongly competed against by the surrounding spruces of twice the height.

One of the causes of the widespread distribution of the oak is the transport of acorns by jays and squirrels. However, there is information to suggest that squirrels may not be of much significance for nut and acorn dispersal. It has been shown that they have an exceptional ability to find nuts or acorns which they have dropped during carrying (Daubenmire 1959, p. 303). However, this information pre-

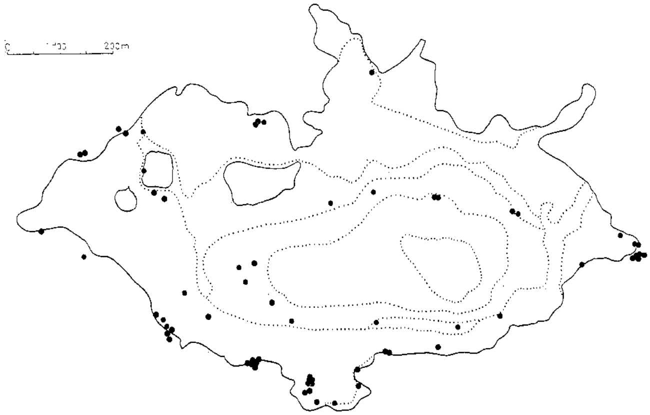

Fig. 17. *Populus tremula*. See text.

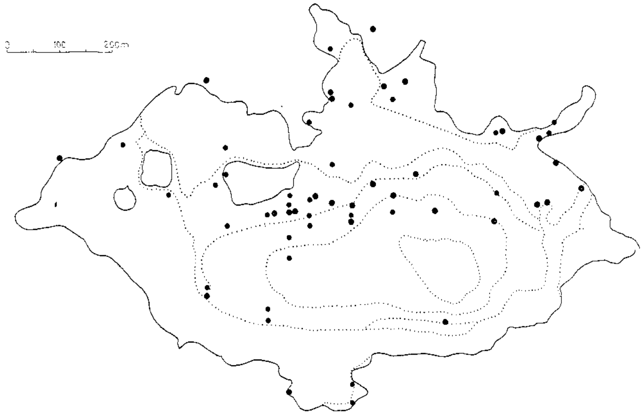

Fig. 18. *Corylus avellana.* The map includes seedlings as well as older, stronger bushes.

sumably refers to American squirrels, which belong to another species and may behave differently from our native squirrel.

Even with the complete dispersal throughout the area which should occur, the oak is infrequent in meadow-wood communities, especially those with few dwarf shrubs. Large-leaved herbs and densely growing grass have competed against the oak in its earliest development stage, even though the light requirement of the seedling is said to be less than that of the mature tree (Weimarck 1953, p. 165).

Ulmus glabra* ssp. *scabra occurs in five localities on the peat land (Fig. 20). Because of its high requirements (see for example Dahlbeck 1953, p. 212) all these are only a short distance from the non-

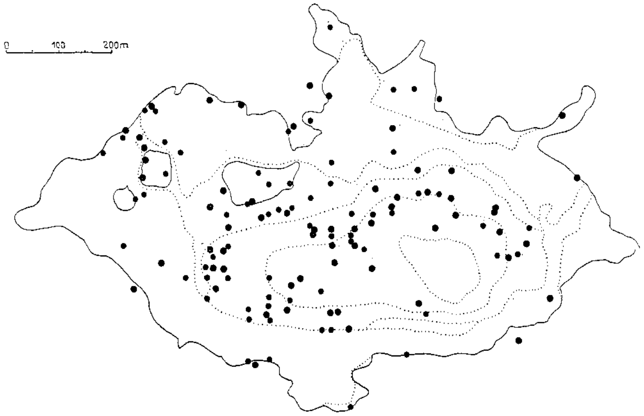

Fig. 19. *Quercus robur.* The map includes all the observed occurrences of oak. Only few of the occurrences were more than 2 m tall trees.

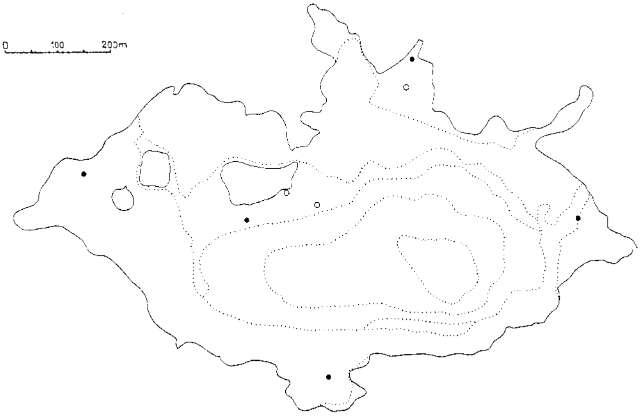

Fig. 20. *Ulmus glabra* ssp. *scabra* (●) and *Sorbus intermedia* (○). Only two of the *Ulmus* occurrences were trees, one of which was 14—15 m tall.

peaty land, where the peat layer is thin (20—40 cm) and intermixed with mineral constituents. In two of the localities it forms trees up to ca. 14 m high, whereas in the others it occurs as bushes.

Ribes alpinum occurs mainly in areas where the soil surface layer consists of well-decomposed humus from deciduous leaves or *Carex* fen ('peat mull'), i.e. mainly in the meadow-wood communities. It is fairly widespread there (Fig. 21) but there are large gaps in the distribution.

Ribes spicatum is much more rare than *R. alpinum* and the places where it occurs are concentrated in the eastern part of the area (Fig. 22).

Fig. 21. *Ribes alpinum*. See text.

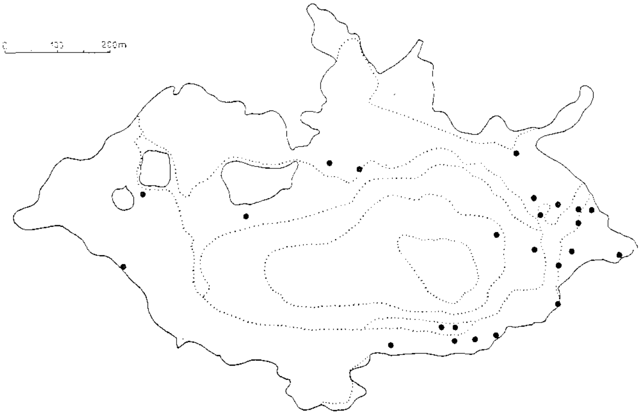

Fig. 22. *Ribes spicatum.* See text.

Sorbus intermedia is represented on Jägarmossen only by a few 2—3 m high bushes.

Rowan *(Sorbus aucuparia)* has been found evenly distributed throughout the area, although it is rare in the two pine wood communities (Fig. 23). It has always a somewhat twisted form and only exceptionally attains a height of 10 m. Malmström (1949, p. 129) wrote of the habitat of rowan "it does well on almost all kinds of ground except for mires" (transl.). A similar opinion was put forward by Lagerberg (1950). Its present occurrence on Jägarmossen shows that this assertion does not hold good for all types of mires. However, it must be remembered that the environment at Jägarmos-

Fig. 23. *Sorbus aucuparia* has a uniform distribution over the whole peat land, with the exception of the pine dominated area where it does not occur.

sen has been greatly modified as a result of draining and of the stands of spruce and pine which have now grown up. Sylvén (1953, p. 233) does not put forward a definite habitat type for rowan but considers that "it occurs on all land . . . where the seeds can find a seed-bed" (transl.). The present distribution of rowan on the peat land shows that it can tolerate a peat substratum, provided only that this fulfils certain not very stringent requirements for nutrient, aeration and water factors.

Wild raspberry *(Rubus idaeus)* mainly belongs to the luxuriant communities rich in herbs. It often occurs there in quantity, together with *Urtica dioeca,* in gaps in the tree stand. In a few cases it enters the characteristic heath communities, but then forms only small, spindly stems which fail to regenerate after few years. As is well known, the raspberry is regarded as a "nitrate species" (Hesselman 1917). In its most luxuriant form it is restricted to the parts of the peat land which are high in nitrogen ($2^1/_2$—$3^1/_2$ % nitrogen in the surface layer), where at least moderate nitrification would be expected. See also the site descriptions for *Alnus glutinosa.*

Prunus padus has approximately the same distribution pattern as the other "mull plants" discussed, but it is found especially in the *Oxalis*-spruce wood region. Occasionally it extends across the boundary to the heath-coniferous region.

It is fertile only exceptionally, and then always in open sites in the meadow-coniferous wood. It often forms rather long but very slender, thin-stemmed individuals, which have a tendency to grow parallel with the ground for a large part of their length. Diameter at breast height is not more than 12—14 cm.

Acer platanoides has in the main the same distribution as the other demanding tree species in the area (Fig. 24). Thus it does not tend to extend outside the meadow-wood communities. Nor does it seem to stand the competition which obtains in the grass-rich communities in Mjölnar fen. Most of the examples of *A. platanoides* are $^1/_2$—1 m high seedlings, but there are some 5—7 m tall trees. Occurrence in the heath-wood is probably temporary. It germinates there, lives for a few years and then disappears again from the locality.

One of the things stated about the habitat preferences of *A. platanoides* is that it seems to require a substratum poor in calcium for its best performance and reproduction (Lindquist 1953, p. 193). On deeper peat it grows rather slowly. Otherwise it is described as being a rapidly growing tree in the young stages, with low light requirement (Dengler 1935, p. 310; Tschermak 1950, p. 436). From this one gets the impression that a pure peat substratum is not favourable for this species, even though the plant nutrient content of better fen peat meets quite high requirements (for several elements).

Trees of *A. platanoides* occur first, characteristically, in the immediate vicinity of the non-peaty land and on the surrounding non-peaty land.

Rhamnus frangula is the commonest bush on the peat land (Fig. 25). Except for the *Ledum*-pine wood, it occurs in all communities. However, it shows a clear preference for the nutrient-rich peat in the peripheral areas, and it is there that it first appears to do well and to attain a significant height (2—2½ m). The typical locality for *R. frangula* is the former deciduous tree and *Carex* fen, where it is sometimes so common that it is included in the quadrat analysis. Its high frequency is also shown by the fact that it occurs in 9 out of 12 sample areas, and for woody plants this is exceeded only by birch, spruce, and wild raspberry.

Rhamnus cathartica is an occasional species which has been observed in one place at Mjölnar fen.

Small-leaved lime *(Tilia cordata)* has its few occurrences in the central part of the *Oxalis*-spruce wood (Fig. 25). It may be said with certainty that at least one of these localities dates from the period preceding drainage, since *Tilia* was recorded there as 1—2 m high trees 5 years after completion of ditching. The marked increase in closure of the stand after drainage is apparently disadvantageous to *Tilia* in spite of its preference for shady habitats. This is shown, for example, by poor growth and procumbent, almost creeping, badly rot-infected stems. It has also been subject to grazing by elk (see Herz 1925; Tschermak 1950, p. 438) which has further contributed to the decrease in its vitality. *Tilia* has not been observed fruiting, so its continuation must at present be based entirely on vegetative reproduction, which is common in this species (Herz 1925, p. 110).

Daphne mezereum has the main part of its distribution in Mjölnar fen and in the parts of the *Oxalis*-spruce wood nearest the non-peaty land (Fig. 26). It obviously tolerates only the best soils and avoids heavily shaded places. It usually occurs in the form of single, spindly stems about ½ m high, but where conditions are specially favourable it forms vigorous groups more than 1 m high.

Empetrum nigrum has been recorded only from two places in the bilberry-pine wood.

Ledum palustre. In the first half of June the splendid flowers of *Ledum palustre* give a characteristic appearence to the central part

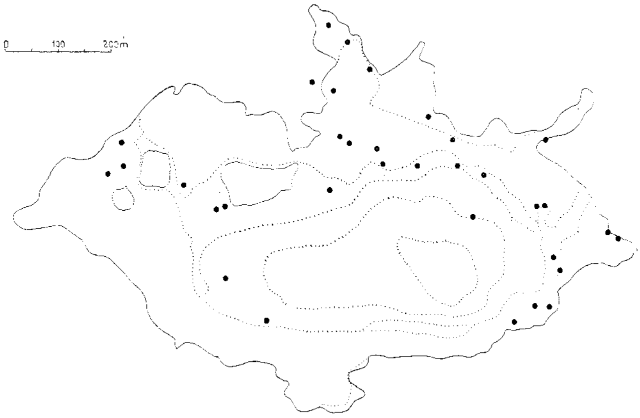

Fig. 24. *Acer platanoides*. Seedlings as well as trees are noted on the map.

of the peat land (description Ch. 4. B.). Figs. 5 and 14 show that the range of distribution of *Ledum palustre* corresponds practically completely with the general occurrence of pine. Hence it grows together with the commonest field layer dominants in the pine wood, i.e., *Vaccinium myrtillus, V. vitis-idaea* and *V. uliginosum.* Information about the occurrence of these species, and of *Andromeda polifolia,* is given in the plant community descriptions.

Calluna vulgaris is rare (Fig. 16), but is recorded from a few more localities than *Empetrum.* It does not extend outside the boundaries of the heath-wood communities. *Calluna* has often been said to be a calcifuge species (Lagerberg 1950), but there is so much evidence to the contrary that it is best not to be too categorical about the question.

Fip. 25. *Rhamnus frangula* has a similar distribution to *Sorbus aucuparia.*

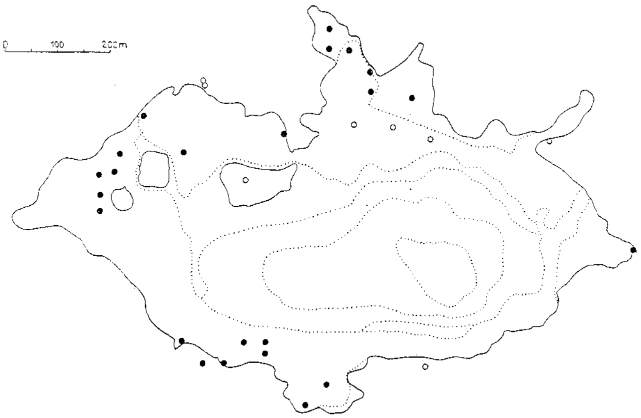

Fig. 26. *Tilia cordata* (○) and *Daphne mezereum* (●). Both are strongly restricted to the margin of the peat land.

Olsen (1936) pointed out that the majority of "acid soil plants" and "basic soil plants" often have a wide amplitude in respect to the acidity of the substrate. *Calluna*, for example, occurs on a pure limestone substratum on Öland (see Stålfelt 1960, p. 301, and references cited by him; Olsen 1921a, p. 88). McVean and Ratcliffe (1962, p. 170) write "*Calluna* is a frequent component of calcareous rock face vegetation in the Highlands, sometimes in habitats where the feeding roots could hardly avoid contact with free calcium carbonate, and the species undoubtedly grows at times on soils which have a high content of exchangeable calcium."

Fig. 27. *Fraxinus excelsior* is strongly restricted to the meadow-forest area on Jägarmossen. Several of the occurrences are large trees, about 20 m tall.

Ash ***(Fraxinus excelsior)*** shows a high degree of restriction to the herb-rich peripheral areas (Fig. 27) with peat rich in phosphorus, calcium and nitrogen.

There is probably no doubt that ash has very high demands on the habitat. Thus Halden (1928) wrote categorically that it is highly dependent on the distribution of calcareous areas. This should probably not be interpreted simply to mean that ash is specifically dependent on calcium, but rather that it is favoured by the generally high fertility which is usually associated with calcareous habitats. But ash is also found on fertile soil where there is no calcium carbonate, even at its northern limit in Sweden, for example at Garpenberg (Sjörs, personal communication).

Huldén (1941), who has written a monograph on ash, considers that the best conditions for its growth are offered by calcium-containing glacial till (op.cit., p. 136), and according to Wardle (1961, p. 741) it is most frequent in areas with calcium-containing bed rock. Rancken (1953, p. 182) reported that ash undoubtably has a higher requirement for soil fertility than other Scandinavian tree species. He further defined its requirement as being for a moist, calcium- and nitrate-containing soil. A pH of at least 5.8 is good for root growth, and maximum root growth is at pH 6.3—6.5 (Huldén 1941, p. 156). Wardle (1961) considers that it is usually absent if the pH of the surface of the soil is < 4.2.

Weis (1927) has also pointed out the high requirement of ash for inorganic nitrogen compounds, but about phosphorus his view is that "The demand of ash for phosphate (possibly also potassium) is so strikingly small that large amounts may possibly have a deleterious effect on it" (transl.). He probably means here such a high phosphorus content in the substratum that inhibition of growth can occur. This phenomenon is also mentioned by Lindquist (1938, p. 116). However, Møller (1941, p. 21 and 31) considers that ash has a high phosphorus demand, since he writes "Ash has the highest demand for phosphate of our common tree species" (transl.).

These contrasting opinions indicate that it is wiser at present to accept Tansley's (1939, p. 253) less precise estimate of the nutrient demand of ash: "Ash demands a good supply of mineral salts and avoids all markedly acid soils."

The comparatively little material from Jägarmossen supports this assertion of the generally high nutrient demand of ash. Of the separately investigated components of the habitat complex (mainly the plant nutrient status) the highest analysis figures have, in general,

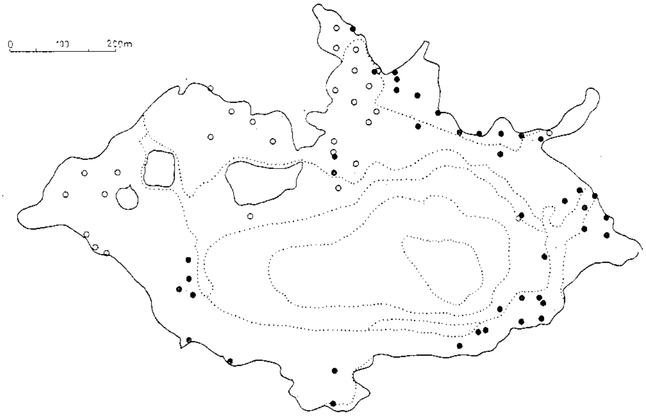

Fig. 28. *Lonicera xylosteum* (○) and *Viburnum opulus* (●). See text.

been obtained for those parts of the area where ash is present. This is so primarily for nitrogen and calcium contents, and other important factors also reach a maximum here, e.g. ash content, apparent density, degree of neutralization and total phosphorus content. However, there are certain characteristic exceptions. Thus the contents of total potassium, ammonium lactate-soluble potassium (K-AL) and hydrochloric acid-soluble potassium (K-HCl) are not significantly higher within the area of ash distribution than in other parts of the peat land. However, the quantities expressed per unit of surface area are as a rule greater, as a consequence of the higher apparent density of the peat in the herb-rich communties. On the other hand, the lowest recorded contents of ammonium lactate-soluble phosphorus (P-AL) are in the plant communities with ash. The above-cited information in the literature about pH demand of ash holds only to a limited extent. As a rule, the pH values of the substrate where ash is present are in the range 4.2—5.6. (For more exhaustive treatment of plant nutrient conditions see part II).

In several cases, ash has attained considerable dimensions, although the environment is not the most favourable for the species. The tallest trees reach 20 m, although the diameter at breast height is not more than about 20 cm. As a rule the trunks are rather crooked, and unsuitable for quality timber.

Viburnum opulus and ***Lonicera xylosteum*** finally may be mentioned. These two bush species belong to the category of "mull plants" already named. This comprises species which in the area only exceptionally extend over the boundary of the heath-wood communities (Fig. 28).

Of these two species, only *Viburnum* occurs, in two cases, in the heath-coniferous wood. It should be remembered that the boundaries between communities on the map are not distinct lines but an estimated centre of a gradual transition, "ecotone" (Weaver and Clement 1929, p. 53), between two adjacent plant communities.

Lonicera and *Viburnum* as compared show a very peculiar feature of distribution, namely that there is hardly any overlap of the two areas of distribution. Thus with two exceptions *Lonicera* is restricted to the NW in the area, and *Viburnum* to the N, E and S. At first sight these distribution conditions may be regarded as arising by chance. Of the factors which have been of most importance for the species' distribution, i.e., historical development, dispersal conditions, and habitat factors, the first two would be expected to operate with similar effect throughout the whole area. However, habitat factors are more variable. But none of those investigated shows any feature which might allow a simple explanation of the peculiarity of the distribution pattern.

Chapter 5. Some features of the development of the vegetation during the period since drainage

A. Survey and methods

Succession in plant communities has been studied for a considerable time, both here in Sweden and in other countries. Braun-Blanquet (1951, p. 443) writes, for example, that as early as the beginning of the 19th century attention was paid to the natural succession in the vegetation.

In Sweden, succession in plant communities has been to a great extent a practical question, and the result of certain treatments such as clear-felling, thinning and burning of forest land, draining marshy land, grazing, addition of fertilizers, etc. has been studied. However, the results of these treatments have not been followed during the whole of their process to a more or less stable final stage ("climax") —this is in fact seldom possible during one man's lifetime—and "opinions have been based on single observations made on a large number of habitats rather than on long term, profound studies of the development of the vegetation at a single place" (O. Tamm 1940, p. 227; transl.).

The various features of vegetational changes proceed at different rates, depending on the habitat factors (climate, soil type, etc.), the type of change (colonization of drained areas, encroachment of vegetation at the edges of open water, development after fire, etc.). Tanttu (1915, p. 23) pointed out that on drained peat soils the new forest type appears first after several decades, and that the changes are seen only along the drainage channels if drainage has been slight, an observation which is generally confirmed, for instance by work in Switzerland (Grünig 1955, p. 481). Grünig also said that in some cases drainage may bring about only slight changes in fen vegetation ("Flachmoorvegetation") in 15 years. On the other hand, Pearsall (cited by Tansley, 1939, p. 604) showed the rapid course of change which may be associated with the encroachment of vegetation at the edges of open water during a similar length of time.

The present type of change, i.e., drainage of a peat area with a permanent water table at or just under the surface, has been studied at several places, but practically without exception only the state following upon drainage. It probably need not be questioned that the conclusions which have been drawn with regard to the vegetational development are completely correct in their main features, but many details have had to be omitted.

In the first decades of the 20th century, when research on peat land was very active both in Sweden (Sernander, von Post, Melin, Osvald, Malmström, etc.) and Finland (Cajander, Auer, Rancken, Tanttu, etc.), and in central Europe (Weber, etc.), thorough work of a pioneer character was done and this has since been a guide for later investigations of similar type. With the stratigraphy of the peat, etc., as a background the main lines of the mode of origin and development of peat lands were established. Since at that time, peat land had higher economic value than it has nowadays, for cultivation, forestry, preparation of peat for fuel, etc., the drained peat land was also of considerable interest, but unfortunately no base for future studies of the development of recent vegetation was laid down. For example, no permanent quadrats were marked out.

Now, when direct observations of the development cannot be used, other available sources must be taken up in the attempt to reconstruct the past sequence. Summaries of the various methods with their advantages and disadvantages have been given by Du Rietz (1930), Lüdi (1930), Braun-Blanquet (1951) and Ellenberg (1956), among others.

In this context, peat boring records, vegetation and habitat descriptions and a number of extensive quadrat analyses made 5 years *after* ditching was completed on Jägarmossen have been used as a basis for a description of change in the vegetation. Peat boring records are from three transect lines laid out over the peat land, along which borings had been made at least every 40 m, and at the same time general notes were made on the characteristic features of the species composition of the tree and field layers. In addition, the 10 × 10 m quadrats laid out by Dr. Carl Malmström were distributed very evenly over the area and when these are put in on the survey map (Fig. 2) made at that time (1927) they provide a good basis for a comparison with the present-day state of the vegetation. The marks for the quadrats are naturally not still in place, but their position can be determined with relatively good accuracy. In the subsequent comparison it should be borne in mind that there is some uncertainty involved here, despite all possible care, since to some extent this can affect the species content. However, this effect should be small and as a rule negligible. To get some check on this, when the site of the quadrat had been established its sides were increased by 1 m in each direction, so that a 12 × 12 m quadrat was formed. Within this larger quadrat the 10 × 10 quadrat has been shifted so that one corner and two sides have always coincided with those of the larger quadrat and the species thereby coming into or disappearing from the survey have been recorded. The total of these, together with the observations on the original quadrat, have been used to decide whether a species should be included in the data or not.

The presentation below differs from the original only technically. The older quadrats (from 1927) have been called "quadrats 1—14" and the new (1959—1960) "sample areas Jm 1—Jm 12" (Fig. 2).

The various features of the development refer, in the main, only to the vegetation units distinguished as associations. The material does not allow vegetational changes within lower rank units to be treated. From a practical point of view these are of minor significance, since in forestry the association is the most useful sociological unit. It corresponds most closely to "forest type".

The arrangement follows that used above for the plant community descriptions, but to compress the material some similar associations have been taken together.

B. Vegetational development

Ledum-pine wood and bilberry-pine wood

Of Jägarmossen's plant communities, the *Ledum*-pine wood has the most conservative features. By this is meant that the changes which have taken place in the species composition of the vegetation after drainage have been insignificant (see Table 8, quadrats 1 and 2). The main reason for this can be assumed to be that the draining effect in this part is relatively small. The blocking up of the ditches dug in this area, as a consequence of encroachment of vegetation and of material which has fallen in, is sufficient to retain a high water table (see water table measurements, part II) and to decrease or sometimes prevent oxygen diffusion to any depth in the peat, and hence limit the extent of the plant rooting zone. Therefore as long as the present condition obtains, the *Ledum*-pine wood will retain at least the main features of its character. There is still slight peat formation in patches and humification of the peat is prevented to a great extent by the high water table.

Because of the clearly relatively small changes in the habitat which have come about after drainage, the conditions are fairly favourable for retention of the original plant community. Thus the vegetation comparisons which have been made show that only small shifts have taken place, both quantitatively and qualitatively, in the field and bottom layers.

Vaccinium myrtillus, which had reached the outer part of the *Ledum*-pine wood according to a record of the vegetation from 1927 (Table 8, quadrat 2), has now extended in over the boundary of the central and poorest (in plant nutrients) part of this community. Both *V. uliginosum* and *V. vitis-idaea* show noticable increase in degree of cover and in patches *V. uliginosum* reaches 100 per cent degree of cover. *V. vitis-idaea* is important in the "lower" field layer. *Ledum* still has its earlier position, while *V. oxycoccus* and *Rubus chamaemorus* have decreased. In the bottom layer *Aulacomnium palustre* has decreased as well as *Sphagnum fuscum* and *S. magellanicum;* but *S. parvifolium* has remained surprisingly unchanged. *Dicranum scoparium* has replaced *D. bergeri.* The slight recorded increase for *Pleurozium schreberi* (2 to 3) is perhaps not so insignificant as it might seem. It has been shown that patches with *Pleurozium* are significantly drier in the surface layer than are the *Sphagnum* patches, and that under these there is often a thin layer of well-humified plant remains with the appearance of mor. Presumably this is a more suitable sub-

Table 8. Changes in the vegetation in quadrats 1—4 within the pine wood communities between 29 June, 1927 and 20—21 July, 1960. — Changes in the vegetation in quadrat 9 in the bilberry-spruce wood between 30 June, 1927 and 21 July, 1960

	1927				1960			
Trees	1	2	3	4	1	2	3	4
Betula pubescens	2	-	3	3	1	1	2	1
Picea abies	1	2	1	1	1	3	1	3
Pinus silvestris	1	-	3	2	4	1	4	3
Quercus robur	-	-	-	-	-	-	1	-
Dwarf shrubs								
Andromeda polifolia	1	1	-	1	1	1	-	-
Ledum palustre	2	3	2	3	2	1	1	-
Vaccinium mytillus	-	1	1	1	1	1	4	5
oxycoccus	3	3	1	1	1	1	-	-
uliginosum	3	3	3	3	4	3	1	1
vitis-idaea	1	3	2	3	3	2	3	2
Grasses and herbs								
Chamaenerion angustifolium	-	-	1	-	-	-	-	-
Dactylorchis maculata	-	-	1	-	-	-	-	-
Dryopteris spinulosa	-	-	-	-	-	-	1	-
Eriophorum angustifolium	-	-	-	1	-	-	-	-
vaginatum	2	3	4	1	2	2	1	-
Galeopsis tetrahit	-	-	-	-	-	-	1	-
Luzula multiflora	-	-	1	-	-	-	-	-
pilosa	-	-	-	-	1	-	-	1
Melampyrum pratense	1	-	1	-	1	-	-	-
silvaticum	-	-	-	-	-	-	-	1
Rubus chamaemorus	4	3	3	3	2	1	1	1

	1927				1960			
Mosses and lichens	1	2	3	4	1	2	3	4
Aulacomnium palustre	3	3	3	1	1	-	-	-
Brachythecium rutabulum	-	-	-	-	-	-	-	1
Dicranum bergeri	1	-	-	-	-	1	-	-
polysetum	1	1	-	1	2	2	3	-
scoparium	-	1	-	1	1	1	1	1
Hylocomium splendens	-	-	1	1	-	-	2	2
Orthodicranum montanum	-	-	1	-	-	-	-	-
Plagiothecium denticulatum	-	-	-	1	-	-	-	1
Pleurozium schreberi	2	1	2	2	3	3	4	3
Pholia nutans	1	2	1	1	1	1	1	1
Polytrichum strictum	-	-	2	2	1	1	-	-
Ptilium crista-castrensis	-	-	-	1	-	-	1	-
Rhytidiadelphus triquetrus	-	-	-	-	-	-	-	1
Sphagnum fuscum	2	1	1	-	1	-	-	-
magellanicum	2	1	1	2	1	-	-	-
nemoreum	-	-	-	3	-	-	-	-
parvifolium	3	4	3	-	3	1	-	-
Cladonia cenotea	-	-	-	-	-	1	-	-
cornuta	-	-	-	-	1	1	-	-
crispata	-	-	-	-	-	1	-	-
deformis	-	-	-	-	1	-	-	-
fimbriata	-	1	1	-	-	-	-	-
rangiferina	1	1	1	1	1	1	-	-
silvatica	1	1	1	-	1	1	-	-

Changes in the vegetation in quadrat 9 in the bilberry-spruce wood between 1927 and 1960

	1927	1960
Trees		
Alnus glutinosa	1	-
Betula pubescens	3	1
Picea abies	3	5
Pinus silvestris	1	1
Sorbus aucuparia	1	1
Bushes		
Rubus idaeus	-	1
Salix aurita	2	-
Dwarf shrubs		
Vaccinium myrtillus	4	1
vitis-idaea	4	-
Grasses and herbs		
Calamagrostis sp.	2	-
Chamaenerion angustifolium	1	-
Cirsium vulgare	-	1
Dactylorchis maculata	1	-
Dryopteris spinulosa	1	1
Galeopsis tetrahit	-	1
Luzula pilosa	-	1
Lycopodium annotinum	2	2
Maianthemum bifolium	2	1
Melica nutans	-	1
Oxalis acetosella	-	1

	1927	1960
Potentilla erecta	1	-
Rubus chamaemorus	2	-
Trientalis europaea	1	-
Mosses and lichens		
Aulacomnium palustre	1	-
Brachythecium rutabulum	1	1
Dicranum fuscescens	-	1
majus	-	1
polysetum	1	1
scoparium	-	1
Hylocomium splendens	2	4
Plagiothecium denticulatum	-	1
piliferum	1	-
Pleurozium schreberi	4	4
Pohlia cruda	1	-
Polytrichum strictum	1	-
Rhodobryum roseum	1	-
Rhytidiadelphus triquetrus	1	1
Sphagnum nemoreum	1	-
palustre	1	-
wulfianum	1	-
Cladonia cornuta	-	1
fimbriata	1	-

strate for species requiring good soil than the moister *Sphagnum* patches.

The increased degree of cover for pine is entirely due to increase in the projection of the crowns of the pines, since the number of individuals has decreased rather than increased during the intervening years (1927—1962). In the older description it is said that "dwarf shrub bog" — this includes the bilberry-pine wood—"has had fairly large pines, far apart, which were felled 1916—1917, and single birches and very stunted pines" (transl.). The present *Ledum*-pine wood "was grown with trees hardly useful even for thin timber" (transl.). To judge from the age determinations the "stunted pines" were also felled.

Historically, the bilberry-pine wood (Table 8, quadrats 3 and 4) can be said to be one stage after the *Ledum*-pine wood, since this latter is closer to a purely ombrotrophic (Du Rietz 1954, p. 572) nutrient economy. At the stage just before drainage the *Ledum*-pine wood may have been completely dependent on the precipitation falling on its surface for its water and nutrient economy. The very low contents of plant nutrients in its surface layer indicates this. The bilberry-pine wood differs from the central community in having generally higher contents per unit of dry weight (see part II), but above all larger total amounts of nutrients. The surface layer of the soil also has a different appearance, since the somewhat more humified peat is covered by often well-developed mor. However, it is often not possible to separate F-and H-layers.

Immediately after drainage "this part bore good pines which as a rule yielded two lengths of timber 14′—16′" (when cut in 1916—17). In quadrat 3 there were fairly large pines before felling "while the present" (1927) "pines have mostly come up directly after felling. The bog surface is clearly tussocky. The tussocks are formed partly by *Sphagnum,* and partly have formed around tree stumps. *Eriophorum vaginatum* here, in contrast to quadrats 1 and 2"—the *Ledum*-pine wood—"forms fairly tall, strong tussocks. It seems to have fruited heavily. The young pine and birch seedlings have good growth. The majority of birches have stump shoots. *Ledum* is taller and more luxuriant than in quadrats 1 and 2. *Sphagnum* spp. seem to be on the decline. Here and there are bare patches with *Pohlia*" (transl.).

The present status of the community, shown with the aid of quadrat 3 (Table 8) is a well-closed stand of pine with an understorey of birch and vigorously growing spruce. Note that spruce was not mentioned in the earlier description. The present boundary of distribution of spruce growing in stands goes just E of the area (see pine distribution map, Fig. 14 and Fig. 3). *Betula pubescens* occurs in the area only as thin-stemmed individuals up to 3 m tall. *Quercus robur* is new among the tree species—but only as minor bushes.

The stumps in the area and its immediate vicinity show that there has been repeated felling there. The oldest stumps are generally now grown over with moss and together with "fossil" tussocks give the ground a rough appearance.

In general, the changes in the tree layer that have occurred in this part are modest, but earlier seedlings have now grown up into trees, and the tendency towards spruce development is very strong.

Vaccinium myrtillus which was previously a species of no quantitative significance has now increased and taken a dominant position, while *Ledum* and *Vaccinium uliginosum* have clearly receded. *V. oxycoccus* has disappeared completely, neither is it seen in the immediate vicinity of the area. *Eriophorum vaginatum* and *Rubus chamaemorus,* which were previously important, have decreased considerably and now have an insignificant physiognomical value. Apart from these changes it can be seen that some species have come in and others disappeared. For hardly any of the latter would the environmental change be expected to have brought about the changes, and they can be attributed to occurrences of a chance nature. For example, felling in the area may have made seed dispersal and seedling survival easier for numerous species on the peat land (see Sjörs 1954, p. 27, and literature cited there).

The bottom layer shows clear traces of a transition to a drier soil. Here it is negative features which are decisive. Thus all the *Sphagnum* species have disappeared together with the moist-soil moss, *Aulacomnium palustre*. However, significant positive features are also noticed. *Pleurozium* has increased and together with *Dicranum polysetum* and *Hylocomium splendens* is dominant in the layer. Finally, it is found that all the lichens have disappeared.

Quadrat 4 lies somewhat closer to the bilberry-spruce wood, but is not affected by this to a noticeable degree, and agrees in its main features with the previous quadrat. It was said in the previous description that the trees in this part of the stand consisted partly of remains from the earlier felling and partly of seedlings come up after that. The dominating pines reached 2.5—3.0 m in height (in 1927). To a large extent the birch had come up as stump shoots. The tree stand as a whole was more open than before felling (1916—1917). In the field layer the dwarf shrub species were tall and well-grown, and *Eriophorum vaginatum* was only sparsely represented (see Table 8, quadrats 3 and 4). Finally, it was pointed out that this part of the mire, in particular, had always been relatively dry.

The most striking change in appearance would be that instead of the young pine wood of about a man's height there is now a closed stand of pine and spruce. Qualitatively, the tree species proportions have shifted, in that spruce has increased significantly at the expense of birch. Pine degree of cover is little changed in spite of the increased crown projection of the individual trees. It is clear that pine has actually decreased in number during the intervening period, a course of development which is also continuing. Development of spruce is very active and it pushes in its crowns into and between those of pine. In a short time it should prevail completely. Nor are pine seedlings seen any longer. The singly occurring birch trees in the stand have ceased to play a part.

The most marked changes in the field layer are in the *Ericaceae.* Three species of the original six remain, and those formerly important, *Ledum, Vaccinium uliginosum* and *V. vitis-idaea,* have been practically completely replaced by *V. myrtillus.*

Even *Ledum* has disappeared from the quadrat but is seen occasionally in the vicinity. *V. oxycoccus* has also gone. Both *Eriophorum* species are now absent, and *Rubus chamaemorus,* which was formely fairly common, now occurs only as single individuals. There are only two new species, both with low degree of cover.

From the bottom layer, both the two *Sphagnum* species and *Aulacomnium palustre* have gone. They have been replaced by *Hylocomium* and *Pleurozium.* In this connection, occurrence of the relatively demanding mosses, *Brachythecium rutabulum* and *Rhytidiadelphus triquetrus,* is worthy of note.

Using as a background this description and the indicated directions of development in the *Ledum-* and bilberry-pine wood, a general summary about what is known of the most nearly corresponding vegetation types from nearby places with similar treatment may be useful, in order to throw light on the connection with these.

Eriksson (1912) considers that pine bog can arise from an open raised bog, if this is drained very effectively. Thus on Stormyren at Bälinge in Uppland a line of pine wood grew up transversely across the bog, after a channel had been dug. The "*Vaginatum*—facies" (Eriksson, p. 171) cut across on this occasion may be linked with Melin's "*Vaginatum*—bog" mentioned below, and comes close to Sarasto's (see below) *Sphagnum – Eriophorum – Ledum* combination. A connection with Almquist's (1929, p. 275) *Pinus – Eriophorum vaginatum – Sphagnum angustifolium*—mire wood is also possible.

Melin's (1917) work on forest vegetation on drained mires in central Norrland has its value for reference in this connection in that the author has succeeded in finding very old drainage areas (the oldest from the 1830s). However, this also applies a limitation, in the large degree of uncertainty which must prevail in reconstructing the various parent communities (see, e.g., Du Rietz 1930, p. 469 and Lüdi 1930). The microscopical analysis made of the peat cannot give the composition of the community in which it was formed with sufficient precision (see Malmström 1923, p. 65). An important limitation in the present context is that these forest communities, very advanced in the succession, described by Melin, are from an area about 500 km north of Jägarmossen, so that it is hardly advisable to use his results directly. But through the attention which Melin (1917, p. 295) also gave to some mire areas in eastern Central Sweden, there is a possibility of finding a connection with one or two of his "associations" (see also Lundberg 1914, with a number of pictures).

The two associations, *Ledum*- and bilberry-pine wood should thus be related to "afforested *Vaginatum*-bog" (transl., Melin 1917, p. 115, 121 and 300) which, after good drainage, changes towards "wood of *Myrtillus – Vaccinium* type (Melin 1917, p. 241; transl.).

Sarasto, who has studied corresponding communities in Finland, considers that the following sequence, among others, may occur: a *Sphagnum – Eriophorum vaginatum – Ledum* combination changes towards a *Pleurozium – Ledum* combination (Sarasto 1951, p. 74), i.e., the present condition on Jägarmossen. However, this latter composition should not be taken to be a final stage of the *Ledum*-pine wood development but as a middle link in the succession towards a community similar to a forest vegetation type on non-peaty land.

Melin's (1917) *Myrtillus – Vaccinium* type, mentioned above, is the community most closely linked to related non-peaty vegetation. But before the *Ledum*- and bilberry-pine wood reaches this stage—provided that the water table is lowered more than at present—it will go through several sociologically important stages of development, whose appearance is not known. It is therefore best at present to speak uncategorically, like Lukkala (1920, 1929 a), of "a mire type corresponding to drier conditions" (transl.), during the first stages. Almquist (1929, p. 274) also expresses himself generally on the development of pine bogs by saying that they change to moss-rich *Ledum*-pine wood after drainage.

The development is slow and there are no good examples to show later stages of succession in the peat land type treated here. However, a short description by Tolf (1900, p. 18) is not without interest. This is of a clearly late stage in *Ledum*-pine wood development after drainage: "In the vegetation . . . there was nothing reminiscent of the common plant communities on peat. *Sphagnum* spp. were observed only very rarely, but the peat was covered completely by *Hylocomium* spp., characteristic forest mosses on good soil. *Ledum, V. myrtillus* and *V. vitis-idaea* were the dwarf shrub representatives" (transl.).

Therefore, it is probably not possible to follow the development of the vegetation in detail, other than for a fairly limited period directly after drainage. The special character of each area must be taken into account, since the stratigraphy of the peat finally has a decisive effect, anyway on the more deeply-rooted vegetation. As far as peat land is concerned that originates from filling-in of a body of open water (which in eastern Sweden was most often of eutrophic nature), the shrinkage of the peat will lead to access to nutrient sources of varying richness, from more or less bog-type peat at the surface to different fen peat types, gyttja, etc., further down or near the non-peaty land.

Bilberry-spruce wood

Bilberry-spruce wood, *Maianthemum*- and *Oxalis*-spruce wood have developed towards types which are already similar to a large degree to wood communities on the non-peaty land. The proportion of mire plants in the species list is very low, or, as is usually the case, they are absent. Unfortunately, there is only one earlier-studied quadrat (Table 8, quadrat 9) from the bilberry-spruce wood, so that the variations in the development of the community cannot be discussed as comprehensively as one would wish. From a forestry viewpoint this part was regarded (1927) as a good, well-closed stand composed of birch, alder, spruce and pine, and it showed a large increase in growth after drainage. The stand was said to be "in great need of thinning, especially in crowded groups of spruce and birch. Greatest height 10 m. Scattered stumps of previously felled trees. Ground often covered by a carpet of *Hylocomium*. Under the densest spruces the ground is bare or covered by needles and birch leaves. In the more open parts, dwarf shrubs and herbs are dominant. *Vaccinium myrtillus, Maianthemum* and *Rubus chamaemorus* are most important physiognomically. The plant community seems to be very vigorous. Long shoots are produced on the trees. Bilberry fairly tall and luxuriant" (transl.).

The above account shows that the quadrat presents a different picture in practically all its details from that of only about 35 years ago. Like pine, birch has mostly been felled, and there remain only the well-decayed stumps of alder. In a stand estimate made in 1931 the stem numbers were distributed as follows: pine 36 per cent, spruce 37 per cent, broad-leaved trees 27 per cent. However, in 1959 there was virtually 100 per cent spruce, and birch and pine occurred only occasionally. The maximum height of spruce is now 18—20 m.

The impoverishment of the field layer is striking. This earlier (Table 8) consisted of *Vaccinium* spp. There are now only minor remnants of these in the form of single plants or scattered groups. *V. vitis-idaea* is generally absent (see also Table 4, sample areas Jm 9 and Jm 10). The number of herb species is about the same on the two occasions, but with only two species in common, viz., *Maianthemum* and *Dryopteris spinulosa. Sphagnum* spp. and *Aulacomnium palustre* have disappeared from the bottom layer.

Comparison with other parts of the community gives the impression that the above description applies fairly generally to its typical parts. However, Långholmen, a part of which is bilberry-spruce wood, is somewhat divergent. The differences which occur can be attributed partly to the earlier (natural) drainage of this area, and partly to forest practice.

According to the older notes, soon after drainage the present bilberry-spruce wood was an *Eriophorum vaginatum* community rich in dwarf shrubs. Except for Långholmen, this in turn was the first result of drainage of a probably fairly wet community in the transition area between the lagg, in the restricted sense, and the drier parts in the centre.

The community which is assumed to precede the bilberry-spruce wood, on undrained peat, has been described in one or two places in the literature. Thus Eriksson (1912, p. 162) wrote that "*Eriophorum vaginatum* bog has elements which are found in fen and *Carex*-bog as well as in *Calluna*- and pine-bog" (transl.). Almquist (1929, p. 170) also thinks that the type exists, although he has himself seldom seen it. He places it in *Eriophorum vaginatum – Sphagnum recurvum* bog, but as an intermediate form. As Almquist also suggests, it can be linked with Melin's *Vaginatum*-bog.

In this part the upper layer of the peat is too strongly humified for a microscopic analysis. The only identifiable remains in two samples were fragments of birch bark and leaves of *Drepanocladus fluitans*.

The topographical position of the former *E. vaginatum* community fits well into the "normal" pattern of vegetational zonation on a forest bog or at the edge of a pine bog or an east-Swedish raised bog (see Eriksson 1912, fold-out map, Du Rietz and Nannfeldt 1925, Du Rietz 1950, Gorham 1952, etc.).

The lower vegetation layer of the bilberry-spruce wood is at present so well adapted to the moisture conditions that possible further lowering of the water table in the peat would not have any positive effect on the field- and bottom-layer vegetation. The present water table conditions can probably be regarded as almost optimum for bilberry-spruce wood. The moss-rich bilberry-spruce wood as such is also a stable community on a mineral soil substratum, as shown for Uppland by Almquist (1929, p. 302), for example. The development which may take place is brought about by change in the tree layer, as Almquist points out as follows, "the density of the dwarf shrub stand is seen to remain, within a wide range, inversely proportional to that of the tree layer" (transl.). There is also an example of this in the present case (see Table 4, sample areas Jm 2, Jm 9 and Jm 10). Also continued shrinkage of the peat, clear-felling, etc., may affect future development.

Maianthemum-spruce wood and Oxalis-spruce wood

All the communities described below belong to the peripheral part of the peat land which during their existence before drainage have had complete access to mineral soil water for their nutrient supply. Consequently they have had—and still have—a clearly eutrophic character, with the present *Oxalis*-spruce wood having the highest degree of eutrophy.

On the forest map from 1912—1913, the peripheral part of Jägarmossen is treated as a unit, as fen or unspecified wet ground, and it is clearly considered worthless. Thus on the map there is no suggestion of differentiation between the fen communities. However, on the forest map of 1924 (two years after completion of ditching) Långholmen is distinguished as a stand with a timber standing crop of 30 m^3 per hectare (Ch. 3. D). Other parts were apparently not of such a type that a forest estimate in them was thought to be worthwhile. But obviously drainage had already had such a favourable effect that large parts of the area north of the main run-off channel were no longer regarded as unproductive wet ground.

The classification of the communities near the non-peaty land (the lagg communities) in Ch. 4 depends on the qualitative and quantitative properties of the present-day vegetation. In attempting to reconstruct the condition at the time of drainage it may be assumed that units which are now different probably correspond to previously different vegetation types. This is certainly true for the main part of the area, but the connection is complicated for parts where the tree stand has been thinned severely, or where an overcrowded stand hinders the full development of the lower layer of vegetation. A small part burnt by a forest fire is another example of similar divergence. In the thinned stand, decreased competition has stimulated the field layer to a special luxuriance which would not exist in a more balanced ecosystem. In the overcrowded stand, on the other hand, only the tree and bottom layers are developed, and in extreme cases the bottom layer may also have disappeared, but probably more as a consequence of heavy leaf and twigfall than of the low light intensity. Finally, the fire has removed the tree layer and indirectly favoured the growth of a vegetation type, otherwise very atypical of the area, which includes a number of hemerophytes. The following list is an example of the composition of the "burnt-ground phase". The relatively large number of species which normally occur in a moist environment (marked as +) should be noticed. Hemerophytes are marked ○.

	Betula pubescens
	verrucosa
	Rubus idaeus
	Salix cinerea
○	*Achillea millefolium*
	Agrostis tenuis
(○)	*Anthoxanthum odoratum*
○	*Anthriscus silvestris*
	Calamagrostis arundinacea
(+)	*canescens*
○	*Campanula patula*
+	*Carex canescens*
	digitata
(+)	*echinata*
(○)	*Cerastium vulgare*
	Chamaenerion angustifolium
+	*Cirsium heterophyllum*
+	*palustre*
○	*Dactylis glomerata*
	Deschampsia flexuosa
	Dryopteris spinulosa
	Epilobium montanum
+	*palustre*
	Fragaria vesca
	Galeopsis tetrahit
+	*Galium palustre*
	Luzula multiflora
	pilosa
	Maianthemum bifolium
	Milium effusum
	Moehringia trinervia
+	*Poa palustris*
+	*Poa trivialis*
	Potentilla erecta
	Roegneria canina
○	*Rumex acetosa*
○	*acetosella*
○	*Scrophularia nodosa*
	Solidago virgaurea
○	*Sonchus arvensis*
	Taraxacum sp.
○	*Dicranella cerviculata*
	Pleurozium schreberi
○	*Pohlia nutans*
	Polytrichum commune
	juniperinum
○	*Marchantia polymorpha*

The burnt area is instructive in showing that as soon as competition from the tree layer decreases or stops, *Calamagrostis canescens* grows luxuriantly and becomes the most important species physiognomically. Thus in this respect the development reverses to the state which obtained just after drainage, and which still obtains in localities with similar conditions.

The much greater difficulties in attempting to reconstruct the previous species composition in the peripheral zones than in the central zone are apparent from the above discussion. In addition to these factors, the parent community of these areas is only exceptionally identifiable in the present vegetation and the peat material in the surface layer is often destroyed out of all recognition. Therefore for these areas, comparison with notes from previous surveys and also with descriptions in literature from nearby equivalent vegetation types are more important than they have been earlier.

Maianthemum-spruce wood (Table 9, quadrat 14) has originated from the least eutrophic of the parent communities of the meadow-spruce wood, which was former a wooded fen or carr with birch as the most important species but with a conifer element, mainly spruce, probably also present. Stumps of *Alnus glutinosa,* bored through in the course of the peat investigation, show that this species was also present, although the stumps are now commonly at a depth of more than 50 cm, but its frequency has been low. Plants of *Menyanthes trifoliata* and *Iris pseudacorus,* even from some time after drainage, give an indication that the locality has been fairly wet. *Iris* still occurs as a relict in one or two places in the tree stand, but its normal habitat is in the large main run-off channel. Various *Cyperaceae,* mostly *Carex* spp., were probably the most important species in the field layer, and the bottom layer consisted of *Drepanocladus* spp. From this the plant community can be said to be parallel with some of Almquist's (1929, p. 106) *Carex*-fens, but having a tree layer. The reason for this assumption is the occurrence in 1927 of *Carex elata* and *Carex nigra, Drepanocladus intermedius,* and probably a *D. exannulatus* form. In addition, there are several herbs in common with Almquist's list: *Caltha palustris, Potentilla palustris, Galium palustre, Iris, Lysimachia* spp., *Menyanthes,* etc.

Development immediately after drainage was characterized by the major improvement in the conditions for spruce, which responded by a marked increase in growth, and further, by movement of *Calamagrostis canescens* out into the gaps between the tussocks, where it rapidly became the dominant species. In this phase, *Vaccinium vitis-idaea* had quite a high degree of cover although it occurred on the tussocks.

Table 9. Changes in the vegetation in quadrats 10, 11 and 14 in the herb-rich spruce wood between 30 June, 1927 and 19 July, 1960

	1927			1960		
Trees	10	11	14	10	11	14
Acer platanoides (seedlings)	-	-	-	1	-	-
Alnus glutinosa	1	2	1	1	-	1
Betula pubescens	2	2	4	1	1	-
Picea abies	2	2	3	2	4	4
Pinus silvestris	1	1	1	-	-	-
Prunus padus	1	1	-	1	-	-
Sorbus aucuparia	1	1	-	1	-	-
Tilia cordata	-	1	-	-	1	-
Bushes						
Juniperus communis	-	1	-	-	-	-
Rhamnus frangula	-	1	1	1	-	1
Rubus idaeus	1	1	1	1	-	1
Salix aurita	1	-	2	-	-	-
cinerea	-	2	-	-	-	-
Dwarf shrubs						
Vaccinium myrtillus	3	3	1	1	-	1
vitis-idaea	3	2	3	-	-	1
Grasses and herbs						
Athyrium filix femina	2	2	-	2	2	-
Calamagrostis canescens	4	4	4	1	-	-
Caltha palustris	1	1	-	-	-	-
Carex digitata	-	-	-	-	-	1
elata	-	-	2	-	-	-
elongata	-	-	-	1	-	-
Chamaenerion angustifolium	1	1	-	-	-	1
Chrysosplenium alterniflorum	-	-	-	-	1	-
Cirsium palustre	-	1	-	-	-	-
Dryopteris spinulosa	1	1	-	1	1	1
Equisetum limosum	-	1	-	-	-	-
Filipendula ulmaria	2	2	1	1	1	-
Fragaria vesca	1	1	-	1	1	-
Galeopsis tetrahit	1	-	-	1	1	-
Galium palustre	1	1	1	-	-	-
Geum rivale	1	1	-	-	-	-
Iris pseudacorus	-	-	1	-	-	-
Lactuca muralis	-	-	-	1	1	1
Lastrea dryopteris	1	1	-	4	3	-
phegopteris	-	1	-	-	-	-
Luzula pilosa	1	-	-	1	-	1
Lycopodium annotinum	-	-	-	-	-	1
Lysimachia thyrsiflora	-	-	1	-	-	-
vulgaris	1	-	2	-	-	-
Maianthemum bifolium	2	2	1	1	1	1
Melampyrum pratense	-	-	-	-	-	1
silvaticum	-	1	1	-	-	-
Melica nutans	-	-	-	1	-	-
Menyanthes trifoliata	-	-	1	-	-	-
Milium effusum	-	-	-	1	-	-
Oxalis acetosella	1	1	1	3	5	3
Paris quadrifolia	-	-	-	-	1	-
Poa trivialis	1	-	-	-	-	-
Potentilla palustris	-	-	1	-	-	-
Pyrola rotundifolia	1	[illegible]	-	-	-	-
Ranunculus reptans	1	1	-	-	-	-
Ramischia secunda	1	1	1	-	-	1
Rubus saxatilis	2	3	1	1	1	1
Solidago virgaurea	-	1	-	-	-	-
Taraxacum sp.	1	1	1	-	-	-
Trientalis europaea	2	1	1	1	-	1
Urtica dioeca	-	-	-	-	1	-
Viola palustris	-	-	-	1	-	-
Mosses and lichens						
Aulacomnium palustre	-	-	1	-	-	-
Brachythecium rutabulum	-	-	-	2	3	3
salebrosum	1	-	-	1	1	-
Bryum capillare	1	1	-	-	-	-
Calliergonella cuspidata	1	1	-	-	-	-
Ceratodon purpureus	1	-	-	-	-	-
Cirriphyllum piliferum	-	-	-	-	-	1
Climacium dendroides	1	2	1	-	-	-
Dicranum polysetum	-	-	1	-	-	-
scoparium	-	1	-	-	1	1
Drepanocladus uncinatus	1	-	1	1	-	-
Hylocomnium splendens	1	3	3	2	1	3
Hypnum cupressiforme	-	-	-	1	-	-
Mnium cuspidatum	-	1	-	-	-	1
punctatum	1	-	-	-	-	-
silvaticum	-	1	-	-	-	-
Orthodicranum montanum	1	-	-	1	-	-
Plagiothecium denticulatum	-	-	-	-	-	1
silvaticum	-	1	-	-	-	-
Pleurozium schreberi	1	1	2	-	-	2
Polytrichum commune	-	1	-	-	-	-
juniperinum	-	-	1	-	-	-
Ptilium crista-castrensis	-	-	-	-	-	1
Rhodobryum roseum	-	-	-	-	-	1
Rhytidiadelphus triquetrus	2	2	1	2	2	1
Sphagnum girghensonii	-	-	1	-	-	-
Lophocolea heterophylla	-	-	-	1	1	1
Ptilidium ciliare	1	-	-	-	-	-
Cladonia cenotea	-	-	1	-	-	-
fimbriata	-	-	1	-	-	-
rangiferina	1	-	1	-	-	-
silvatica	1	-	1	-	-	-

The habitat changes in the intermediate period can be traced in all the vegetation layers, both quantitatively and qualitatively (Table 9, quadrat 14). They are most marked, however, in the field layer. The tree layer has lost two of its four species, but this is due to the influence of man, as is the fact that spruce has not attained a higher degree of cover. An obvious result of the changed environmental conditions is that *Salix aurita* has disappeared (this only applies to quadrat 14 and its immediate vicinity). This species requires fairly good light and water supply in order to do well. The field layer has mostly undergone negative changes. Dwarf shrubs are strongly reduced throughout and occur on root bases or as unimportant remnants on the shrunken tussocks. Among grasses and herbs it is seen that *Calamagrostis canescens* is no longer represented in the closed tree stand, although single sterile relicts are present in the community. The hygrophilic element (see above) has also disappeared. *Oxalis acetosella* is the only one of the species earlier present to have shown a clear increase. In the bottom layer, *Brachythecium rutabulum* has increased considerably, whereas the species which were important earlier, *Hylocomium splendens, Pleurozium* and *Rhytidiadelphus triquetrus,* have not changed significantly.

In spite of the close relationship of the *Oxalis*-spruce wood with the *Maianthemum*-spruce wood, for reasons given above it has been considered justified to regard the two as separate associations. Such a division could also be based on edaphic characteristics, such as the physical nature of the peat layer, which may now be considered (for nutritional conditions, etc., see part II). In the *Oxalis*-spruce wood the peat is dark, almost black (dark brown when in a dry state), and it is always almost completely humified in the surface layer ("peat mull"). In the *Maianthemum*-spruce wood the surface layer is somewhat lighter in colour and of a more powdery consistency. On the basis of the existence of differences in the structural characteristics of the peat, etc., it is justified to assume that there were also differences between the two communities when the mire was undrained.

The original vegetation type of the sites now occupied by *Oxalis*-spruce wood was probably intermediate between Almquist's (1929, p. 372) tussocky birch fen and alder fen, to a large extent having both *Alnus glutinosa* and *Betula pubescens.*

According to old notes on the vegetation, "the original vegetation consisted of a tussocky birch-alder fen with occasional spruce" (transl.). Certain parts directly south of the main run-off channel, where this leaves Jägarmossen, were probably close to Almquist's (1929, p. 377) alder-ash-spruce fen. Here the peat is well-humified from the surface to the bottom (H_8—H_{10} on the von Post scale) and the consistency when dry is crumbly-granular, greasy when wet. The substrate gives the impression of being very fertile. This is especially apparent where the peat layer is so shallow that the plant roots reach the underlaying layer. However, as will later be shown (part II) the clay gyttja—which is most often the uppermost layer under the peat with a high content of mineral constituents—is not particularly rich in plant nutrients (expressed per unit weight).

In this part the soil surface directly after draining was "markedly tussocky", and the tree layer was composed of birch and alder together with single spruces. "Birch seedlings are fairly abundant. The field layer is dominated by dense grass *(Calamagrostis)*, bushes of *Salix, Rhamnus frangula, Sorbus aucuparia,* etc. The soil dug out from the main run-off channel is covered by an almost head-high, particularly dense stand of *Urtica dioeca.* Older spruce, birch and alder were felled in the years 1916—1917" (Ullén 1939; transl.).

The description refers to the area on both sides of the main run-off channel, so that the features of the development of the part south of the ditch cannot be followed in detail. This was obviously considerably wetter than the N part and quite clearly different, e.g., in being more tussocky and in having more alder. Hence, the tree layer is rather uneven, with gaps without trees here and there, where increased light penetration, "Lichtflecke" (Walter 1949, p. 345), has favoured good growth of herbs (sample area Jm 8, Table 6). From the available evidence, it is apparent that the structure of the community has changed completely during the period following drainage. The composition of the tree layer has shifted towards spruce dominance (as compared with the earlier "single spruce"), while birch and alder each make up ca. 20 per cent of the stem volume of the stand S of the main run-off channel (sample area Jm 8), but together only 15—20 per cent of the stand N of the channel (sample areas Jm 3 and Jm 4). *Calamagrostis,* previously dominant, has disappeared from the field layer and has been followed by a comparatively herb-rich community, which has some species in common with the earlier one (among the herbs *Urtica dioeca* is most noticeable, and among woody plants, *Rhamnus frangula, Salix cinerea* and *Sorbus aucuparia*).

The *Oxalis*-spruce wood probably had two different vegetation types as forerunners, viz., the recently mentioned wet type with little spruce, and a spruce-rich, less wet type. These subsequently converted towards the *Picea – Oxalis* association. The less wet type is exemplified by quadrats 10 and 11 (Table 9). It has progressed to the "normal" (*Oxalis*-dominated) form of the community (see also sample area Jm 3, Table 6). *Lastrea dryopteris* occasionally occurs locally in large quantities (quadrat 10).

As for *Maianthemum*-spruce wood, a decrease caused by man in the number of tree species, favouring spruce, can be discerned. However, there has been no systematic removal of other tree species, so that both *Acer platanoides* and *Tilia cordata* are present in the sample quadrats.

In the field layer there has been a considerable reduction in the number of species (see quadrats 10 and 11, Table 9). Only a few individuals of *Vaccinium myrtillus* remain, and among the other field layer species the particularly insignificant position of *Calamagrostis canescens,* as compared with earlier, is noticeable. At the same time, the species characteristic of moist conditions have disappeared completely. In addition, there are a number of changes which are of fundamental interest; *Oxalis* and *Lastrea dryopteris* have increased strongly, *Melica nutans* and *Milium effusum* have come in, whereas the species more frequent in heath-wood, *Maianthemum, Pyrola rotundifolia* (probably also *P. minor,* although this is not in the species list for 1927), *Ramischia secunda, Rubus saxatilis,* etc., have all decreased or disappeared.

As earlier, the bottom layer is comparatively weakly developed, and it shows no large changes. However, it has lost half of its number of species, and *Brachythecium rutabulum* is commonly the dominant species.

The above comparison, between the state of the vegetation directly after drainage and that now, has shown for the herb-rich communities that the previous division of the field- and bottom-layer vegetation, into relatively xerophilic vegetation of a heath character on the tussocks and stump bases, and more hygrophilic on the open surfaces in between, no longer exists. With unimportant exceptions, the species are now evenly distributed over the whole surface. To a large extent, the tussocks have rotted down and form only minor elevations of the surface of the ground. However, it is a common phenomenon that trees now living grow on the shrunken tussocks (see Ch. 4. C. Spruce).

As shown by the data in the tables, in all cases the number of species in the herb-spruce wood has decreased. This is so in all layers of the vegetation and is mainly attributable to changes in light and water factors. However, the opposite development has taken place in the field layer in the parts of Långholmen where the tree layer has been thinned (see below "Others", and summary Ch. 5. C.).

Grass-rich birch-spruce wood

There is probably no doubt that in its main features this area at the present time represents a successional stage which is probably very similar to that which the two preceding associations (*Maianthemum*-spruce wood and *Oxalis*-spruce wood) passed through directly after drainage. It is a characteristically moist community having a tree layer with gaps and a grass-rich field layer. This community is usually labile, but has changed only slowly during the period since ditching, when drainage of the surface peat has elsewhere been effective. However, it seems as if the S and SW part of Jägarmossen were exceptional with respect to drainage, for a considerable time after the ditches were dug, the area was so poor from a forest production point of view that it was the only one that was omitted from the forest survey of 1927 and 1931. Besides, it was stated of part of the area that it was "of less interest, since ditching has not been fully effective, and the stand is still afflicted with water" (transl.). It is probable that the conditions for forest production were also judged not to be good, since it was found that "the majority of the pine and spruce seedlings which came up between the tussocks with deciduous trees have died out" (transl.).

Thus the habitats in this part of the peat land have begun only very slowly to change their character (see also Ch. 6., diagram of annual rings). The plant community has therefore had a good chance of retaining some of the original features, i.e., those prevailing at the time of drainage. Before drainage the appearance of the vegetation probably was very similar to the collective type distinguished as 'bush lagg' ("busklaggen") by Eriksson (1912, p. 126), comprising the two main types 'birch-alder-lagg' and 'Salix-lagg'. It is interesting to compare Katz' (1926, p. 198) "*Betula alba* – *Calamagrostis lanceolata* – *Sphagnaceae* association" which occurs on mires in central Russia, and Kulczyński's (1949, p. 289) "willow-birch bogs" in Poland. These two types are perhaps not identical with the stage preceding the grass-rich birch-spruce wood, but in all probability they are very near it.

In Mjölnar fen a gradual transition can be distinguished, from the parts in the W least affected by drainage via the E intermediate types to the purely meadow-spruce wood communities. This situation is useful in that it gives indications which support the assumptions made about the stages preceding the meadow-spruce wood.

Of the material available for comparison, quadrat 13 (Table 10) illustrates the vegetation type which has been least affected by the changed environmental conditions. It is informative to quote notes about the area made on 30.6.1927: "The community is originally a grass-*Carex* fen with scattered birch-*Salix* groups. The fen surface is covered to a large extent with *Carex Goodenowii* and *Festuca rubra*. In this community, *Menyanthes, Comarum, Sonchus* and *Galium uliginosum* also occur, with *Taraxacum* here and there. There is usually

Table 10. Changes in the vegetation in quadrats 7, 8 and 13 in the grass-rich birch-spruce wood between 29—30 June, 1927 and 14 July, 1960

	1927			1960		
Trees	7	8	13	7	8	13
Alnus glutinosa	1	1	1	1	-	-
Betula pubescens	4	4	3	1	2	1
verrucosa	-	1	-	-	-	-
Praxinus excelsior	1	-	-	-	-	-
Picea abies	1	1	1	3	2	3
Pinus silvestris	-	1	-	-	-	1
Prunus padus	1	-	-	1	1	-
Sorbus aucuparia	-	1	-	1	-	-
Bushes						
Juniperus communis	-	-	1	-	-	-
Rhamnus frangula	1	1	1	1	1	1
Ribes alpinum	-	-	-	-	1	-
Rubus idaeus	1	1	-	1	2	1
Salix aurita	1	-	-	-	-	1
cinerea	1	-	1	-	-	-
nigricans	1	-	-	-	-	-
pentandra	1	-	1	-	-	-
phylicifolia	1	-	-	-	-	1
repens	-	-	1	-	-	-
Viburnum opulus	1	-	-	-	-	-
Dwarf shrubs						
Vaccinium myrtillus	1	1	-	-	-	-
uliginosum	-	-	-	-	-	1
vitis-idaea	-	1	-	-	-	1
Grasses and herbs						
Anemone nemorosa	-	2	-	1	1	-
Angelica silvestris	-	1	-	-	1	-
Anthriscus silvestris	-	-	-	1	-	-
Athyrium filix femina	-	1	-	-	-	-
Calamagrostis canescens	1	3	1	1	2	3
Caltha palustris	1	1	1	-	-	-
Carex appropinquata	2	-	-	-	-	-
elata	3	-	4	-	-	1
elongata	-	1	-	-	-	-
nigra	-	-	1	-	-	-
panicea	-	-	1	-	-	-
Cerastium vulgare	-	1	1	-	1	-
Chamaenerion angustifolium	1	3	-	-	-	-
Chelidonium majus	-	-	-	-	1	-
Cirsium palustre	1	-	-	-	-	-
Convallaria majalis	-	-	-	1	-	-
Corallorhiza trifida	-	-	1	-	-	-
Deschampsia caespitosa	1	-	-	-	-	-
Dryopteris cristata	-	-	-	-	-	1
spinulosa	1	1	1	1	1	1
Epilobium montanum	-	1	-	-	-	-
Equisetum palustre	-	-	-	-	-	1
Festuca rubra	-	-	2	-	-	-
Filipendula ulmaria	4	1	1	2	1	1
Fragaria vesca	-	1	-	-	1	1
Galeopsis tetrahit	-	1	-	-	-	-
Galium palustre	1	-	1	-	-	-
uliginosum	-	-	2	-	-	-
Geum rivale	2	1	-	1	-	1
Lactuca muralis	-	-	-	-	1	-
Lastrea dryopteris	1	2	-	1	2	-
Luzula pilosa	-	1	-	-	-	1
Lycopodium annotinum	-	-	-	-	-	1
Lysimachia thyrsiflora	-	-	-	1	1	1
vulgaris	1	1	1	1	-	1
Maianthemum bifolium	1	2	1	1	1	1
Melampyrum pratense	-	-	-	1	-	1
silvaticum	-	1	-	-	-	-
Melica nutans	-	-	-	1	1	1
Mentha arvensis	1	-	-	-	-	-
Menyanthes trifoliata	1	-	1	-	-	-
Milium effusum	-	-	-	3	1	1
Moehringia trinervia	-	-	-	1	1	-
Oxalis acetosella	1	1	-	3	3	-
Paris quadrifolia	-	1	-	1	-	-
Peucedanum palustre	1	-	-	-	-	-
Poa nemoralis	1	-	-	-	-	-
pratensis	-	1	-	-	-	-
trivialis	1	1	-	-	-	-
Potentilla erecta	1	-	-	-	-	1
palustris	1	-	1	-	-	-
Pyrola rotundifolia	-	1	-	-	-	1
auricomus	1	-	-	-	-	-
Ranunculus repens	-	-	-	-	1	-
reptans	-	1	-	-	-	-
Ramischia secunda	-	-	-	-	-	1
Rubus chamaemorus	-	1	-	-	-	-
saxatilis	1	2	1	1	1	1
Rumex actosa	-	1	-	-	-	-
Scutellaria galericulata	-	-	-	-	1	-
Sonchus arvensis	-	-	1	-	-	-
Stellaria palustris	-	-	1	-	-	-
Taraxacum sp.	1	1	1	-	-	-
Trientalis europaea	1	1	1	1	1	1
Tussilago farfara	1	-	-	-	-	-
Urtica dioeca	-	-	-	1	3	-
Valeriana officinalis	-	-	-	-	-	-
Veronica chamaedrys	-	1	-	-	-	-
Vicia sepium	-	-	-	-	1	-
Viola epipsila	1	-	1	1	-	1
palustris	1	-	1	-	1	-
riviniana	-	-	-	-	-	1
Mosses and lichens						
Aulacomnium palustre	-	-	1	-	-	-
Brachythecium rutabulum	-	-	-	1	1	3
salebrosum	-	-	-	1	1	-
velutinum	-	-	-	1	1	-
Bryum bimum	1	-	-	-	-	-
ventricosum	1	-	-	-	-	-
Calliergonella cuspidata	1	-	-	-	-	-
Campylium stellatum	1	-	-	-	-	-
Ceratodon purpureus	-	1	-	-	-	-
Climacium dendroides	1	-	1	1	1	-
Dicranum bonjeani	-	-	1	-	-	-
majus	-	1	-	-	-	-
scoparium	-	1	-	-	1	-
Drepanocladus fluitans	1	-	-	-	-	-
intermedius	-	-	2	-	-	-
Fissidens adianthoides	1	-	-	-	-	-
osmundoides	1	-	-	-	-	-
Hylocomium splendens	1	1	1	1	1	1
Mnium cuspidatum	1	-	-	1	1	1
punctatum	-	-	-	-	-	1
Plagiothecium denticulatum	-	-	-	-	-	1
silvaticum	1	-	-	-	-	-
Pleurozium schreberi	1	1	-	1	1	1
Pohlia nutans	-	1	-	-	-	-
Polytrichum juniperum	-	1	-	-	-	-
Rhodobryum roseum	-	-	-	-	1	1
Rhytidiadelphus triquetrus	1	1	-	1	1	1
Lophocolea heterophylla	-	-	-	1	1	1
Cladonia fimbriata	1	1	-	-	-	-

no bottom layer. The ground is largely covered by *Carex* and grass shoots of the preceding year. However *Amblystegium* is present in the wettest parts. Species preferring drier conditions, *Hylocomium* spp., *Trientalis, Majanthemum,* etc., are completely restricted to the tussocks, on which trees and bushes grow. *Spirea ulmaria, Calamagrostis lanceolata* and *Dryopteris spinulosa* also tend to occur around or on tussocks with bushes growing on them. After drainage of the fen, *Taraxacum* has probably come in. No forest tree seedlings have appeared yet on the fen surface" (transl.).

A comparison between the species lists of 1927 and 1960 reveals a quantitative increase and a considerable qualitative change. However, the increase is only in dwarf shrubs and mosses. Among tree species, birch and spruce have increased (see below). Alder has disappeared and pine has come in, but only as a single seedling about $^1/_2$ m in height. Among bushes, only *Rhamnus frangula* remains. Dwarf shrubs, formerly absent from the area, are now represented by *Vaccinium vitis-idaea* and *V. uliginosum.* The number of other field layer species has remained the same, but of the original 23 only 9 are left. Thus 14 have disappeared and been replaced by others. The number of species of mosses has increased from five to nine, but not one of these is the same as those previously present.

Of the important community-builders in the lower layers, only *Calamagrostis canescens* is in common now and previously. In the bottom layer, as in many other parts of the peat land, *Brachythecium rutabulum* has become most important, and in Mjölnar fen it has succeeded *Drepanocladus intermedius.* This is of special interest because it clearly shows the wet nature of the previous environment.

Another clear change is the gradual disappearance of the distinction between the vegetation on the tussocks and on the flat surface in between them. Because the surface layer of the ground has gradually become fairly thoroughly drained, plants which are restricted to a drier substrate have also been able to move in from the surrounding land. For example, *Pyrola* spp., *Ramischia secunda, Trientalis, Veronica chamaedrys,* etc., are distributed relatively uniformly in the community. We may be reminded of the quite opposite development in the *Oxalis*-spruce wood. But this may also be considered as an expression of the development of the community, since when the more open wood at Mjölnar fen becomes closed, the present condition in the herb-rich spruce wood will probably eventually be reached. Dwarf shrubs and other elements of the heath wood are here restricted to refuges on the remains of tussocks or overgrown stumps, where they can still compete successfully with the herbs, mainly *Oxalis*. But a number of species somewhat favoured by moist conditions have come in, e.g., *Equisetum palustre, Geum rivale, Milium effusum, Scutellaria galericulata.*

The important position taken by *Melica nutans* in the field layer is characteristic of the vegetation of Mjölnar fen. From being generally unrepresented in any of the quadrats from there, it has now become one of the most important species of the association, in some parts alone and in some in a mixture with *Calamagrostis canescens.*

Since drainage the tree layer has developed strongly. From being entirely localized to the tussocks, spruce, in particular, and birch have now secured a position on the "open fen surface". However, it should be pointed out that there are still large grass areas where the only woody species is thin-stemmed birch (Fig. 11).

Sample area Jm 12 represents a variant of the type described above, and has a very small amount of spruce. Identifiable stumps which can be found show that there has been no spruce there in the immediately preceding tree generation. There is a good basis for assuming that at the time of drainage there was a fairly even bush layer of birch and sparse tree layer of alder; as opposed to the foregoing type with large, open fen surfaces with *Carex,* broken by the bush vegetation on the tussocks.

In the SE part of Mjölnar fen there are two quadrats which clearly represent a more luxuriant and herb-rich former vegetation than that just described. The above-mentioned "bush lagg" (Eriksson 1912) and Almquist's (1929, p. 328) "*Ulmaria*-rich meadow-deciduous wood" are very similar to this. The 1927 survey shows that quadrat 7 represented a tussocky community with *Carex appropinquata* and *C. nigra* (?) as tussock formers. *Filipendula ulmaria* was important physiognomically although it was distributed unevenly over the surface. It was pointed out that, "the bottom layer is usually absent. *Amblystegia* occurs only very infrequently. The previous year's leaves of *Carex* spp. form a fairly dense and impenetrable mat. Birch originally grew on the fen. After felling of the birch the ground was burned to improve grazing" (transl.). Quadrat 8 has also been subject to interference, since "tall spruces, which formed a fairly closed stand" (transl.) were felled in 1916—1917. After felling there was vigorous growth of birch, grass and herbs. In 1927 the thin-stemmed birch was $^1/_2$ to $1^1/_2$ m in height. "Spruces and pines which are present in the community have partly come in after felling, and partly were present before, in the form of stunted bushes" (transl.). The poor development of the bottom layer is illustrated by quadrats 7 and 8 (Table 10). It was also said that "between the stumps there is bare ground, or ground, covered by a dense mat of previous year's leaves of *Calamagrostis*" (transl.).

The present character of these quadrats shows that there has been a decrease in the number of higher plant species, and this has been mainly in the field layer. Trees, as a crop which is harvested occasionally, are judged less easily in this respect. Of the three species formerly common to both quadrats (alder, birch and spruce), birch and spruce remain. It is strange to find that all the *Salix* spp. have gone from the bush layer, since the environment would not be expected to be unfavourable for the occurrence of at least some of them. In this layer *Rhamnus frangula* and *Rubus idaeus* are the species in common. In the bottom layer there is a slight tendency towards a decrease in the number of species, but probably an increase in the degree of cover of those species which occur, because the condition "the bottom layer is usually absent" does not now apply, at least half of the surface area being covered by mosses.

It is interesting to find that several of the field layer species which are most important in the present community were already present at the time when the quadrats were established. They have naturally been subject to quantitative changes, but nevertheless they show a surprising constancy (as in other cases, with reservations because of possible differences in estimation of degree of cover).

Others

Three of the available quadrats (no. 5, 6, 12; Table 11) have not yet been discussed, because they were considered not to be very suitable for showing the development of the various plant communities after drainage. Two of them are in Långholmen, where they have been affected by thinning the tree stand and the consequent increased illumination. The third is in the N part of the peat land where the density of the stand of spruce has practically completely prevented the development of a field layer.

The quadrats in Långholmen are both in the boundary zone between *Maianthemum*-spruce wood and bilberry-spruce wood, and this is why they have been treated separately.

These two quadrats were not particularly comparable with one another at the beginning stage. Thus *Rubus chamaemorus* was the field layer dominant in one, and *Maianthemum* and *Trientalis* in the other.

Of the 12 field layer species (apart from dwarf shrubs) there were

Table 11. Changes in the vegetation in quadrats 5 and 6 in the meadow-spruce forest, and in quadrat 12 in a part of it with a very poorly developed field layer between 29—30 June, 1927 and 21 September, 1960

	1927			1960		
	5	6	12	5	6	12
Trees						
Alnus glutinosa	-	1	1	-	-	-
Betula pubescens	2	1	2	1	1	1
Picea abies	3	?	3	3	4	5
Pinus silvestris	1	-	1	-	-	-
Populus tremula	1	-	-	1	-	-
Prunus padus	-	-	1	-	-	-
Quercus robur	1	1	-	-	-	-
Sorbus aucuparia	1	2	1	1	1	1
Bushes						
Juniperus communis	1	-	1	-	-	-
Rhamnus frangula	1	1	1	1	1	-
Ribes alpinum	-	-	-	-	1	-
spicatum	-	-	-	-	1	-
Rubus idaeus	-	-	-	2	2	-
Salix aurita	-	-	1	-	-	-
cinerea	-	-	2	-	-	-
Viburnum opulus	-	-	1	-	-	-
Dwarf shrubs						
Linnaea borealis	-	-	1	-	-	-
Vaccinium myrtillus	5	4	2	2	1	-
uliginosum	-	-	1	-	-	-
vitis-idaea	5	4	2	1	1	-
Grasses and herbs						
Anemone nemorosa	-	-	1	-	-	-
Anthoxanthum odoratum	-	-	1	1	-	-
Calamagrostis canescens	-	2	2	-	-	-
epigejos	-	-	2	-	-	-
Carex flava	-	-	1	-	-	-
loliacea	-	-	-	1	-	-
nigra	1	-	1	-	-	-
panicea	-	-	2	-	-	-
vaginata	-	-	-	-	1	-
Cerastium caespitosum	-	-	-	1	-	-
Chamaenerion angustifolium	-	1	-	1	-	-
Chelidonium majus	-	-	-	1	1	-
Convallaria majalis	-	-	1	-	-	-
Crepis paludosa	-	-	1	-	-	-
Dactylorchis maculata	-	-	1	-	-	-
Deschampsia caespitosa	-	-	1	-	-	-
flexuosa	-	-	-	2	-	-
Dryopteris spinulosa	-	1	-	1	1	-
Epilobium montanum	-	-	-	-	1	-
Equisetum palustre	-	-	1	-	-	-
silvaticum	-	-	1	-	-	-
Eriophorum vaginatum	-	-	1	-	-	-
Festuca rubra	-	-	1	-	-	-
Filipendula ulmaria	-	-	2	-	-	-
Fragaria vesca	-	-	1	1	1	-
Galeopsis tetrahit	-	-	-	1	1	-
Geum rivale	-	-	1	-	-	-
Juncus effusum	-	-	1	-	-	-
Lactuca muralis	-	-	-	1	1	-
Lastrea dryopteris	-	2	-	-	2	-
Luzula pilosa	1	1	-	1	1	1
Lycopodium annotium	3	1	1	1	1	-
Maianthemum bifolium	1	4	2	2	1	-
Melampyrum pratense	1	1	-	2	-	-
Melica nutans	-	-	1	2	1	-
Milium effusum	-	-	-	1	1	-
Moehringia trinervia	-	-	-	1	1	-
Oxalis acetosella	-	1	-	1	3	-
Paris quadrifolia	-	-	-	-	-	1
Poa trivialis	-	-	-	1	1	-
Potentilla erecta	-	1	2	-	-	-
Pyrola rotundifolia	-	-	1	-	-	-
Rubus chamaemorus	4	1	-	-	-	-
saxatilis	-	-	1	-	-	-
Sesleria coerulea	-	-	1	-	-	-
Solidago virgaurea	-	-	1	-	-	-
Sonchus arvensis	-	-	-	-	1	-
Taraxacum sp.	-	-	-	1	1	-
Trientalis europaea	2	4	1	1	1	-
Urtica dioeca	-	-	-	1	1	-
Viola palustris	-	-	1	-	-	-
Mosses and lichens						
Aulacomnium palustre	-	-	1	-	-	-
Brachythecium rutabulum	-	1	-	1	3	-
salebrosum	-	-	-	-	-	1
velutinum	-	-	-	-	-	1
Calliergonella cuspidata	-	1	-	-	-	-
Dicranum bonjeani	1	-	-	-	-	-
majus	-	1	-	-	-	-
polysetum	-	1	-	1	1	-
scoparium	1	1	1	1	1	1
Hylocomium splendens	5	5	1	2	4	1
Hypnum cupressiforme	-	-	-	-	1	-
Mnium cuspidatum	-	-	-	-	1	-
Orthodicranum montanum	-	-	-	-	-	1
Plagiothecium denticulatum	1	-	-	1	1	1
Pleurozium schreberi	5	3	1	2	2	-
Pohlia nutans	1	-	-	1	-	-
Polytrichum commune	1	-	-	-	-	-
Ptilium crista-castrensis	-	-	-	-	1	-
Rhodobryum roseum	-	-	-	1	1	1
Rhytidiadelphus triquetrus	1	2	1	1	1	1
Sphagnum nemoreum	1	-	1	-	-	-
palustre	-	-	1	-	-	-
parvifolium	-	-	1	-	-	-
rubellum	-	-	1	-	-	-
Lophocolea heterophylla	-	-	-	-	1	1
Ptilidium ciliare	-	1	-	-	1	-
Cladonia fimbriata	1	1	1	-	-	-
rangiferina	-	1	1	-	-	-
silvatica	-	-	1	-	-	-

only four in common, in contrast to the present situation where there are 15 out of 25. A marked increase in number of species has taken place.

Quadrat 5 (Table 11) represents a vegetation type which since drainage has undergone a complete metamorphosis from a species-poor "moss-rich spruce wood with *Rubus chamaemorus*"—fairly close to a marshy spruce wood—to a species-rich spruce wood with low herbs. Two of the field layer species, *R. chamaemorus* and *Carex nigra,* have disappeared, but no less than 18 species have come in.

Quadrat 6 (Table 11) has also undergone extensive changes, but not as pronounced as in the foregoing. Four out of ten species have disappeared from the field layer and 14 have come in. In both quadrats the bottom layer has changed to a fairly moderate extent. However, it is clear that there is a shift from heath-wood towards meadow-wood species. The supremity of *Hylocomium splendens* and *Pleurozium schreberi* is no longer clear and these species have to a large extent been replaced, mainly by *Brachythecium rutabulum,* and secondly, in patches, by rich occurrences of *Mnium cuspidatum; Rhodobryum roseum* is constant but with low degree of cover. Those parts of the area which have no bottom layer have probably increased somewhat in extent.

Quadrat 12 (Table 11) is an example of drastic change in the vegetation attributable to the particular effect of two important factors of the environment—drainage and dense shading. The quadrat is situated in the N part of the peat land not far from the edge and when it was established in 1927 it was little affected by the drainage. In notes from this time is written "the reaction after drainage not yet particularly obvious" (transl.). The area is characterized by an "uneven stand, with some gaps, of older birch, pine and dwarfed spruces together with some younger birch, alder and spruce" (transl.). The trees were also said to be frost-damaged to a large extent. Otherwise the quadrat is described as follows: "The ground surface is clearly tussocky. The tussocks have arisen around the tree bases. *Hylocomium* spp., dwarf shrubs, *Maianthemum* and *Trientalis,* together with *Linnaea borealis,* are mainly localized to the tussocks. In the wetter parts grasses and sedges are most successful. The occurrence of *Calamagrostis epigejos* is worthy of note. In the wetter parts mosses are often absent, although *Sphagnum* occurs with variable frequency. The most common *Carex* in the wet parts is *C. panicea*" (transl.).

The position of the quadrat in the transitional region gives the species composition the character of a mixture of fen and dryer habitat species, but some particular features lead to its inclusion under Eriksson's (1912, p. 134) fen-meadow term. However, it is modified by the occurrence of the trees and the tussocks with their characteristic heath-wood vegetation. The physiognomic importance of *Carex panicea* is also a reason for placing it near "*Carex panicea* formation" (op. cit.), which, however, like Almquist's (1929, p. 124) "*Carex panicea* association", has no tree layer.

On re-examination of the quadrat there is hardly a single character in common with those at the time of establishment. For example, none of the recorded field layer species is still present. The bottom layer has even less than 5% cover; other parts are covered by needles and twigs.

C. General remarks on the vegetational development

In the summary in Table 12 are shown the changes since drainage in the number of species in the various layers of the vegetation. The data are derived from the 14 quadrats which have been discussed in Ch. 5. B. and were established in 1927 and re-examined in 1960 (see Ch. 5. A.). The figures I—VI represent the present-day plant communities, in the order of description in Ch. 4. B.; and 0 is a community which has not been specially distinguished, with poorly developed field and bottom layers.

In areas where the vegetation has developed "normally", i.e., where felling and thinning of the tree layer has not disturbed the development to any large extent, there has usually been an impoverishment of the flora. The exceptions are the quadrats (5 and 6) affected by felling, where the number of species has increased somewhat, as in the *Ledum*-pine wood. For Mjölnar fen (quadrat 13) the increase is mainly in the mosses.

In general it seems that drainage of this type of peat land favours an increase of species which have a larger nutrient demand than the species which were part of the original vegetation of the mire. At the same time the less demanding species decrease in quantity. For example, in the bottom layer the heath-coniferous wood mosses, *Hylocomium, Pleurozium* and *Dicranum* spp., give way to *Brachythecium, Rhytidiadelphus, Mnium* spp., etc.; and in the field layer the dwarf shrubs are displaced by herbs, e.g., *Oxalis* and *Maianthemum*. The invasion of spruce into pine-dominated woods is a related feature. In the most nutrient-deficient parts the changes are from poor-fen species towards heath-wood species. *Sphagnum* spp. disappear and are replaced by the above-listed heath-coniferous wood mosses. *Eriophorum vaginatum, Vaccinium uliginosum, V. oxycoccus,* etc. in the field layer are followed by *V. myrtillus* and *V. vitis-idaea,* etc. (see development scheme below).

In general, drainage leads clearly to an increase in eutrophy of the

Table 12. Summary of the changes in numbers of species in the various layers of the vegetation in quadrats 1—14 during the period 1927—1960

	Trees				Bushes				Dwarf shrubs				Grasses and herbs				Mosses				Lichens				Total			
	1927	1960	+	—	1927	1960	+	—	1927	1960	+	—	1927	1960	+	—	1927	1960	+	—	1927	1960	+	—	1927	1960	+	—
I (1)	3	3	—	—	—	—	—	—	5	6	1	—	3	4	1	—	8	9	2	1	2	4	2	—	21	26	6	1
I (2)	3	3	—	—	—	—	—	—	6	6	—	—	2	2	—	—	8	7	2	3	3	5	3	1	22	23	5	4
II (3)	3	4	1	—	—	—	—	—	5	4	—	1	6	4	2	4	9	6	3	6	3	—	—	3	26	18	6	14
II (4)	3	3	—	—	—	—	—	—	6	3	—	3	3	3	2	2	11	7	2	6	1	—	—	1	24	16	4	12
III (9)	5	4	—	1	1	1	1	1	2	1	—	1	9	8	5	6	13	9	4	8	1	1	1	1	31	24	11	18
III—IV (5)	6	4	—	2	2	2	1	1	2	2	—	—	7	22	17	2	9	9	3	3	1	—	—	1	27	39	21	9
III—IV (6)	5	3	—	2	1	4	3	—	2	2	—	—	12	20	13	5	9	13	6	2	2	—	—	2	31	42	22	11
IV (10)	6	6	1	1	2	2	1	1	2	1	—	1	22	17	5	10	12	8	3	7	2	—	—	2	46	34	10	22
IV (14)	4	2	—	2	3	2	—	1	2	2	—	—	16	12	7	11	9	11	8	6	4	—	—	4	38	27	15	24
V (11)	7	3	—	4	4	—	—	4	2	—	—	2	22	13	5	14	11	6	3	8	—	—	—	—	46	22	8	32
VI (7)	5	5	1	1	8	2	—	6	1	—	—	1	29	21	10	18	13	9	4	8	1	—	—	1	57	37	15	35
VI (8)	6	3	1	4	2	3	1	—	2	—	—	2	31	23	11	19	8	11	7	4	1	—	—	1	50	40	20	30
VI (13)	3	3	1	1	5	4	3	4	—	2	2	—	23	23	14	14	5	9	8	4	—	—	—	—	36	41	28	23
0 (12)	6	3	—	3	5	—	—	5	4	—	—	4	29	2	2	29	9	9	6	6	3	—	—	3	56	14	8	50

Explanation: I, II, III, IV, V, VI are the association numbers according to the description in the text (Ch. 4). 0 is a community which has not been studied.

+ : species which have come in during the period 1927—1960

— : species which have disappeared during the period 1927—1960 environment, i.e. not an increase in the reserves of plant nutrients but an increase in their availability.

To conclude this chapter, an attempt is made to give a schematic survey of the succession in the forest communities on Jägarmossen. This reconstruction is undoubtedly hypothetical on some points, but the information presented above contributes some certain indications so that it seems justified to include the scheme as a basis for further discussion.

(I)—(VI) represent the present-day communities, as in the vegetation description and the earlier communities go back only to the time of drainage.

Pinus – Vaccinium spp. – Pleurozium schreberi ass. (without mire plants
↑
(I) Pinus – Ledum – Pleurozium ass. → (II) Pinus – Vaccinium myrtillus – Pleurozium ass.
↑ ↑
Pinus – Ledum – Sphagnum parvifolium ass. Pinus – Ledum – Eriophorum vaginatum S. parvifolium ass.

(III) Picea – Vaccinium myrtillus – Pleurozium ass.
↑
Picea – Betula – Vaccinium spp. – Pleurozium ass.
↑
Pinus – Picea – Betula – Vaccinium spp. – Eriophorum vaginatum – Pleurozium ass.

(IV) Picea – Oxalis – Maianthemum – Brachythecium rutabulum ass.
↑
Picea – Betula – Calamagrostis canescens – Brachythecium rutabulum ass.
↑
Betula – Salix – Carex nigra – Drepanocladus spp. ass.

(V) Picea – Oxalis – Brachythecium rutabulum ass.
↑
(VI) Picea – Betula – Calamagrostis – Melica – Brachythecium rutabulum ass.
↑
Betula – Salix – Carex elata – Drepanocladus intermedius ass.

Dwarf shrub-pine wood (I and II) is seen to show two lines of development, which gradually converge. The two beginning stages are well-known because of their general occurrence, and there is hardly any lack of certainty about their position as preceding stages of the present (I and II) communities. However, it may be doubtful whether it is correct to call the *Eriophorum vaginatum*-rich type an association, but since the two communities develop somewhat differently during a period of their existence—one leads to *Ledum*-pine wood and the other bilberry-pine wood (with *Ledum* in the intermediate stages)—they should be kept separate. The horizontal development I→II is at present taking place on Jägarmossen, and may be accepted as well-substantiated. The final stage without mire plants is hypothetical, but there is certainly evidence for it in the literature (see Tolf 1900 and also Almquist 1929). The final stage as well as II often contains spruce in important amounts. This has not been represented in the scheme.

The stage immediately preceding the bilberry-spruce wood (III) is known from an earlier observation but its origin on undrained peat land must be sought in a comparison of the literature about similar vegetation in other places. It is clear that in this case also, *Eriophorum vaginatum* has been important in characterizing the community. It has been distinguished in some cases as the peat-forming constituent in the community. Other important components have been *V. uliginosum* and *V. vitis-idaea*, and among tree species, pine, spruce and birch, growing on tussocks, have been part of a thin, weakly-growing stand.

The two meadow-spruce wood communities have had fairly similar beginning stages but the somewhat different plant nutrient conditions in the two have had a differential effect to a minor extent. Thus *Maianthemum*-spruce wood (IV) seems to have originated from a bush community with *Carex nigra* as an important field layer species and non-specific mosses of wet ground (*Drepanocladus fluitans, D. exannulatus* etc.) in the bottom layer. In contrast, *Oxalis*-spruce wood (V) has had a *Carex elata* community as a forerunner, with bottom layer species comprising somewhat more demanding mosses (*Drepanocladus intermedius, Campylium stellatum, Tomentypnum nitens,* etc.), *Mniaceae* etc. There were bushes on the large tussocks, *Salix* spp., *Rhamnus frangula,* birch etc. Both communities have passed through a grass-rich intermediate stage (VI) with *Calamagrostis canescens* as the field layer dominant in the first (IV), and *Melica nutans* as co-dominant with *C. canescens* in the second (V).

Chapter 6. The effect of drainage on the growth in diameter of the trees (annual ring measurements)

To show clearly and simply the effect of drainage of Jägarmossen on the growth of the trees a number of cores bored during the forest survey have been carefully measured. The measurements have subsequently been used to construct some annual ring diagrams. For technical details about the method of measurement see Eklund (1949).

Of ca. 250 cores examined, half have been from the base of the trunk and half from breast height (130 cm above ground level). In the annual ring diagrams it is the measurements from breast height which are shown. Annual rings from stump height are often distorted as a result of root buttresses, so that the values obtained are not fully comparable. An investigation of the "distortion" in the material showed that for spruce the ratio between the width of an annual ring at 130 cm to that at the base of the trunk was 0.8—1.0 : 1.0 (mean 0.92 : 1.00).

Pine cores have been measured from three sample areas (Jm 1, Jm 6 and Jm 10; composite diagram for these in Fig. 29), from the *Ledum*-pine wood, bilberry-pine wood and bilberry-spruce wood. As a rule, the measurements go back to the time of drainage and for some trees they go back considerably longer. During the time when ditches were dug, and directly afterwards, pine grew similarly on sample areas Jm 1 and Jm 6, but from 1925 onward (3 years after ditching had been completed) the curves diverge and for a 10 year period they are quite distinct from one another. In Jm 6, vigorous growth starts early and reaches a maximum in 1929. In the same period, there is a steady, even rise in the curve for Jm 1, broken in 1936 by a marked increase in growth, but it first reaches a maximum in 1939, 17 years after completion of ditching, when the width of the annual rings attains the same value as does Jm 6 in 1929. The curves correspond fairly well after this, but that for Jm 6 (bilberry-pine wood) usually lies somewhat higher. It is fairly certain that this difference in development is connected with the water conditions in the peat. The central *Ledum*-pine wood was at first drained with difficulty, but gradually the outer layer became sufficiently dry for the root systems to be able to extend somewhat deeper. However, this extension is still very weak (see Ch. 4. C. Pine), although sufficient to bring about an increase in the tree growth. This in turn increases the magnitude of the total

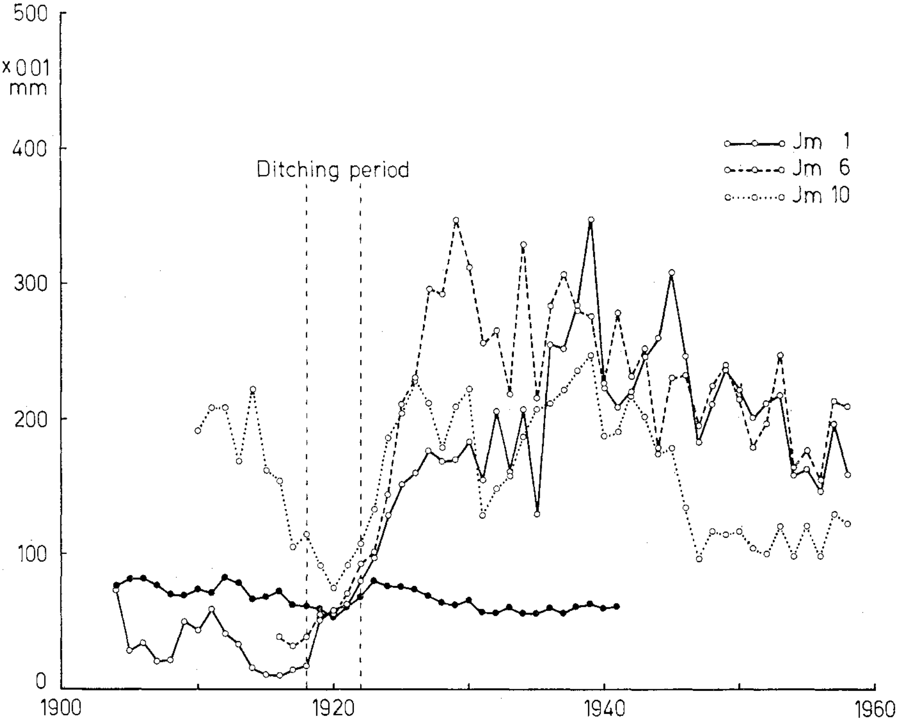

Fig. 29. Annual ring diagrams for pine within the *Ledum*-pine wood (Jm 1), the bilberry-pine wood (Jm 6) and the bilberry-spruce wood (Jm 10). Note especially how the maximum ring widths in the *Ledum*-pine wood and the bilberry-pine wood occur at different times. For comparison, the annual ring development (solid circles) of trees on ground unaffected by drainage has been included. The width of the annual rings is given in hundredths of a mm. The trees were bored at breast height. For all the single curves there were more than 10 trees measured.

transpiration, completing the biological drainage—root development cycle.

In the more peripheral sample area, Jm 6, drainage was earlier very effective and this brought about acceleration in growth shortly after ditching. As in Jm 1, the annual ring width has recently decreased somewhat.

An interesting feature of the annual ring curves is that they agree in some respects with the trends in annual ring width described by Eklund (1954) for pine, which are thought to correspond with the "growth year" character. Thus 1928 was said to be a poor growth year, followed by an improvement reaching a maximum in 1931. However, the years 1934 and 1939, said to be average growth years, are good years in the Jägarmossen material. Of the particularly bad growth years, 1935 and 1938, only 1935 is apparently as bad here.

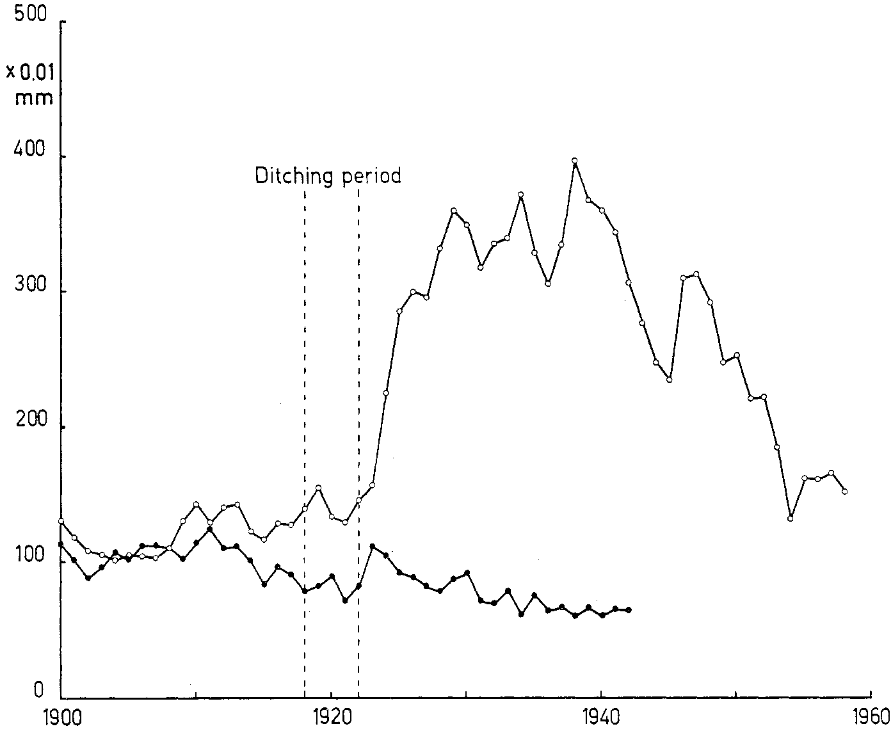

Fig. 30. Annual ring diagram for all measured spruces within the bilberry-spruce wood, the *Maianthemum*-spruce wood and the *Oxalis*-spruce wood. See text to Fig. 29.

The annual ring development (Fig. 30) of spruce after drainage at first shows the same features as pine, viz., an obvious increase in width of the rings. The first maximum is in 1929 (for the total annual ring width in all the measured trees, except for those from Mjölnar fen) and there is a minimum in 1931 followed by a maximum again in 1934. After this the curves for the two species agree only in their main features. However, as for pine, after an absolute maximum at the end of the 1930s there is a continuous decrease in annual ring width interrupted by temporary minor increases which are possibly a consequence of felling or thinning.

The first year when there was a noticeable increase in growth of spruce is 1924. Ditching had commenced six years previously and been concluded two years previously. The main run-off channel and the large lateral ditches had been dug in 1918—1921. Thus the effect of drainage was already apparent in the third year after the main ditches were dug, and in the eighth year the effect was "complete", i.e., the water level as such was no longer a limiting factor for growth.

After that the width of the annual rings was for a time determined mainly by the general features of the climate which govern tree growth in the region as a whole. After the time of the later maximum (1938) it may be assumed that the stand's demand on the substrate had reached such a level that nutrient availability became a factor which to a large extent determined the annual ring width.

The decrease with age (Eklund 1954, p. 29 ff.) was apparently of no significance in the decrease in recent years in the measurements (see below). However, as has been mentioned, both thinning and felling have doubtless left traces in the diagram, although it is unfortunately not possible to date these processes.

The separate sample areas may be more or less different from the general picture which has been described. The annual ring widths in Jm 2 and Jm 8 reach a first well-marked maximum in 1929 and an absolute maximum 1934. After 1934 the curve from Jm 2 already shows a downward trend. There is a weaker increase in 1947—1948 and two pronounced minima in 1945 and 1954. In contrast, Jm 8 has three very marked maxima after that in 1929, in 1937, 1946—1948 and 1953. Closely agreeing with Jm 2 are Jm 11, and also Jm 9 after 1929. Jm 9 is somewhat divergent in the almost explosive development there immediately after completion of ditching. Thus it reaches a well-marked maximum as early as 1925, followed by a slight decrease in 1927, then it agrees with the features described above. This sample area is very close to the main run-off channel, with one side parallel to it (see Fig. 2), and two of the other sides are also close to ditches, which have also contributed to a rapid and effective drainage. This area should have had the most favourable potential drainage of all.

It seems as if proximity to the main channel has been of importance for rapidity of growth reaction of the trees. Sample areas Jm 3 and Jm 4, which are rather similar to one another, but are further from the main run-off channel than Jm 8 and Jm 9 (Fig. 2), certainly have the same steep rise in the annual ring curves as Jm 8 and Jm 9 in the first stage after ditching, but their absolute maximum is not until 1938, 16 years after ditching.

In their important respects these observations agree with those for drained peat land in Finland. Thus Lukkala (1937) states that diameter growth of the trees begins to increase some years after ditching and successively rises to a maximum within 15—20 years. After this there is a decrease, which may be followed by secondary maxima lower than the first.

In the above account, annual ring measurements in sample areas

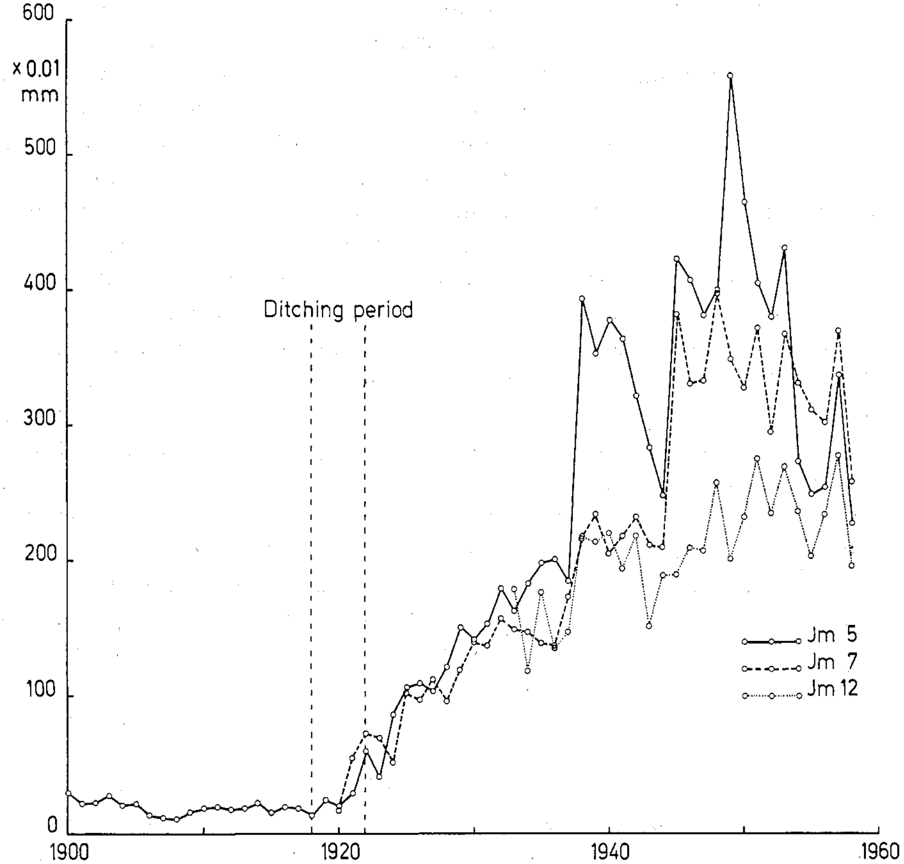

Fig. 31. Annual ring diagrams for spruce within the grass-rich birch-spruce wood. Note the difference between the growth of the annual rings in this community and in the pure spruce wood communities (Fig. 30). See text to Fig. 29.

from the open birch-spruce wood with grass have not yet been mentioned. These, Jm 5, Jm 7 and Jm 12, have such different backgrounds (see vegetation descriptions Ch. 4. B.) from all the others that they cannot be treated as equal in their development history, nor, therefore, in spruce annual ring development. These areas are part of a community characterized by the sparse occurrence of bush-type spruces on tussocks, and after ditching the growth conditions improved only slowly. Surface water remained in the area for a long time and probably because it was open, frost damage took place. There is therefore a very characteristic annual ring development in this part of the peat land (Fig. 31).

The few spruces occurring within Jm 5 from the time before ditching grow extremely slowly, on average only 20 per cent as fast as spruces in other parts at the same time. This supports the hypothesis that at least in this part of Mjölnar fen tree growth suffered more from the unfavourable conditions than in other parts of the peat land. After ditching, a distinct but slight increase of annual ring width can be discerned for sample areas Jm 5 and Jm 7. Jm 5 reaches a first maximum in 1938 but this is followed in the early 1940s by a marked decrease and then a very pronounced increase toward the end of the decade. The maximum attained in 1949 is the highest absolute value of all the means for several trees measured on Jägarmossen. The annual ring for that year was as much as 5.6 mm in width, corresponding to a diameter increase of more than 11 mm. After that the curve goes down again, with secondary growth peaks in 1953 and 1957 and pronounced depressions in 1952 and 1955. Sample area Jm 7 shows only a minor increase at the end of the 1930s, nor does it have such marked changes as Jm 5. However, like Jm 5, it has a growth peak in 1945, but its absolute maximum is attained in 1948, one year earlier than Jm 5. As in all the other annual ring measurements there is a decrease in growth in these two sample areas in 1958, the last year of measurement.

In this material there is no clear decrease in annual ring width with increasing tree age, nor is there any clear evidence as to whether trees of different ages react at different speed to drainage. To study this to some extent the measurements were sorted into five age classes from 30 to more than 70 years. However, the material is somewhat heterogeneous (for example there are only four trees in the lowest age class and two in the highest).

The class > 70 years reaches its maximum first (1926) but after this it has about the same annual radial increment as the other classes, during a 15 year period up to about 1941. However, after that its growth decreases relatively more rapidly than that of the other classes. For the remaining classes the maximum falls in the order: 31—40, 61—70, 51—60 and 41—50 years (1928, 1929, 1938 and 1938, respectively). It should be remembered that the age classes correspond to a certain extent with site on the peat land, so that the substrate and drainage factors can change very significantly from class to class, and therefore affect growth (see Heikurainen and Kuusela 1962).

How growth varies with age, in this particular case, can be shown suitably in a simple table of mean annual ring widths of spruce during different periods, in relation to a standard:

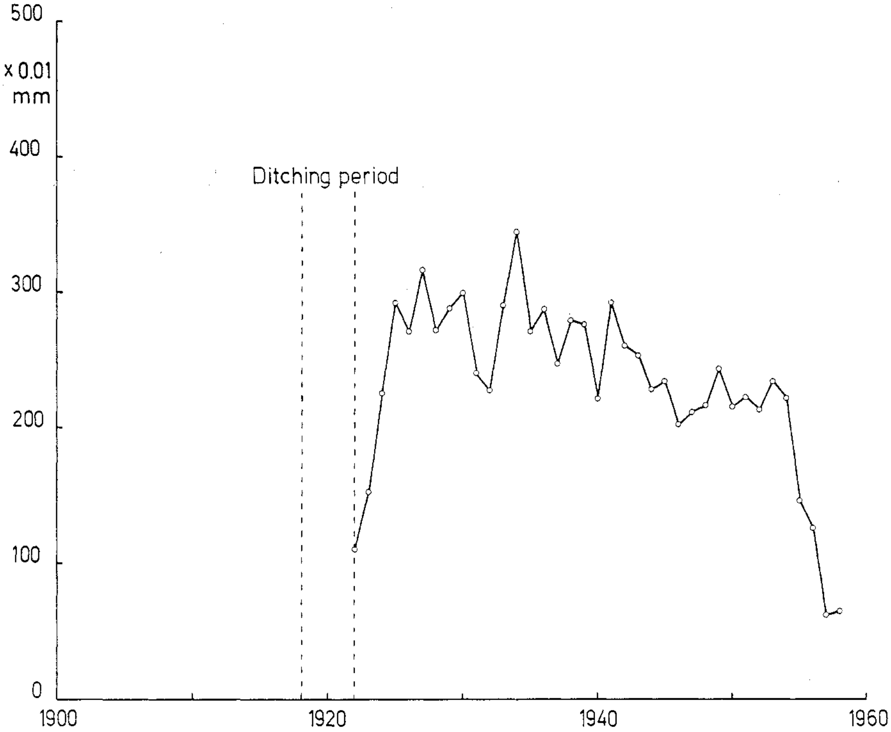

Fig. 32. Annual ring diagram for birch (Jm 12). The birch rapidly attained maximum growth rate after drainage, but this period was short. After less than 30 years, growth fell off very markedlv.

Mean relative annual ring width for different age classes and different periods

Age class, years	31—40	41—50	51—60	61—70	> 70
No. of cores	4	39	12	13	2
Before 1923	116	100	107	77	74
1923—1958	172	199	208	219	153
Total measurement period	166	172	177	166	123

Class 41—50 years has been taken as the base value as it includes the largest number of measured cores.

It should be pointed out that these measurements are for age at breast height (130 cm above ground). The absolute age is often considerably greater. Mean age at breast height for all the measured trees is 31 years but the range of variation is great, from 4 to 83 years.

To judge from the annual ring measurements, *Betula pubescens* (Fig. 32) first became more general in the communities of the peripheral zones as a consequence of drainage. In the years immediately after ditching the annual ring development is mainly the same as for the other measured tree species, but afterwards the only point of agreement is the maximum in 1934. This is also the absolute maximum annual ring width of birch. After this there is at first a weak downward tendency, with minor fluctuations. From 1953 onwards the downward tendency has become more pronounced (see also Ch. 4. C. "Birch").

The pattern of annual ring growth on various parts on Jägarmossen is not uncommon on drained peat lands, even if other sites may show a more or less divergent development.

Part II

Habitat conditions in the area of detailed study

Chapter 7. Geological features

In the investigation started in 1927 of forest production on Jägarmossen, the substratum was also studied fairly thoroughly. However, the result of this study is represented only by a peat boring record and a sketch of two peat profiles based on that record.

From notes and the profile sketch it is apparent that different kinds of sediments as well as sedentary soils (peat) are to be found. The sediments are algal gyttja, clay gyttja, chalk gyttja (see Kubiëna 1950) and alluvial clay, and they were all deposited in open, calm water. The basin was cut off from the sea 4500—5000 years ago (Ch. 3).

The most common sediment is the clay gyttja (clay mud), which covers the mineral soil substratum (glacial till, sand and clay) over the largest part of the peat land. The general properties of the clay gyttja, as well as of the other soils occurring, are fully described by von Post and Granlund (1926) and Osvald (1937). Hence only observations made within the area will be discussed. The terminology used by von Post and Granlund and Osvald (op. cit.) has been followed.

The clay gyttja stratum is often very thick: in the deepest parts of the basin (Fig. 33) it may be almost 2 m. Towards the shore of the former lake it becomes thinner but a few meters from the shore-line it is still easy to discern it in most parts (see Fig. 33, in which it can be seen that the clay gyttja only 20 m from the shore-line is as much as 7—8 dm thick).

The occurrence of clay gyttja near the boundary between the former lake and the present-day non-peaty land means that peat formation has not extended beyond the shore-line of the lake further than the thickness of the peat layer since the time when the lake was filled-in. Accordingly, the surrounding land has not become paludified to any noticeable extent.

Within small parts in the NW of the peat land the clay gyttja is not typical, but forms a transition to pure clay. Clay is thus the layer nearest to the overlying peat in that part. The ash content of the clay is 90 % or more in comparison to 75—80 % for the clay gyttja in the other sites and the apparent density of the clayey matter is about 1300 g/dm^3 as against 400 g/dm^3 for the clay gyttja proper.

A peculiar formation in the southern part of the area is the hollow, filled up by clay and silt, below the clay gyttja. It is easily seen in both the peat profiles (Fig. 33). This hollow is of interest because its extension within the peat land completely coincides with Långholmen, the only part of the area with a comparatively good tree stand before the ditching, i.e., with good natural draining.

The clay gyttja is throughout very poor in fossils, but shells of *Mytilus* in the gyttja as well as in the transition layer to the underlying sand provide evidence of the marine epoch of the former lake. Remains of "brown mosses" have also been found embedded in the gyttja. Information on some of the chemical properties of the clay gyttja is given later. It has not been investigated microscopically, therefore it is not possible to decide how much of it is of brackish or fresh-water origin.

After the clay gyttja, the algal gyttja (algal mud) is quantitatively the most important of the sediments. This occurs in the central and deepest part of the former lake. The algal gyttja is a characteristic dull reddish brown and has a firm jelly-like consistency. It is nowhere particularly thick; about 70—80 cm is the maximum. Because it is only in the deeper parts, it does not occur in any of the vertical profiles for peat sampling, but it has been cut through in some deep peat profile pits immediately S and N of the pine wood communities, in both places at a depth of 160—180 cm. In contrast to the clay gyttja, the algal gyttja contains some identifiable remains, e.g., fruits of *Alnus, Betula, Tilia* and *Acer* and leaves of *Alnus, Betula* and *Salix* sp. Since the algal gyttja is not the immediate substratum for the vegetation at any site, it has not been chemically analysed.

Between the clay gyttja and the algal gyttja, there are a few smaller areas with calcareous gyttja. These areas lie N and S of the central part at a depth of 2—3 m below the ground surface. The thickness is up to 40—50 cm. The large number of broken shells of various molluscs and of lime concretions give the gyttja a pronounced granular structure which causes its easy break-down into small pieces when dug up. Here and there in the gyttja, as well as in the transition zone to overlying and underlying sediments, there is often a large number

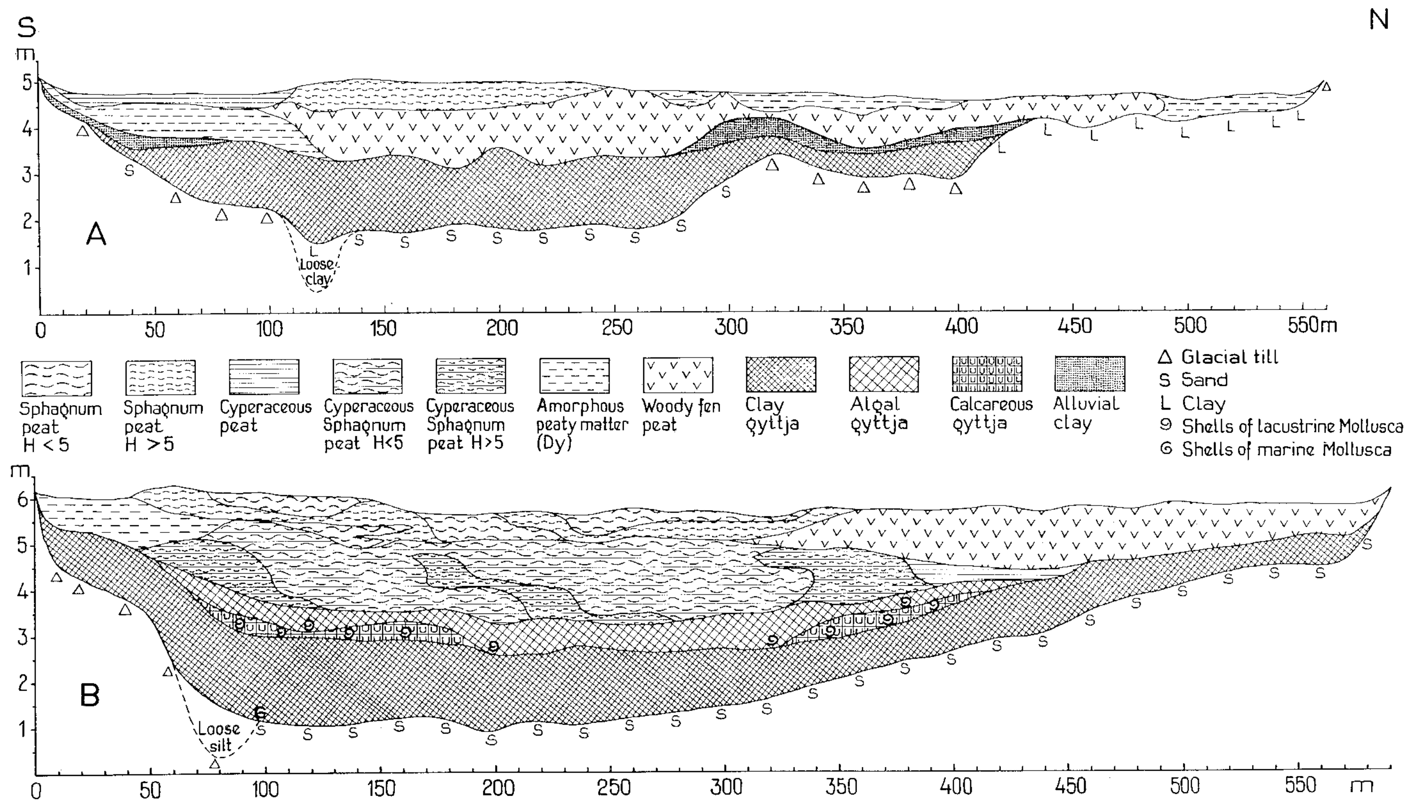

Fig. 33. Jägarmossen. Profiles through the peat. For A and B, see Fig. 34.—Largely based on a sketch by N. Willén from borings made in 1927.

of undestroyed shells of bivalves and snails. The high carbonate content of the calcareous gyttja is easily demonstrated by pouring hydrochloric acid upon it. It then effervesces strongly.

The alluvial clay in the W part of the peat land has a relatively small area of distribution. It has presumably been formed from the clayey moraine and clay deposits which constitutes the substratum of the former lake and also its immediate surroundings in that area.

These soils, in general far out of reach of the roots of the living vegetation, have been treated in relatively great detail because they give an instructive picture of the conditions for the formation of the peat land and also, to a certain extent, of the properties of the surrounding non-peaty land.

In general, the peat-forming plant communities grew over an only slightly concave lake bottom, because the sediments had filled up the deepest parts. In the shore zones the bottom was more steeply sloping. This shallow basin was progressively filled up and today there is a hint of convexity in the surface profile in a small part in the centre of the area.

The limnic peat types are very sparse; remains of *Phragmites communis* occur in only a few places and then as extremely thin layers in the profile. In the peripheral areas the sediments are mainly overlayered by different kinds of woody fen peat and, in the centre, by *Sphagnum*-cyperaceous peat, indicating that the open water surface was first over-grown by a quagmire; the peripheral areas were then already very wet fen communities. The quagmire for a time consisted of tall *Carex* species, mainly *C. lasiocarpa,* the fruits of which have often been found in the peat samples. Remains of *Menyanthes trifoliata* and, above all, of *Scheuchzeria palustris* have also been found. Remains of the latter species (mainly fruits) have been found in nearly all of the peat samples from the deeper levels within the area studied. Within the area which now corresponds to the *Ledum*-pine wood, such remains also occur at considerably shallower depths; at a level 60—70 cm below the surface there is a large number of *Scheuchzeria*-rhizomes. The dominating mosses in the quagmire have been different *Sphagnum* species able to tolerate the very wet site, but "brown mosses" have also been observed (*Paludella squarrosa* is the only identified species; *Drepanocladus* was also represented).

As a consequence of the continuing filling-in process the quagmire gradually sank down and settled on the sediments. The surface layer generally became more firm and less wet and plant communities favoured by the wet site were succeded by others. Finally the central part was filled-in, but it is still possible to find lenses of water enclosed in the peat. In the surface layer of the central area drier communities have developed with less wet-demanding *Sphagnum* species and with *Eriophorum vaginatum* as the quantitatively most important species. The peripheral communities have remained very wet even up to some time after draining. Once formed, the woody fen and the *Carex* fen communities have maintained the main features of their appearance up to the time of drainage. During a period of their development these communities also extended over the *Sphagnum*-cyperaceous communities in the central part (see Fig. 33). However, these latter communities later recolonized the lost areas.

Today only a small area, very nearly coincident with the *Ledum*-pine wood, has a low-humified *Sphagnum* peat (*S. fuscum, S. magellanicum, S. parvifolium*). In the direction of the peripheral area from the *Ledum*-pine wood, there is a wide section, comprising the main part of the bilberry-pine wood, the bilberry-spruce wood and also tongues of the *Maianthemum*-spruce wood, with a moderately or highly humified *Sphagnum* peat which in large areas is strongly mixed with or substituted by *Eriophorum vaginatum* peat. Between that section and the boundary with the non-peaty land, different, rather highly humified fen peat types follow. In the most superficial layers, humification can be complete (H_{10}) and the peat is then characterized as "peat mull" ("muck soil"). However, small parts of the SW area of Mjölnar fen have only moderately (H_5) humified *Carex* peat even in the surface layers. It is particularly the tall *Carex* species (*C. lasiocarpa* and *C. elata*) which contribute to the firm structure with still identifiable plant remains.

In the area SW-SE of sample area Jm 2 the surface peat is completely humified (H_{10}). This peat is probably partly composed of low-growing *Carex* species (*C. nigra, C. panicea,* etc.) and partly of fen "dy" (amorphous peaty matter) i.e., a kind of peat deposited by a *Carex* community without a bottom layer "in which the plant remains are decomposed to an amorphous 'dy' under the influence of water rich in oxygen" (von Post and Granlund 1926; transl.).

Chapter 8. Topography of the peat land, thickness of the peat, and area distribution of different depths

The peat land slopes weakly from N to S and from W to E. The levelled profiles (Fig. 33, A and B) show that in the N—S direction the slope is at the most, about 1 in 400 (profile C, not shown in Fig. 33). If the comparatively steep rise in the transition zone to the non-peaty land is disregarded, the slope of the peat land is only 1 in 800 for profile C, < 1 in 1000 for profile B (580 m long) and 1 in 1000—2000 for profile A (560 m long), i.e., angles of inclination < 0.°1.

The westernmost profile (A) shows a weak convexity in the surface contour. The part may be an offshoot of the central "bog area". Profile B, however, which cuts across "the bog", is hollowed out in that part which is sometimes thought of as ombrogeneous. There are two possible explanations for this: (1) "The bog" area has never been raised above the surroundings, and was perhaps not even ombrotrophic (see also Ch. 10. a., cation exchange properties). (2) The peat has subsided as a consequence of draining. An average rise in the profile of at least 50 cm would be needed for the surface of "the bog" area to lie above the level of surrounding fen areas. If this were so "the bog" would be cut off from mineral soil water. The subsidence, if it occurred, must have happened between the ditching period and the first borings in the area, i.e., within a period of five years, because the thickness of the peat then (1927) and now (1960) is identical there.

According to Lukkala (1929 a), subsidence of the peat in "Weissmoore" and "Braunmoore", as a consequence of ditching, can reach 50—80 cm during the first five years after drainage with ditches 1.5 m deep. Within "the bog" area the depth of the ditches was 0.8—1.0 m when dug. Hence it is possible that subsidence of the peat in the area amounted to 25—40 cm, i.e., hardly sufficient to explain the ombrogeneous character. Therefore it is uncertain at present whether the central part of Jägarmossen was ever ombrotrophic.

The greatest measured thickness of the peat layer of Jägarmossen is 3.1 m, a figure which is fairly moderate in comparison with other places. The total thickness of the organic matter is, however, more than five meters.

For some German peat lands, Früh and Schröter (1904, p. 155) mention 8—13 m as highest values, while in a site in East Prussia

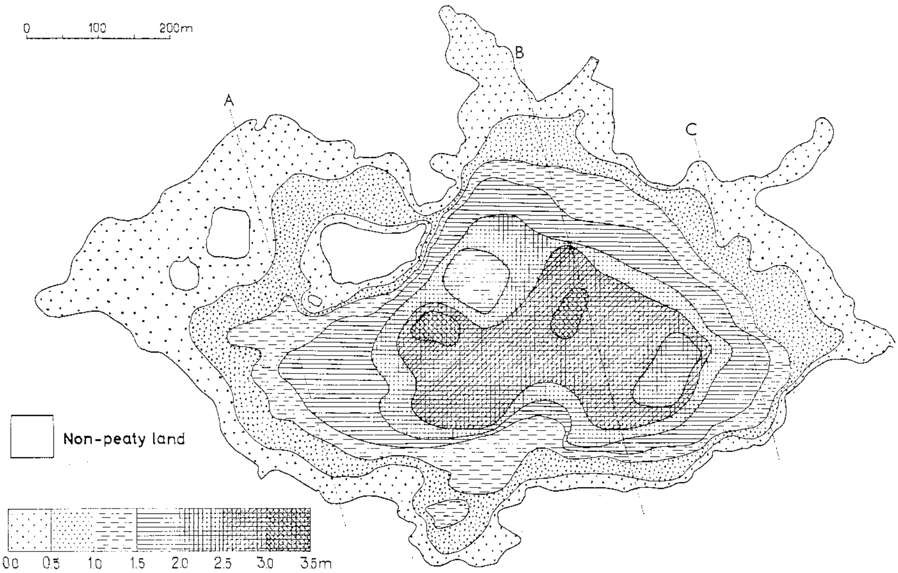

Fig. 34. Jägarmossen. Contours of the peat depth. A—C topographical sections, and investigated peat profiles; see also Fig. 33.

bottom had not been reached at a depth of 24.6 m. From Finland, Backman (1919) reports peat depths up to 7 m. The following Swedish measurements may be mentioned: Skagerhult bog (province Närke) 8 m (von Post and Sernander 1910), Degerö mire (province Västerbotten) 7.8 m (Malmström 1923), Åkhult mire (province Småland) 13 m (Malmer 1962 a).

The map (Fig. 34) shows the thickness of the peat layer on Jägarmossen. This map is based on borings at a rectangular spacing of 20 by 40 m. The percentage distribution of different classes of peat thickness is seen from the following table:

Table 13. The percentage distribution of peat in different depth classes

Peat depth class m	Area-%	Cumulative area-%
0.0—0.5	31.5	31.5
0.5—1.0	19.5	51.0
1.0—1.5	12.5	63.5
1.5—2.0	14.0	77.5
2.0—2.5	9.5	87.0
2.5—3.0	12.0	99.0
>3.0	1.0	100.0

It is seen that half the area of the peat land has peat layers more than 1 m thick. This implies that nearly all the living vegetation is cut off from connection with the mineral soil substratum, and hence is wholly dependent on the store of nutrients in the peat for nutritional support.

At the same time as the peat depths were determined, an attempt was made to determine the change of the boundary between peaty and non-peaty land during the period after draining.

It must be emphasized that such a determination must be imperfect because the method used previously to distinguish between peat and mineral soil is not known and because it is in general also difficult to distinguish between these two kinds of soil in the boundary zone.

On this occasion the boundary was fixed subjectively. A distinct layer of organic matter more than two decimeters thick, below the earlier stated limit to the non-peaty land, has been regarded as peat. Through the activities of earthworms earlier shallow peat land has generally become strongly mixed with mineral soil matter. Here and there the peat is mull-like, with a granular-crumbly structure.

In general it can be stated that the peat land has receded 2—5 m where the surrounding non-peaty land borders on the peat land with a fairly slight slope. The ground thus 'gained' can at present be estimated at about 1.5 hectares, i.e., ca. 3 % of the total area of Jägarmossen.

Chapter 9. Water relations and ditching

The catchment area of Jägarmossen is estimated to be about 220 ha (Ch. 3.C.), of which about one-fifth is peat land. The yearly mean run-off which is "an excellent measure of the water balance" (O. Tamm 1959, p. 1; transl.), precipitation-evaporation, is for this region calculated to be near 200 mm. In a more detailed study (Dr. T. Ahl) made at the Limnological Institute, University of Uppsala, the annual run-off (for an average year) was calculated to be ca. 170 mm for an area immediately N of Jägarmossen.

Before ditching a large quantity of water gathered in the basin filled in by peat every year. This water was considerably slowed down

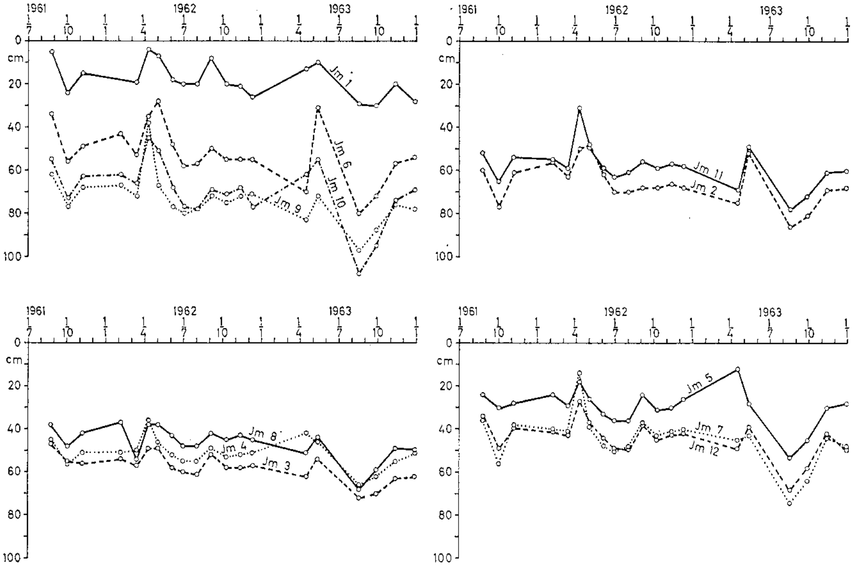

Fig. 35. The depth of the water table below the peat surface on Jägarmossen in sample areas Jm 1—12, in the years 1961—63. The diagrams are grouped according to heath-forest (Jm 1,6,9 and 10); *Maianthemum*-spruce wood (Jm 2, 11); *Oxalis*-spruce wood (Jm 3,4 and 8), and grass-rich birch-spruce wood (Jm 5,7 and 12). The measurements will be put in relation to precipitation data in connexion with a later treatment of water chemical analysis.

in its movement and rose to a higher level than today, since the passage out of the depression was higher. Before draining, the area S of the main ditch and E of the power-line (Fig. 2) was said to be impassable in summer, since the water stood high between the tussocks; and the area N of the main ditch was characterized as very wet. To make the area suitable for forest growth it was essential to draw off the surplus water. Hence a fairly extensive ditching undertaking was planned and was carried out during the years 1918—22. The main ditches were dug in 1918—21 and the secondary ditches in 1922.

The total length of the ditches on Jägarmossen amounts to about 10 800 m, i.e., about 250 m of ditches per ha. The dimensions of the main run-off channel were considerable: mean depth 1.6 m, width at the ground surface 4.0 m and at the bottom 0.5 m. All ditches were dug by hand.

As expected, the close ditching system had a very marked effect at first on the superficial water run-off. However, the effects were somewhat uneven. In some of the W parts there was an apparent lag in the development of the vegetation and the tree growth. This can only be

Table 14. Lowest water table measured within sample areas Jm 1—12, 15 November, 1959. The symbol > means that the water table wells reached the indicated level but that free water was not seen there

Sample area no.	Peat depth m	Lowest water table cm	Sample area no.	Peat depth m	Lowest water table cm
Jm 1	2.80	80	Jm 7	0.95	>100
2	1.60	150	8	0.60	>120
3	0.50	> 60	9	1.60	>150
4	1.30	>100	10	1.80	>200
5	0.40	> 80	11	1.80	>100
6	2.70	110	12	1.00	120

interpreted on the basis that the drainage was insufficient. There are still peripheral areas which seem still to be too wet to permit good tree growth, and the *Ledum*-pine wood (in the centre) is also at a disadvantage because of too high a water table (see below).

The ground water table has also been subject to a considerable sinking as a consequence of the ditching and of the increased water consumption of the vegetation. However, it is still subject to great fluctuations in certain areas (Fig. 35). In this figure an account is given of a series of water table measurements over a period of more than two years. Supplementary to these measurements are the observations of the lowest water tables encountered within the sample areas. These latter observations are from autumn 1959 after a period with very little precipitation. In 1959, precipitation was about 60—65 % of that in 1962, which was an average year. However, the regular water table measurements did not begin until 1961.

The *Ledum*-pine wood (Jm 1) differs from all the other communities with respect to water relations. The measurements indicate that even in a year with moderate precipitation (1962) there is a water table which effectively stops root penetration in a vertical direction at 20—30 cm below the surface. The sample area Jm 6 (bilberry-pine wood) is most closely related to the *Ledum*-pine wood in the properties of the surface peat and vegetation, but with respect to the water table it is more closely related to the peripheral sample areas. In all but one (Jm 5) of these the water table during the vegetation period seldom reaches a level likely to be inhibitory to the roots of the trees or of other plants with a moderate root depth. The tree roots certainly reach the upper water table levels (50—70 cm) but are not immersed in water for very long. Further, only a very small part of the total root mass reaches as deep as 50 cm. A water table of 70 cm is usually regarded as indicating entirely sufficient drainage of peat land intended for forest growth (Kokkonen 1929). More recent Finnish research also shows that a permanent water table only 30—40 cm below the surface has no deleterious influence on the development of trees, because of the small rooting depth of trees on peat land (Heikurainen 1955, see also Huikari 1959). The water relations of Mjölnar fen (Jm 5, 7 and 12) are somewhat less favourable than in other parts of the area (except for Jm 1). In particular sample area Jm 5 has a high water table during the vegetation period (about 30 cm below the surface in certain wet years). Because of this there are still many gaps in the tree stand in the area.

The lowest water tables measured (Table 14) show that in several sites the water table was greatly lowered when precipitation was very small. Sample areas with a peat layer less than 1 m thick (Jm 3, 5, 8 and 12) had no free water table in the peat in autumn 1959. For some areas with a peat layer more than 1.5 m there was no free water until the transition zone between peat and sediment (Jm 2 and 9) and in one sample area (Jm 10) there was still no free water at a depth of 2 m, i.e., in the calcareous gyttja. Also in this case, Jm 1 differs in having a lowest recorded water table at less than 1 m below surface. After the well had been dug there, the water table was not in equilibrium until after nine days.

Chapter 10. Chemical properties of the peat

A. General remarks

The physical and chemical properties of the soil have a determinant effect upon the vegetation. However, correlations between soil and vegetation in sites influenced by man as well as in virgin sites are extremely complicated. Although such correlations have been studied for a long time, it is still necessary to collect material from different types of vegetation and soil. Nevertheless, there have been several attempts to study the relations between habitat factors and vegetation, and certain evident tendencies have been revealed (see Ch. 13, and literature cited there).

There have also been attempts to relate the production of plant matter to the properties of the substratum. For farming this is an expected approach, since soil analysis is one of the bases frequently used when preparing a fertilization programme (Fredriksson 1961 a, b; Svanberg and Egnér 1961). For forestry, soil analysis has not yet achieved such an importance probably, for example, because of the difficulties in interpreting the highly stratified profiles. But in this case a knowledge of the plant nutrient status is a valuable aid in estimating the potential productivity of a site.

Among other things, the break-through in the manufacture of fertilizers at the end of the 19th and the beginning of the 20th century was responsible for the intensified reclamation of peat lands in N and NW Europe. A number of societies for promoting the cultivation of peat lands were formed. At the same time comprehensive analysis of the physical and chemical properties of peat began. Peat analysis naturally took place outside these societies (Vahtera 1956), but it was through the activity of the peat societies that it became of regional importance.

In forestry, analysis activity was small at that time and the interpretation had to be based upon agricultural experiences, which indeed to a large extent is still the case today.

To characterize different kinds of peat with regard to plant nutrient content, the analyses promoted by the peat societies are excellent because of their multitude. Hjertstedt (1936), e.g., made a summary of more than 7 000 peat analyses made at the laboratory of the Swedish peat society (see also Osvald 1937). A summary of peat analyses is also given by Melin (1917, p. 186). Malmström (1935, 1952) also contributed with peat analyses (only a few published as yet) from various regions, but like Melin (1917) mainly from oligotrophic peat lands. Sjörs (1961 a) has summarized a number of comprehensive peat analyses from different types of peat lands in Sweden; these include total analyses as well as extractable ions. Malmer (1962 a, b) and Persson (1962) have published numerous peat analyses. A large body of analyses are available from Finland (Kaila, Puustjärvi, etc.).

Because of different methods of analysis it is often impossible to make a direct comparison of the numerical values obtained at various times (Vahtera 1956).

B. Peat sampling

The sampling of peat has been done in three parts, the first two of which are concerned exclusively with the special area (Jägarmossen): (1) An "intensive" collection of samples within the sample areas only, i.e., many samples per unit area. (2) An "extensive" grid sampling according to a prefixed spacing with comparatively few samples per unit area. (3) Sampling on other drained peat lands.

It is known that the physical and chemical properties of the soil within even apparently very homogeneous areas may vary considerably (Ferrari and Vermeulen 1956). To characterize a site reasonably well with regard to soil properties great attention must be paid to the collection of samples in the field. "The analysis can be no better than the sample" (Jackson 1958). To avoid subjective influence, the samples have been distributed according to a previously fixed pattern comprising 15 cores per sample area, i.e., an average of one single soil sample per 75—100 m^2. This is much fewer than Aaltonen (1926, 1929) thought was desirable in a more intensive soil investigation, viz., a sample density of one per 20 m^2: "... wenigstens 5—10 Stück aus jedem Bestand auf einem Gebiet von 100—200 m^2". Gjems et al. (1960) also recommend taking about 15 samples from an apparently homogeneous area.

In this way almost 200 samples were obtained from the 0—20 cm level. Each of the 15 samples from the sample areas was treated individually and transported to the laboratory in a polythene bag, usually within a day or two.

In vertical profile, samples have been taken for each 10 cm to a maximum depth of 100 cm, within each sample area. In cases where "the subsoil" (clay gyttja, clay, sand) was reached at shallower depths, the sampling was discontinued earlier (sample areas Jm 3, 5 and 8). Later in the text the clay gyttja is sometimes referred to as a "mineral-rich subsoil" and the like. This must not be taken to imply that the clay gyttja is classified as a mineral soil. It is only a relative concept used to mark the wide differences between peat proper and other organic soils, of which clay gyttja is an example.

The vertical profiles sampled were in the middle of the sample areas and they never coincided with any of the earlier sampling sites. 100 cm was taken as the greatest depth because it was considered that the lower limit of root penetration was then certainly passed. It was also thought that the peat below 100 cm could hardly have any appreciable influence on the nutrient supply to the trees. Lukkala (1920) wrote that "der Torf in einer Tiefe von mehr als einem Meter eine kaum bemerkbare Bedeutung für den Waldwuchs eines Moores besitzt". However, the roots of *Alnus glutinosa* have been seen at a depth of 120 cm.

The second type of sampling comprised 300 peat samples distributed over the whole of Jägarmossen in a quadratic spacing of 40 by 40 m. On certain boundaries this spacing was completed by taking only 10—20 m between the single samples. As the peat land has an area of about 45 ha this corresponds to one sample per 1 500 m^2, i.e., very infrequent sampling with reference to the recommendations mentioned.

The soil sampling on other drained peat lands was made as representative as possible. In general, 12—15 samples were taken from each site. From these one composite sample was later made.

In the sampling process, the cores were taken out with a simple auger made of a slightly conical tube of stainless sheet-iron with saw teeth at the lower end. The cross-sectional area of the tube at the cutting edge was 100 cm². Every 5 cm the tube was partly sawn through so that it was possible to put a knife in the fissures and so divide the core into slices of desired thickness before taking it out of the tube, thus avoiding changes in the degree of compaction.

The mineral soil samples (Ch. 3.A.) were taken from the C horizon. Neither the volume nor the weight was determined, but they comprised ca. two litres of soil with a particle size ≦ 20 mm.

In the laboratory the peat samples have not all been treated similarly. Portions were taken out of samples of the first group for pH determinations on the fresh peat and then the samples were dried in a drying cupboard (25—30° C) with aforced draught. They were weighed air-dry and pH was determined once more. Large roots were then removed. After grinding in a Wiley-mill the surface (0—20 cm) samples from each sample area were aggregated in groups of five and carefully mixed. The three composite samples so obtained from each sample area were subsequently analysed.

The samples of the vertical profiles were treated in the same way but these were not mixed.

On samples of groups two and three, pH and fresh weight of the fresh soil was determined. After air drying, pH was determined again, and the samples were ground. Then the soil was weighed-out for all the other analyses. At the same time per cent oven-dry weight was determined.

No determinations were made on fresh mineral soil samples.

C. Scope and methods of analysis

The scope of the analysis is seen from the following summary:

	Group 1	Group 2	Mineral soil Ch. 3	Plant analysis Ch. 11, 12
Apparent density (bulk density)	+	+	—	—
Residue on ignition (total ash content)	+	+	+	(+)
Mechanical analysis	—	—	+	—
pH (hydrogen ion activity)	+	+	+	—
N total	+	—	—	+
P total	+	—	+	+
K total	+	—	+	+
Ca total	+	—	+	+
Mg total	—	(+)	—	(+)
P-AL	+	+	—	—
K-AL	+	+	—	—
P-HCl	+	+	—	—
K-HCl	+	+	—	—
Specific conductivity	—	+	—	—
Exchangeable metal ions	—	+	—	—
Exchangeable hydrogen ions	—	+	—	—

Symbols: + means analysis made, — means no analysis, (+) means analysis made only on a limited number of samples.

Apparent density (bulk density, volume weight) is the mass of the dry soil (dried at 100—110° C) per unit volume (Buckman and Brady 1960, p. 50; Jackson 1958, p. 10).

Residue on ignition (total ash content) is an approximate expression of the mineral matter content of the soil. It has been determined by igniting the samples in a muffle furnace at ca. 550° C to constant weight.

Mechanical analysis. The particle size of the coarser fractions of the mineral soil has been determined by sieving and of the finer fractions by the hydrometer method (Bouyoucos 1927; Gandahl 1952).

pH (hydrogen ion activity) has been determined electrometrically using a glass electrode (Radiometer 22 pH meter) in a suspension of soil in distilled water.

In spite of the present frequent use of pH determinations, there are still great variations in methods. There are (1) different reagents for extraction, when used at all; (2) different quantities of extraction reagent with regard to quantity of sample; (3) different time of extraction. Further, determinations are sometimes made on dried and stored samples, and sometimes on fresh soil. All these variations may lead to different results. See, e.g., Davis (1943), Gorham (1960), Piper (1950), Puustjärvi (1957), Ramaut (1954).

In the present case the volume ratio soil/suspension has been 1: 2 (Knutson in Malmström 1949). The substitution of soil volume for dry weight, and of suspension volume for quantity of distilled water, reduces the difference between various types of organic soils considerably. But the differences between the two main types of soil (mineral soil and organic soil) in terms of buffer capacity and colloidal content are not overcome completely even with this method. As purely mineral soils are never compared to organic soils this is of no great importance for the present investigation.

The samples were prepared in the afternoon and left until the following day, when they were stirred with a glass rod and left for sedimentation to occur for one or two hours. On measuring, the electrodes were put in the supernatant liquid.

Total nitrogen (N) was determined by the Kjeldahl method, on a macro-scale for the soil samples and on a micro-scale for the plant samples.

The solutions for determination of the ash components in peat, mineral soil and leaves were obtained by wet ashing in Kjeldahl flasks with 25 ml conc. nitric acid and 5—10 ml conc. perchloric acid (see Tamm 1953, p. 13).

Total phosphorus (P) was determined colorimetrically according to Scheel (see Tamm 1953).

Total potassium (K) was determined with an Eppendorf flame-photometer using a propane-air flame (Tamm 1953).

Total calcium (Ca) was determined with the same flame-photometer as potassium, first it was precipitated as oxalate, then the precipitate was dissolved in hydrochloric acid and calcium was determined in an acetylene-air flame (Tamm 1953). For the mineral soil, Ca was determined gravimetrically after oxalate precipitation.

Total magnesium (Mg) was determined with a flame-photometer in an acetylene-oxygen flame, according to Knutson (1957).

P-AL and K-AL. To determine the content of extractable nutrients the so-called AL-method has been in use for some time in agricultural chemistry. Phosphorus and potassium are then determined in the same solution. This is obtained by extracting 5 g of soil with 100 ml of a solution (AL-solution) which is 0.1 M in ammonium lactate and 0.4 M in acetic acid. The pH of the solution is 3.75 and its considerable buffering capacity makes it suitable also for soils with fairly high contents of free calcium carbonate without a disturbing rise in pH. According to the original method the soil is shaken with the solution for 2 hours at 20 ± 1° C (Egnér et al. 1960). However, the modification to 1 ½ hours shaking (Karlsson and Jonsson 1959) has been used in this investigation.

Much of the potassium bound colloidally and that which is superficially adsorbed to the corners and edges of the minerals is by this extraction brought into solution (exchanged with NH_4^+ which is in great excess) and can be determined. Phosphorus present as calcium phosphate is brought into solution and at least a part of that occurring as iron and aluminum phosphate.

To determine the more tightly bound nutrients (reserves) the soil was extracted with hydrochloric acid (Egnér et al. 1960). 2.00 g of fine-grained soil was extracted with 2 M HCl for 2 hours on a steam-bath.

In addition to the easily soluble potassium, this method also extracts the lattice-bound potassium. As a result, very characteristic differences appear between a mineral soil and an organic soil. The organic soils (at least those with a low ash content) hardly contain any lattice-bound potassium in contrast to the mineral soils, this is why the K-AL and K-HCl values, on the whole, are often about the same size (see also Fredriksson 1961 a: Fig. 3). For some analyses the AL values were higher than the HCl values. This is an analytical error which may depend on the fact that the methods have been worked out for mineral soils and are possibly not fully satisfactory for highly organic soils.

The hydrochloric acid extraction dissolves nearly all inorganic phosphates and hydrolyzable organic phosphates.

The difference between the two methods (the AL-method and the HCl-method) from a pedological point of view, is that the former gives an idea of the content of easily "mobilizable fractions" of potassium and phosphorus, while the latter is an expression for the soil reserves of K and P. The hydrochloric acid extraction can also be regarded as an accelerated process of weathering.

The specific conductivity at + 20° C (ohm^{-1} $cm^{-1} \times 10^{-6}$) was measured with a Metrohm Konduktometer E 182 (cell constant 0.66 cm^{-1}) in the same suspension as the soil pH, but before the pH measurement. The values are given as reduced conductivity, i.e., the conductivity due to the hydrogen ions is subtracted from the measured values (Sjörs 1948; Malmer 1962 a, b).

For determinations of cation exchange capacity in soils there are several methods in use today and it is difficult to say whether any one of them is preferable to any other. In the present investigation two methods have been used: (1) The cobalt method. When a soil sample is shaken with a solution containing Co^{2+} this ion will, on replacing other positive ions, be adsorbed on to the soil and an equilibrium will be reached between adsorbed Co^{2+} and Co^{2+} left in the solution. A 0.01—0.1 N Co^{2+} solution has a red colour, the intensity of which can be easily determined colorimetrically. Thus the exchangeable metal ions (S-value) are determined. The hydronium ions are determined after buffering the system at pH $\geqq 7$. A T-value (sum of metal ions and hydronium ions) is calculated according to a formula (see Johansson 1961). (2) Brown's method (Brown 1943), is well-known and easy to handle. In Sweden it has come into use during recent years and it has been critically examined by Sjörs (1961 a). The principle of the method is to determine the pH displacement in a soil extract made of 1 M acetic acid for extractable metal ions and in a soil extract made of 1 M ammonium acetate for extractable hydrogen ions.

Most of the determinations presented below are performed according to the cobalt method.

D. Peat analysis

1. Some relationships studied

As a tool for site classification on virgin peat land the apparent density and the ash content, as such, of the peat have only a restricted value. But both these properties are often fairly well correlated with other properties of the peat. To be able to compute the store of nutrients, apparent density must be known.

The following are examples of average values of apparent density (g/dm^3) of different organic soils:

(1)		(2)		(3)	
Bog peat soils	150	*Sphagnum* peat	95	Mässig zersetztes Hochmoor	90
Fen peat soils	250	*Calluna*-rich peat	125	Gut zersetztes Hochmoor	120
Lacustrine "dy"	350	*Carex* peat	235	Übergangsmoor	180
Gyttja soils	375			Niederungsmoor	250

(1) Osvald (1937, p. 208). (2) Løddesøl (1934, p. 107). (3) Fleischer (cited by Brüne 1948, p. 18).

The lightest kinds of peat are seen to be *Sphagnum* peat, after which come various fen peat types. The sediments (the gyttja soils), in which the mineral matter is often considerable, have the highest densities. The degree of humification of the peat influences also the size of the apparent density, see (3) above. Osvald's comparatively high values for bog and fen peat probably depend on the fact that the soils have been cultivated for farming. On the other hand, undisturbed clay gyttja may have considerably higher values, e.g., on Jägarmossen, up to 700—800 g/dm^3.

As a result af mechanical disintegration of peat, which is accompanied by increase in the "natural" humification through oxidation and microbial activity, the porosity diminishes and the apparent density increases. This is illustrated by the example below.

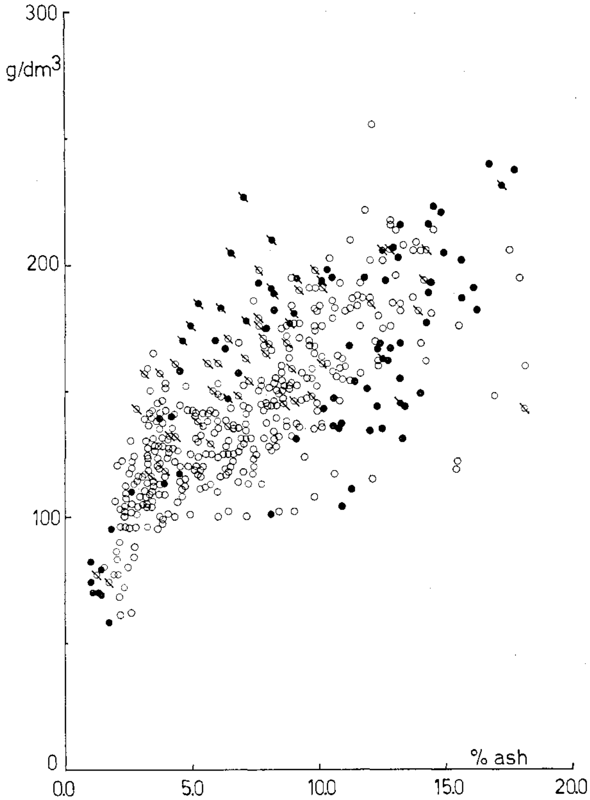

Fig. 36. Relationship between apparent density (g/dm^3) and ash content in peat. Open circles indicate samples from the layer 0—20 cm below soil surface, filled circles indicate samples from >20 cm below soil surface, and an oblique line through the circles indicates that the samples come from other sites than Jägarmossen.

Sample	Apparent density (g/dm^3)							
	1	2	3	4	5	6	7	8
(1) Natural structure......	100	96	92	88	80	153	150	140
(2) Disintegrated.........	292	279	269	216	183	450	439	434

1—5 is a low-humified fen peat composed of different *Sphagnum* spp. and 6—8 high-humified fen peat of "brown mosses", *Carex* spp., etc. (1) Apparent density measured by the usual method (see above, B. Peat sampling), i.e., the peat has its natural structure. (2) Apparent density after grinding. The volume of peat powder was measured in a measuring cylinder, in which it was compacted by shaking.

Roughly, apparent density increases with increasing ash content of the peat, even though there is wide variation (Fig. 36).

Table 15. Distribution of the pH deviations in pH*f* classes and classes of deviation. pH*f* is the pH determinated on the fresh samples. pH*d* is the pH of the same samples after air drying

Classes of deviation pH_f—pH_d	pH_f classes									
	3.0—3.5	3.6—4.0	4.1—4.5	4.6—5.0	5.1—5.5	5.6—6.0	6.1—6.5	6.6—7.0		
	Number of samples								no.	%
+0.39—+0.30		1	1						2	0.3
+0.29—+0.20			1	2					3	0.4
+0.19—+0.10	2	1	2	1	1	1			8	1.0
+0.09—±0	10	8	7	12	7				44	5.7
—0.01——0.10	12	29	14	29	8	3	2		97	12.6
—0.11——0.20	12	38	34	46	19	18			167	21.7
—0.21——0.30	2	29	31	64	27	25	5		183	23.8
—0.31——0.40	4	12	28	29	30	26	18	1	148	19.2
—0.41——0.50		5	10	18	24	13	5	3	78	10.1
—0.51——0.60		5	1	1	4	4	8	1	24	3.1
—0.61——0.70		5	1		1				7	0.9
—0.71——0.80					1		2	1	4	0.5
—0.81——0.90					1		1		2	0.3
—0.91——1.00				2			1		3	0.4

pH. A determination of soil acidity (pH) is often a useful complement to other analyses in site description. It may even be the most valuable of all possible analyses of habitat factors. "Perhaps the most important chemical property of soil as a medium for plant growth is its pH value or hydrogen ion activity" (Jackson 1958, p. 38); see also Buckman and Brady (1960, Ch. 14). The reason for this is that the acidity is often closely correlated with other habitat factors, of which "acid and base status" (Gorham 1953) may be mentioned (see also Lukkala 1929 a; Lundegårdh 1957; Schönhar 1952; Sjörs 1954, 1961 a; Stålfelt 1960). Nutrient availability also is affected by soil pH; it is shown that for wood-sedge organic soils the ideal pH is 5.5—5.8 and for *Sphagnum* peats about 5.0 (Lucas and Davis 1961).

The results of investigations included in the present paper support the opinion that there is an increase in acidity of soil when it is dried and re-wetted before measuring. From Table 15 it is seen that most of the soil samples had lower pH values when dried. Only a few (7—8 %) had higher values. If deviations of ± 0.1 pH unit are regarded as normal analytical errors then less than 2 % of the samples had higher pH after drying. About 18 % did not change at all (deviations < ± 0.1 unit) and the rest (80 %) became more acid. As seen from the table, most of the changes were small, i.e., within ± 0.3 units in more than 60 % of the samples. Changes greater than 0.5 units were exceptional.

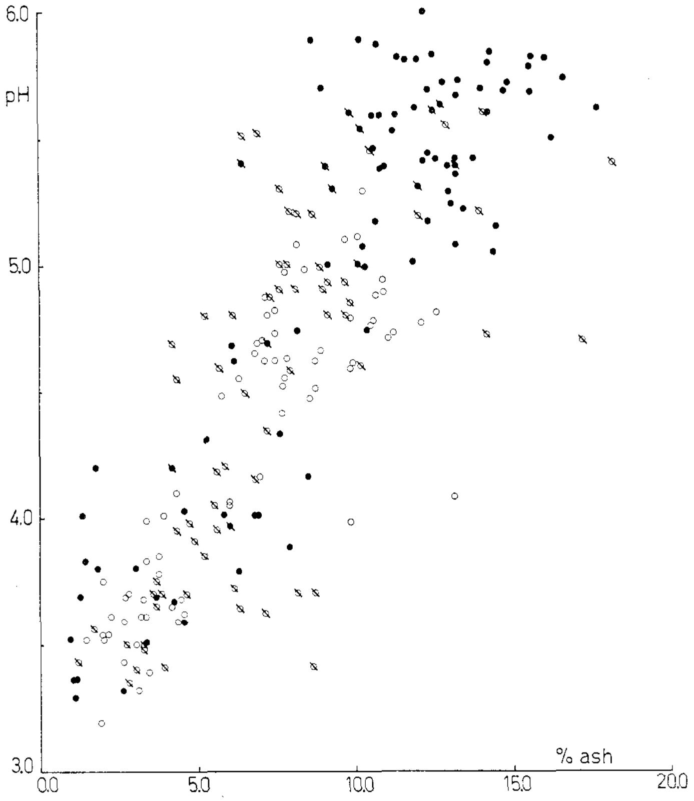

Fig. 37. Relationship between acidity (pH) and ash content in peat.—For symbols, see Fig. 36.

Kivinen (1938) comes to the same conclusion and says decrease on drying can "sogar 0.5 pH-Einheit ausmachen".

It is evident that for peat soils the changes are pH dependent and the relation between the different pH classes is almost linear. Thus drying seems to have only a slight effect on the very acid *Sphagnum* peat and *Sphagnum–Eriophorum vaginatum* peat while the less acid *Carex* peat and *Carex*-"brown mosses" peat becomes considerably more acid on drying.

The reasons for the changes have not been analysed and the literature contains only general discussion with the conclusion that the decrease is a consequence of oxidation and formation of organic acids. A pH increase (Kivekäs 1958) is said to depend on the liberation of NH_4^+ ions, which, as well as amide nitrogen, increase noticeably on drying the soil (Lebendjanzev 1924, cited by Kivekäs 1958). The

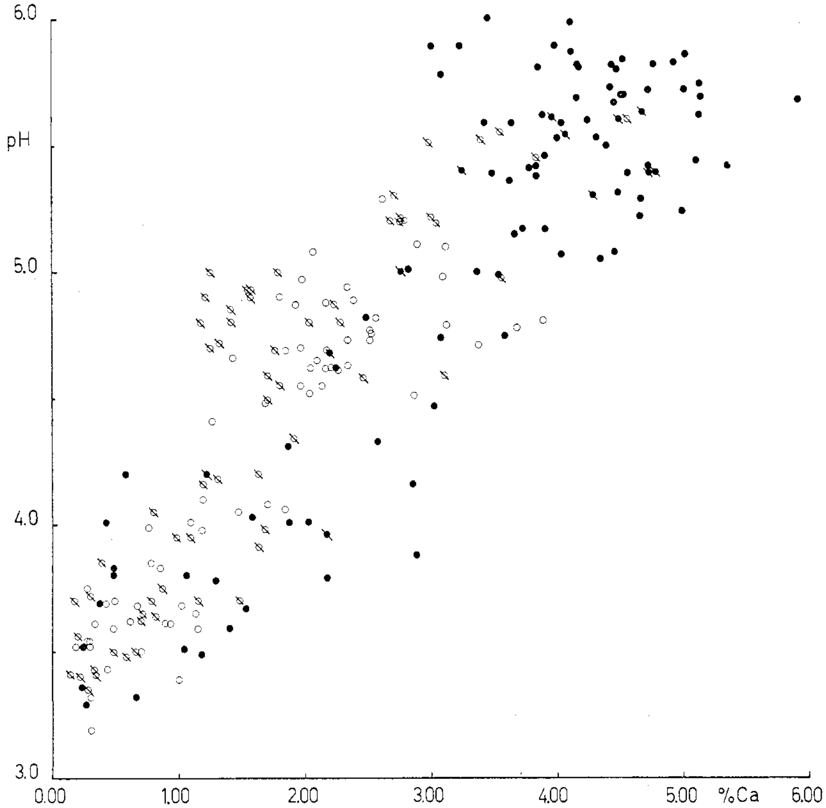

Fig. 38. Relationship between acidity (pH) and calcium (Ca) content in peat.—For symbols, see Fig. 36.

probable importance of the microorganisms is indicated by investigations by Gauger and Ziegenspeck (1930). After rapid drying of the soil there was a noticeable increase of the pH value (0.19—0.65 units), whereas drying for a longer time (14 days) at low temperature was followed by an equivalent decrease (0.22—0.70 units). It is also shown that the amounts of carbon and nitrogen mineralized are increased on soil drying and re-wetting (Birch 1960).

Acidity in relation to ash content of the peat is shown in Fig. 37. For peat in general such a relation was reported by Kotilainen (1928, p. 136), for example; for cultivated peat soils, however, the relation is likely to be less defined. Lundblad (1931, p. 258) even thought that such a relation could not be established. For the peat soils here under consideration there is certainly a fairly obvious relation between pH and ash content, at least for ash contents up to about 20 %. Because a considerable proportion of the ash consists of calcium, which is important in determining the pH value (see below), such a relation might easily be explained.

One of the ecological effects of calcium is its modifying influence on the pH value of acid soils (Stålfelt 1960, p. 314). Hence a certain relation between pH and Ca content of the soil is to be expected; a high Ca content would be expected to be correlated with a high pH and vice versa. This relationship is generally, but not always realized (Lundblad 1931, p. 263). Fig. 38 shows the relation pH/Ca for the peat soils studied.

The main feature of the results support Kotilainen's (1928, p. 136) statement: "— — — ein hoher Kalkgehalt setzt zwar immer einen hohen pH-Wert voraus, umgekehrt setzen jedoch die Hohen pH-Werte nicht immer einen hohen Kalkgehalt voraus, — — —." However, the Ca content corresponding with a particular pH value is generally considerably higher for peat from Uppland than in Kotilainen's analyses from various Finnish sites. In his material all samples with pH < 4.0 have < 1 % CaO (0.7 % Ca), while several samples of peat from Uppland with between 1 and 2 % Ca have pH < 4.0. On the other hand, all Uppland samples with pH > 5.0 have Ca contents > 2 %, and only a few samples with pH 4.5 have Ca contents < 2 %. This agrees with Kotilainen's statements (op. cit. p. 133).

From Fig. 38 it is apparent that samples from other peat lands investigated agree well with those from Jägarmossen in the relationship between pH and calcium. This diagram is closely similar to that of the relation pH/ash (Fig. 37).

Only the macro-nutrients nitrogen, phosphorus, potassium and calcium have been analysed. As a rule, these nutrients are probably the most important in determining the composition and productivity of the vegetation. In common Scandinavian forest soil types it is probably very rare that other nutrients (including micro-nutrients) are so sparse that they become limiting for the growth of trees (see Ingestad 1958).

Since the plant community forming the peat is influenced by the mineral nutrients, it is to be expected that the nitrogen content is also related to the mineral nutrient content. The degree of humification also affects the nitrogen content (Malmström 1952, p. 23). Humification involves, among other things, a decrease in dry matter because of loss of CO_2. This loss causes changes in the weight relations between the constituents of the peat.

The relationships between peat type and nitrogen content are summarized below.

Peat types	%N	Reference
Low-humified *Eriophorum-Sphagnum* peat	$\leqq$1.00	Warén 1924
Moderately-humified sedge peat	>2.50	»
Tall *Carex* peat	1.00—3.00	v.Post and Granlund 1926
Woody fen peat	$\geqq$2.00	»
Sphagnum fuscum-S. magellanicum peat	<1.00	»
Sphagnum peat	1.00—2.00	Kotilainen 1928
Carex-Sphagnum peat	1.00—2.00	»
Carex peat	>2.50	»

Sphagnum peat always has a fairly low nitrogen content, but this rises noticeably when there is an admixture of various vascular plants in the peat.

The following are examples of nitrogen content of some of the individual peat-forming plant species.

Species	%N	Reference
Carex acuta	1.64	Zailer and Wilk 1907
elata	1.29	»
Eriophorum vaginatum	1.31	»
Scheuchzeria palustris	1.85	»
Calliergon spp.	1.23—1.43	»
Scorpidium scorpioides	1.18	»
Sphagnum cuspidatum	1.18	»
cymbifolium	1.08	»
nemoreum	1.21	»
Eriophorum vaginatum	1.20	Mattson and Karlsson 1944
Sphagnum cuspidatum	0.59—0.82	»
fuscum	0.49—0.60	»
nemoreum	0.60	»
Carex elata	1.87	Gorham 1953
Eriophorum vaginatum	1.03—1.79	»
Sphagnum magellanicum	0.91	»
Eriophorum vaginatum	1.15	Tamm 1954
Do., after fertilizing	1.52	»
Carex lasiocarpa, leaves only	1.9—2.1	Malmer and Sjörs 1955
limosa, do.	2.0	»

Analyses of the surface peat (0—20 cm) from Jägarmossen show the following:

Sphagnum magellanicum and *S. parvifolium* peat with some admixture of *Eriophorum vaginatum* 0.75—1.21 % N

Eriophorum vaginatum peat with some admixture of these two *Sphagnum* spp. 1.28—1.68 % N

Peat of tall *Carex* species *(Carex elata, C. appropinquata, C. lasiocarpa)* with some admixture of small *Carex* species *(Carex nigra, C.*

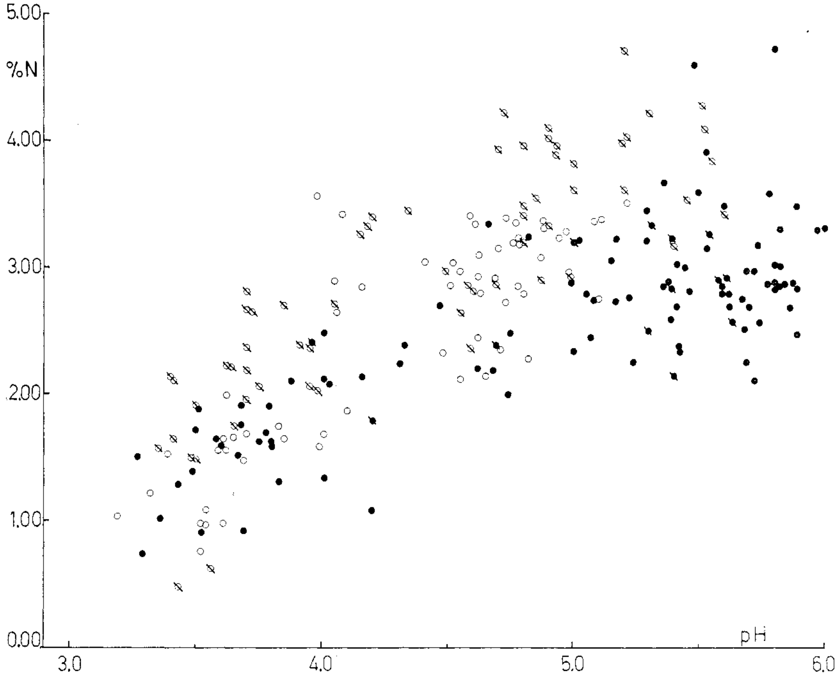

Fig. 39. Relationship between nitrogen (N) content and acidity (pH) in peat.—For symbols see Fig. 36.

panicea) and "brown mosses" *(Drepanocladus, Calliergon, Tomentypnum)* 2.72—3.44 % N

Woody fen peat (not strictly defined as to parent material; however, many herbs have been present in the community) 2.34—3.56 % N

Nitrogen content has been shown to be more or less obviously correlated with many of the other habitat factors analysed, e.g., pH, calcium, phosphorus and ash content and apparent density. There seems to be no correlation with potassium.

The relation N/pH is fairly clear even though the deviations between individual observations are great. Thus there is a regular increase in nitrogen with increasing pH (Fig. 39), at least for the surface samples (0—20 cm). However, for the samples from greater depth (> 20 cm) there is a tendency towards decreasing nitrogen content at pH > 5.5.

There is not always an increasing nitrogen content with decreasing acidity. Sjörs (1954, p. 76) wrote that for various types of meadows the pH dependence of nitrogen is "almost non-existent". Lundblad (1931, p. 261) was of the same opinion about cultivated peat land and this lack of correlation certainly depends on the upset equilibrium

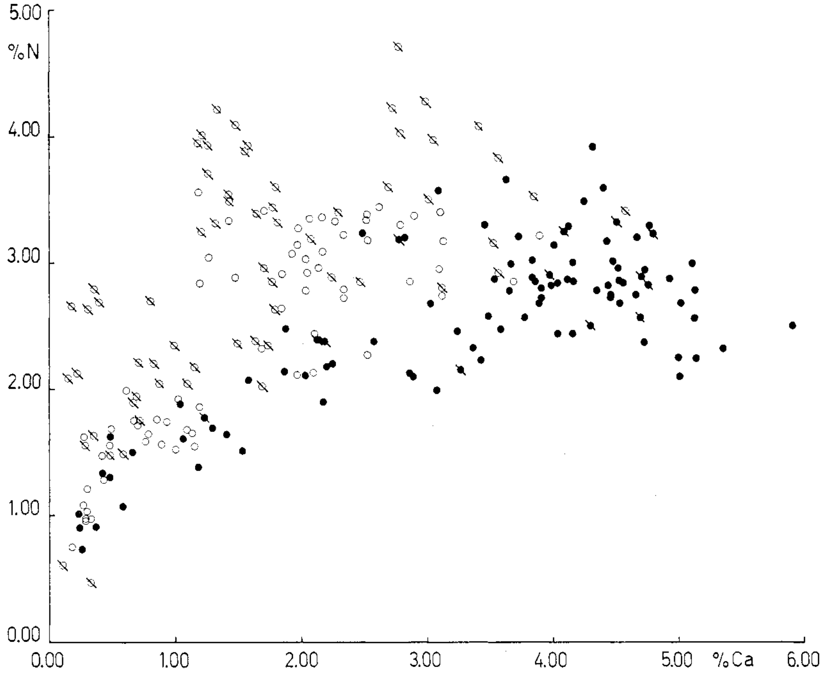

Fig. 40. Relationship between nitrogen (N) and calcium (Ca) contents in peat.—For symbols, see Fig. 36.

between the various processes in the soil consequent upon mechanical working and fertilizing.

The acidity of the peat is an important factor in the different processes of nitrification. Hence for $NH_4^+ \rightarrow NO_2^-$ the lower pH limit probably lies at 3.7—4.0 (Waksman 1957, p. 64) and for nitrate formation, the pH minimum, at least in culture, is at higher values. In fields, nitrate may occasionally be present down to pH 4.0 and sometimes lower, but the nitrification rate becomes negligible below 5.0 (Alexander 1961, p. 274). According to Romell (1953), nitrate formation has been shown in American mor samples at pH 2.9.

Because of strong acidity, in large areas of Jägarmossen there is probably no formation of easily soluble nitrogen through nitrification. Nor is the nitrification likely to be of any great importance for other parts of the area. The nitrogen economy of the plants here, as well as in more acid forest land, is mainly based upon ammonium-nitrogen. However, the nitrification process has been mentioned because nitrate is certainly formed. *Urtica dioeca,* a known nitrate-specific plant (Olsen 1921 a) occurs commonly in many places within the boundaries

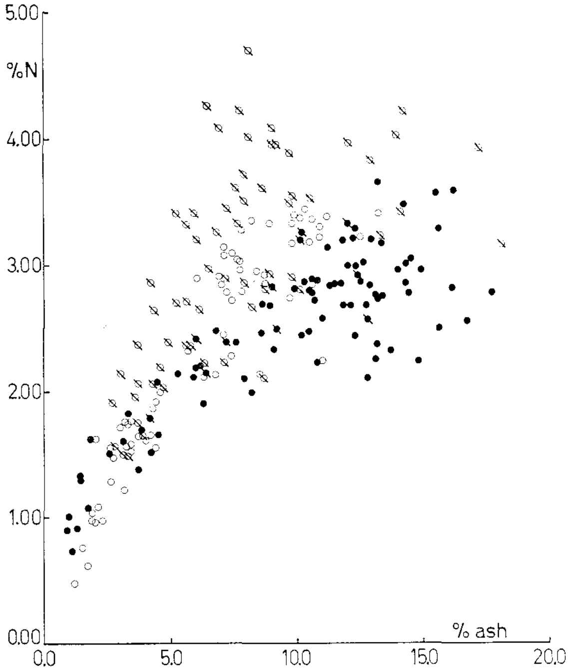

Fig. 41. Relationship between nitrogen (N) and ash contents in peat.—For symbols, see Fig. 36.

of the area, and this must presumably indicate that nitrification does occur. *Urtica* is especially abundant in places where there is little competition from trees, for instance under the power line and along the main run-off channel ("felling area effect"; see Romell 1935) but it is also found in the stands (see vegetation analyses).

Effective drainage has, as far as one can judge, two opposite effects on peat land intended as a habitat for forestry. Humification is hastened as a consequence of increased aeration and of oxidation processes and the contents of the nutrients rise; this is favourable for potential forestry. It has been shown, for instance, that if the humification of the peat is to be satisfactorily rapid, the primary N content should be $> 1.7\ \%$; at lower values humification is delayed or incomplete (Waksman and Tanney 1928). On the other hand, nitrification is retarded by the, on the whole, generally increasing acidity following drying out of the peat. The increase in acidity with drying out is greatest at the higher original pH values, where nitrification would be likely to begin.

The relation N/Ca, Fig. 40, is completely analogous to the N/pH

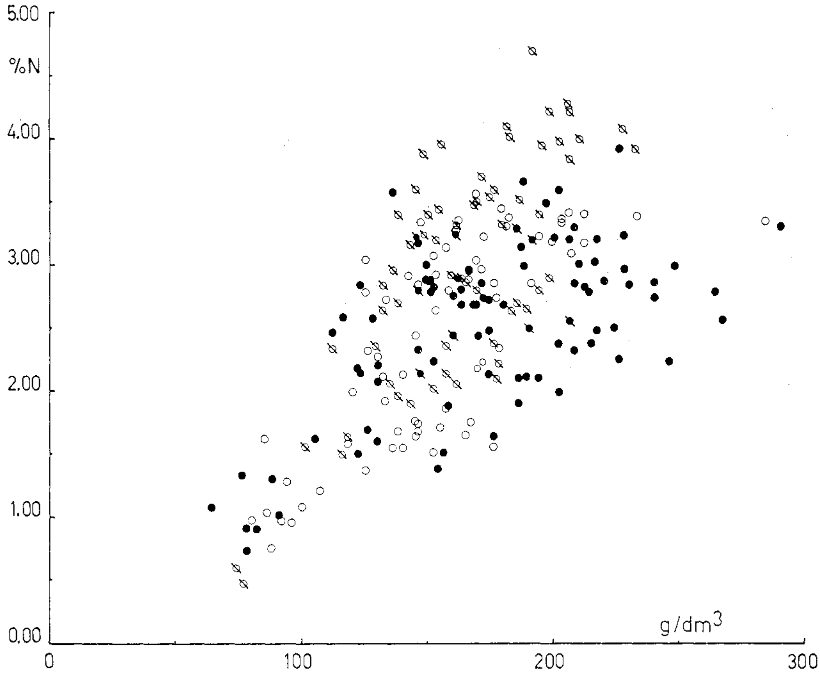

Fig. 42. Relationship between nitrogen (N) content and apparent density (g/dm^3) in peat.— For symbols, see Fig. 36.

relation. This is to be expected, as pH is fairly closely correlated with calcium content (Fig. 38).

A possible reason for the nitrogen increase at higher pH is that denitrification is in progress. The comparatively moderately acid soil and the probably often entirely oxygen-free conditions at depths of the peat greater than the level of the average fluctuations of the ground water, may be favourable for the activity of denitrification bacteria (see Alexander 1961, p. 302—303).

The relation N/ash (Fig. 41) is probably indirect, because at low and moderate ash contents, a great portion of the ash is calcium, which acts as a pH regulator. Thus the relation may be referred firstly to a pH effect and secondly, to the acid and base status.

The relation N/apparent density (Fig. 42) is to a certain degree, related to the relation of nitrogen/ash content and the other correlated factors, and to the degree of humification.

The relation N/P (Fig. 43) shows rather special features. As in the other diagrams, the analyses are classified according to sampling depth. For the surface samples (0—20 cm) there is a slight positive,

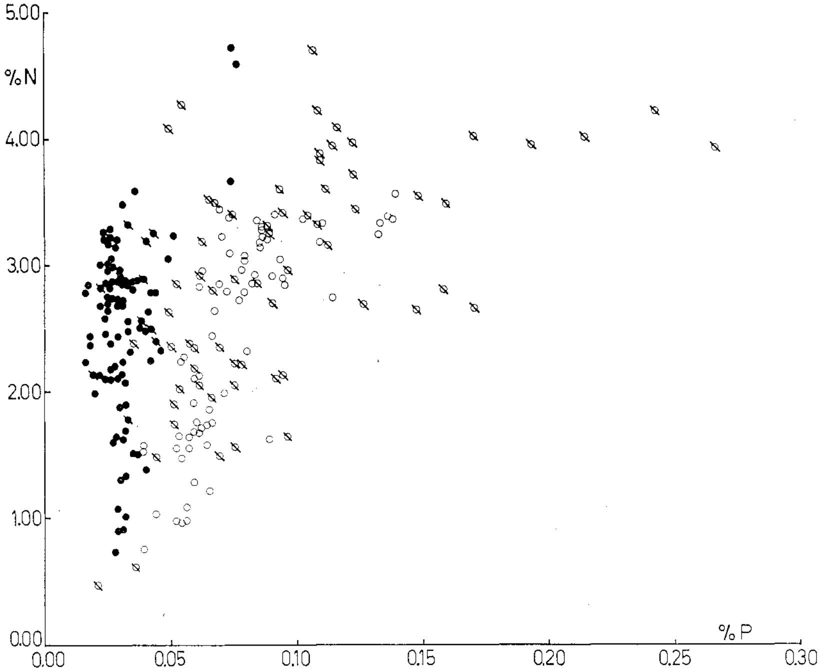

Fig. 43. Relationship between nitrogen (N) and phosphorus (P) contents in peat.—For symbols, see Fig. 36.

probably curvilinear correlation (see Malmer 1962 a, p. 202), i.e., an increasing P content is accompanied by an increasing N content. On the other hand, for samples below this level (> 20 cm) there seems to be no such correlation. Hence the N content increases completely independently of the P content, which lies between fairly narrow limits, about 0.02—0.04 %, i.e., about half the content of the surface peat. The cause of this is likely to be the living vegetation, which has lowered the P content of the substratum to a low and nearly constant level (Tamm 1958, p. 240). Consequently the impoverishment of the store of phosphorus has progressed gradually during the time when new peat has been formed and the thickness of the peat layer has increased (see also below, "Vertical distribution").

Fig. 44, Ca/ash, shows that the relations for samples from the 0—20 cm level and those from > 20 cm below the surface deviate somewhat from one another at higher ash contents in that the former seem to follow a curved line while the latter follow a straight line. Apart from the drying effect, the explanation probably is, that extractable Ca has been leached out of the surface peat which has therefore a low pH

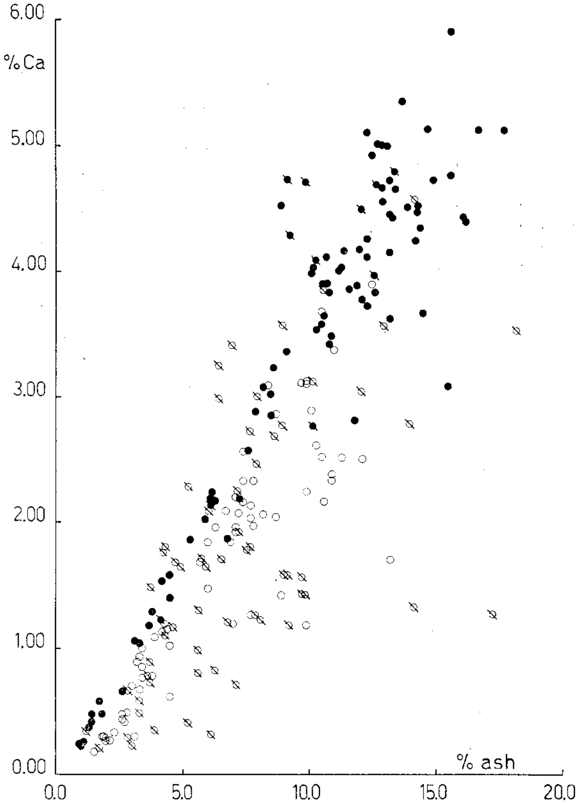

Fig. 44. Relationship between calcium (Ca) and ash contents in peat.—For symbols, see Fig. 36.

but still a high ash content. Peat from greater depths has not been so strongly leached—if leached at all—and so it has a high pH value and a high ash content.

2. Properties of the peat within the different plant communities

a. Horizontal distribution in the layer 0—20 cm below soil surface

The account is based on some maps of the geographical distribution of all analysis values of the individual habitat properties (although all properties studied are not treated in this way) and on some diagrams with representative samples from the plant communties only (see below and Table 28). The same simplified vegetation map as that used for showing the distribution of the woody species is used as a base (Ch. 4. C.; see also Fig. 3). For the sake of conveniance the plant communities may be enumerated:

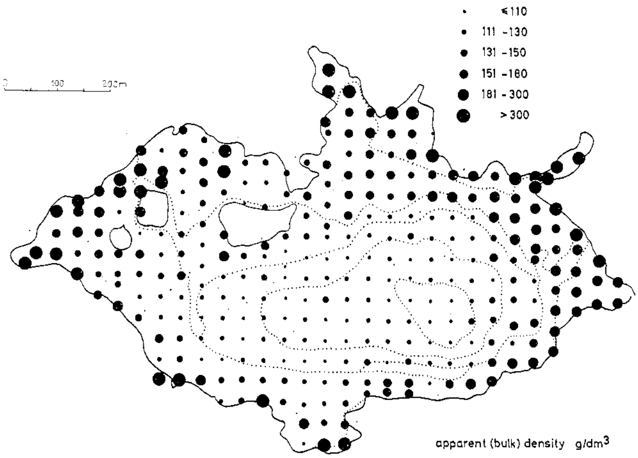

Fig. 45. Distribution of the apparent density (g/dm^3) of the peat on Jägarmossen.—Dotted lines: boundaires between the plant communities.

Heath-forest communities
I. *Ledum*-pine wood
II. Bilberry-pine wood
III. Bilberry-spruce wood

Meadow-forest communities
IV. *Maianthemum*-spruce wood
V. *Oxalis*-spruce wood
VI. Grass-rich birch-spruce wood

In the text and on many of the diagrams the numbers of the communities alone are sometimes referred to. Some of the diagrams have two symbols for the analyses; a stroke for those based on the "extensive" (see Ch. 10. B.) sampling (except for total N, P, K, Ca, for which only

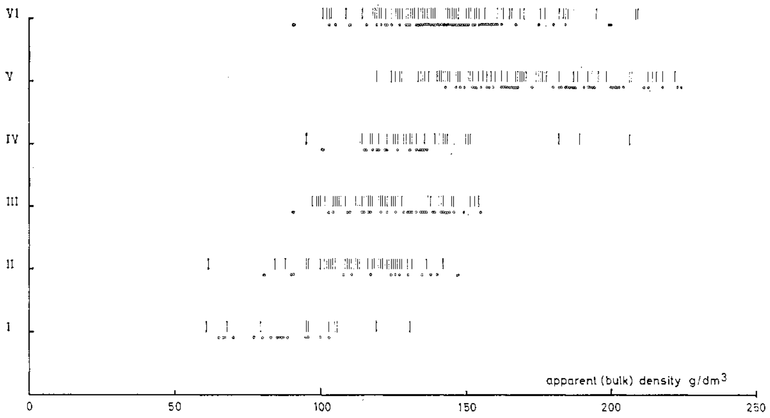

Fig. 46. Distribution of the apparent density (g/dm^3) of the peat in the different plant communities on Jägarmossen.—Each circle indicates a sample from a sample area. Each line indicates a sample from the "extensive" sampling (see Ch. 10.B.). I—VI, see Fig. 3.

sample area analyses are available) and a small circle for those from the sample areas.

The apparent density of peat from Jägarmossen and other sites visited in Uppland agree fairly well with the figures given in Ch. 10.D.1. of average values for various peat types. However, the variations between the separate sampling cores within the same plant community can be considerable (Figs. 45, 46). This is highly dependent on the sampling method. The phenomenon is most evident for the "extensively" taken samples with a rigid sampling space (40 by 40 m generally); this means that the boundaries between the communities, and especially the boundaries with the non-peaty land, are included in the samples. As stated in Ch. 4, the boundaries between the communities are never discrete lines, but zones of varying width with characteristics of both adjoining communities. In the diagram (Fig. 46), the extreme samples are omitted since their high ash contents are not representative of the plant communities (see below). However, they can be seen on the map of apparent density distribution. Apart from these deviations, there is still considerable variation. These may be attributed, for example, to the former distribution of the mire vegetation on tussocks and intervening plane areas. The tussocks, often composed of *Sphagnum* spp. were (and are, where they still remain) very porous and their peat is still often only slightly humified, giving a low apparent density. The intervening areas were composed of a vegetation which has usually given rise to a more tightly packed peat, now moderately to highly humified and having comparatively high apparent density. Thus there are examples of tussock peat from the *Oxalis*-spruce wood with an apparent density of 80 g/dm^3, while it is 175—200 g/dm^3 for the peat in between.

The determinations show that the peat of the heath-forest communities is, on average, considerably lighter than that of the meadow-forest communities. This is due to the properties of the parent material and also to the degree of humification. These variations will greatly affect the evaluation of the store of nutrients in the various communities (see below c.).

Considering the representative samples only, it is seen (Fig. 46) that the samples from the sample areas agree well with those of the "extensive" sampling. This makes it likely that the originally determined boundaries between the plant communities, based exclusively upon the vegetation, also correspond to differencies (boundaries) in chemical properties (see also below, ash content, pH).

The ash content (Figs. 47, 48) has a very wide range, between 1 and

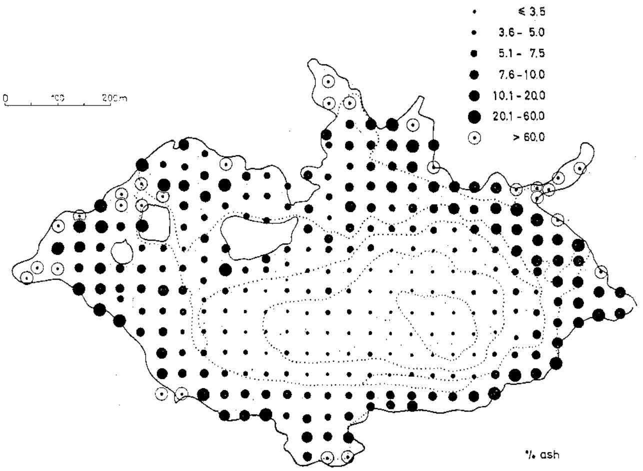

Fig. 47. Distribution of the ash content of the peat on Jägarmossen.—Dotted lines: boundaries between the plant communities.

90 % of dry matter. The only slightly humified *Sphagnum* peat of the *Ledum*-pine wood has about 1 % and then there is a gradual increase towards the boundary with the non-peaty land until there is an average of about 10 % in the peripheral meadow-forest communities. The highest figures are from the mineral soil-mixed peat of the transition zone to the non-peaty land, below the former mire boundary but now areas in many places regarded as non-peaty land.

Fig. 48 shows the varying ash contents within the different plant communities. In this diagram, and also in the others of the same type, no peat samples with more than 20 % ash are included. The ash

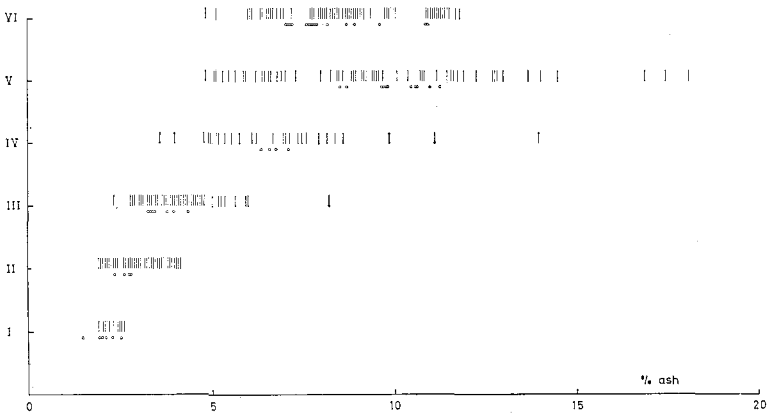

Fig. 48. Distribution of the ash content of the peat in the different plant communities on Jägarmossen.—For symbols, see Fig. 46.

content has therefore determined whether a sample has been designated as peat (< 20 % ash) or as mineral soil-mixed peat (> 20 % ash). This is doubtless a very narrow restriction of the peat concept (see Ch. 2) and it must be emphasized that it is applicable to this case only. The relations between various soil properties studied change markedly at ash contents above ca. 20 %. Up to 20 % ash there are clear, although not necessarily close, correlations between for instance pH/ash, pH/Ca, N/pH, etc. When ash content of the soil rises above ca. 20 %, the spread of the points become more pronounced and gradually so large that no correlations seem to exist. It should be remembered that on maps of distribution of analysis values within the whole area, all "extensively" collected samples are included.

pH determinations. Only determinations on dried samples are shown. The pH diagram (Fig. 50) shows that there are minor deviations between the two kinds of sampling. Thus the sample area peat from the bilberry-pine wood (II) is considerably less acid than peat from the "extensive" sampling. The reason for this is doubtless the position of the sample area (Jm 6) at the outer edge of the community near the bilberry-spruce wood (III). The part of the community between the sample area and the *Ledum*-pine wood, which comprises a fairly large area, thus becomes strongly represented in the diagram, and that area is one of the most acid on Jägarmossen (see also map, Fig. 49).

The pH values show a considerable average increment from the central area towards the periphery (ca. 1.5 unit). None the less the peat of the peripheral meadow-forest communities is very acid. Within the heath-forest (I—III) the mean pH is 3.2—3.7 and in the meadow-forest communities 4.3—4.6. (As to averaging pH it will be referred to Jackson 1958, p. 58 f.) It is characteristic that Heikurainen (1953, p. 138) found considerably higher pH values (5—7) for undrained eutrophic peat lands in N Finland.

There is some indication that the spruce-dominated parts of the area have a somewhat more acid peat than those with many broad-leaved trees, especially birch. The very low pH, as such, does not seem to be unfavourable to the trees. Unfavourable effects may, however, occur because of low mineral contents (Lucas and Davis 1961). On Jägarmossen low pH is accompanied by low content of some nutrients, but the nutrient status of the trees does not seem to be dependent on pH or mineral content of the peat to any noticeable degree, except for the *Ledum*-pine wood where, besides a low nutrient content and a very acid peat, there is at times a high water table which may impede

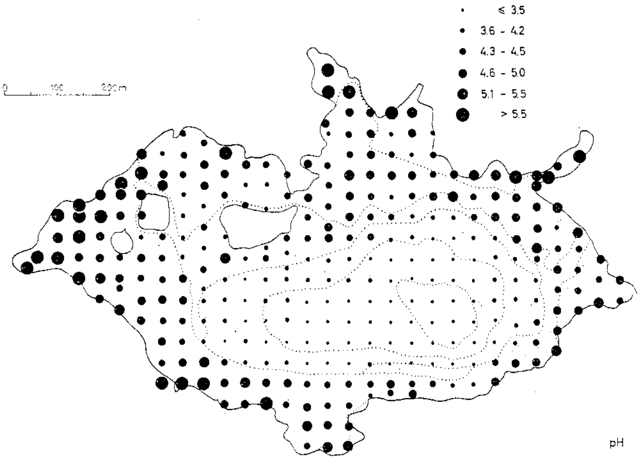

Fig. 49. Distribution of the acidity (pH) of the peat on Jägarmossen.—Dotted lines: boundaries between the plant communities.

nutrient uptake (see also Ch. 11.C.2.). The highest pH values of all, pH 5—7, have been recorded for the mineral soil-mixed peat of the boundary with the non-peaty land, partly a somewhat clayey and partly a somewhat sandy peat.

Before pH determination, the specific conductivity (Figs. 51, 52) was measured in the peat suspension. These figures (dried samples) have the same main features as those mentioned for apparent density, ash content and pH, but the differences between the various communities are not quite as prominent. However, the differences are

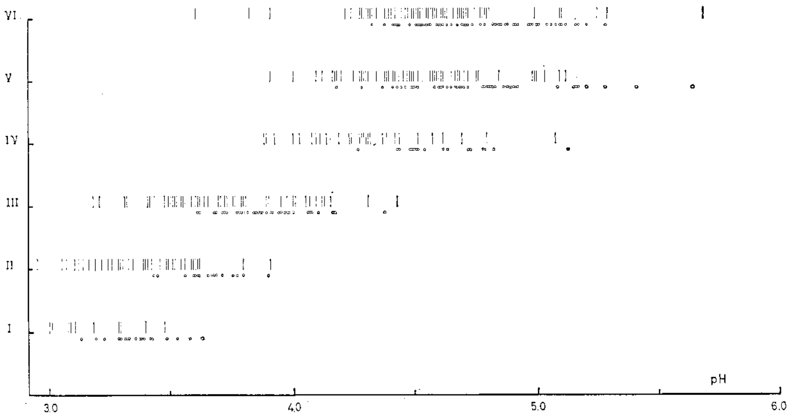

Fig. 50. Distribution of the acidity (pH) of the peat in the different plant communities on Jägarmossen.—For symbols, see Fig. 46.

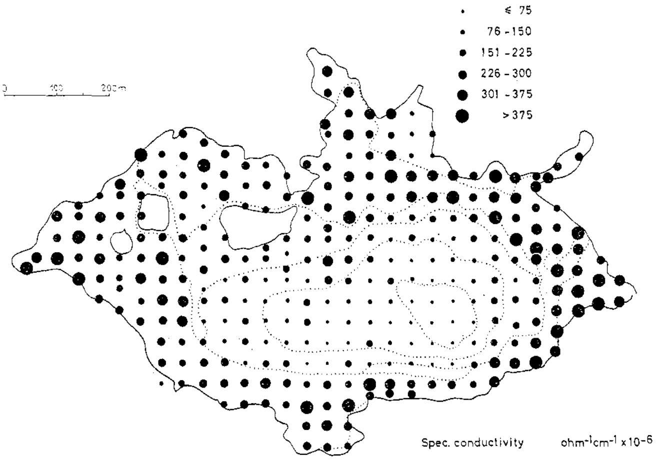

Fig. 51. Distribution of the specific conductivity of the peat on Jägarmossen.—Dotted lines: boundaries between the plant communities.

statistically significant, except between the *Oxalis*-spruce wood and the grass-rich birch-spruce wood.

Nevertheless values of specific conductivity of such a soil suspension must be interpreted with great care. The determinations are highly dependent on various methodical factors and, more particularly, on the concentration of the suspension. For pH, a logarithmic function, the dilution effect is of less importance. In a study of this, it was found (in 16 mineral soil samples) that for a volume ratio soil/water 1:9, the specific conductivity was on average 17×10^{-6} and pH 4.1, and for the ratio 1:1, 66×10^{-6} ohm^{-1} cm^{-1} and pH still

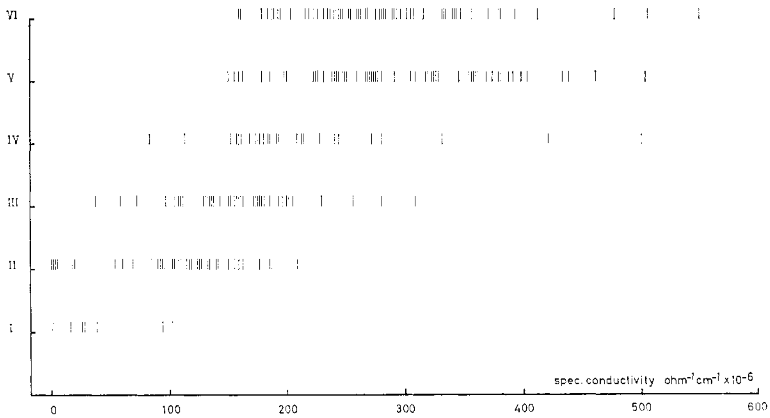

Fig. 52. Distribution of the specific conductivity of the peat in the different plant communities on Jägarmossen.—For symbols, see Fig. 46.

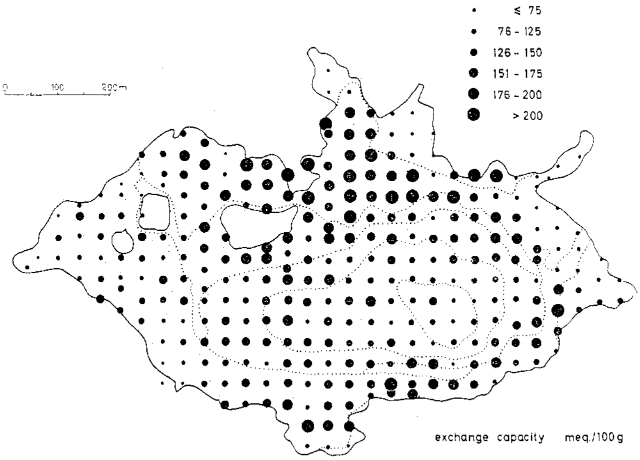

Fig. 53. Distribution of the cation exchange capacity of the peat on Jägarmossen.—Dotted lines: boundaries between the plant communities.

4.1, so that there was a highly noticeable change in specific conductivity while there was no change in pH.

Another factor causing uncertainty is the very great sensitivity of specific conductivity to whether fresh or dry samples are used. For example, for some determinations on fresh samples the specific conductivity had an average range of 10—75 × 10^{-6}, while those on the corresponding dried samples had 40—300 × 10^{-6} ohm^{-1} cm^{-1}, and the ratio fresh/dry determinations varied from 0.07 to 0.44.

In this paper no great stress is laid on the specific conductivity

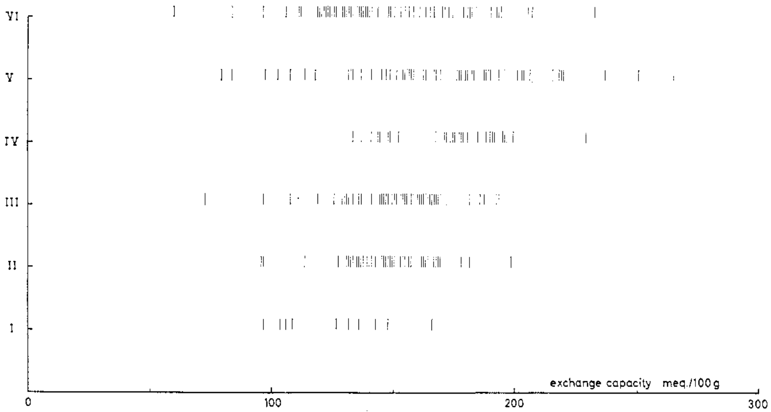

Fig. 54. Distribution of the cation exchange capacity of the peat in the different plant communities on Jägarmossen.—For symbols, see Fig. 46.

determinations in spite of their fairly good agreement with the factors mentioned above. Specific conductivity is only one of the properties used in trying to get different expressions of the complexity of a site. The total value of electrically charged dissolved particles in an aqueous solution might usefully reflect a significant environmental factor. But because of the difficulties in method, it seems wise for the present not to make too broad inferences from specific conductivity determinations on peat.

Cation exchange capacity and degree of neutralization are a common expression of the exchange properties of a soil. These properties are shown in Figures 53—56.

The total exchange capacity (H_3O^+ ions and metal ions) does not vary much between the plant communities (Figs. 53, 54); the average of all samples is within the range 125 to 175 meq./100 g of soil. When computed per unit volume the range increases to about 120—230 meq./dm^3 of soil. However, the variations between separate analyses are much greater. For ash contents < 20 %, the exchange capacity may vary from about 60 to 270 meq./100 g of soil (70—440 meq/dm^3).

In the central area, the cation exchange capacity is highly affected by the great excess of H_3O^+ ions giving rise to fairly high total exchange capacities: 100—170 meq./100 g (60—165 meq./dm^3). However, the highest values on a *weight basis* are recorded from the *Oxalis*-spruce wood. The lowest, on the other hand, are for the boundary with the non-peaty land. The mineral soil-mixed peat, which is very like mull, even has exchange properties suggestive of mull, viz., exchange capacities of 20—150 meq./100 g, which are in general lower values than those of peat proper. On a volume basis, the corresponding values are 180—470 meq./dm^3; and computed on combustible matter, 170—330 meq./100 g, which is on average somewhat higher than Sjörs' (1961 a) values for "forest mull".

In 252 peat samples, mainly from N Finland, Puustjärvi (1956) measured exchange capacities varying between 47 and 167 meq./100 g for various peat types (dried samples). The figures are not strictly comparable to those from Jägarmossen and other sites in Uppland because of the different methods used, but they are useful as relative figures in showing that there is a characteristic order of various peat types, in the same way as is shown in the present paper.

The metallic cations, on the other hand, show distinct differences between the plant communities. The central pine wood area and the neighbouring bilberry-spruce wood have only small quantities of exchangeable metal ions, usually < 50 meq./100 g, whereas the meadow-forest communties have 80—-100 meq./100 g. The mineral soil-mixed peat of the boundary also has a comparatively low value for exchangeable metal ions, 10—50 meq./100 g. The greater part of Jägarmossen rests on a substratum of sand, with clay in places, and doubtless these soils have an important effect on the exchange properties of the peat directly above. Where the admixture of clay is large, the quantity of exchangeable metal ions may even be fairly high, up to 50 meq./100 g, but where there is more sand there are only about 10—20 meq./100 g of exchangeable metal ions.

Sjörs (1961 a, p. 22) gives figures for the exchangeable metal ions for various types of peat land: 14 meq. or less in 100 g of combustible matter in an ombrotrophic bog, 15—49 in poor fen, 45—80 in moderately rich fen and 93 or more in extremely rich fen. In comparison the *Ledum*-pine wood and the bilberry-pine wood fall in the poor fen class, the bilberry-spruce wood and the *Maianthemum*-spruce wood in the rich fen class and the *Oxalis*-spruce wood and grass-rich birch-spruce wood in the extremely rich fen class. Consequently, on the basis of this classification, the *Ledum*-pine wood was never an ombrotrophic area, because the average content of exchangeable metal ions is 26—27 meq./100 g loss on ignition. As yet there has probably been no metal ion supply to the surface peat after drainage, since the ditches are too deep to allow a superficial stream transporting mineral soil-water. Thus the metal ions present were probably present before drainage. But the conditions are somewhat complicated because increased aeration and humification of the surface peat are likely to have changed the exchange properties.

The degree of neutralization probably gives a better description of a site than any of the other exchange properties mentioned. It is also independent of the organic matter content of the soil, as is especially obvious in the samples from the boundary with the non-peaty land, where ash content is very variable. The degree of neutralization (Figs. 55, 56) also agrees better with those properties showing an apparent positive gradient from the centre towards the periphery. The *Ledum*-pine wood has an average of about 20 %, the grass-rich birch-spruce wood about 60 %, and the other communities have intermediate values. About a quarter of all samples from the pine wood area have 20 % or less degree of neutralization and the lowest value recorded is 10 %; these are figures as low as those recorded from various ombrotrophic areas (bogs), where they seem to vary from 16 % downward, "the percentage of neutralization is 16 or less in the true bogs" (Sjörs 1961 a, p. 22, 50; see also Malmer 1962 a: Fig. 57). But experience from other

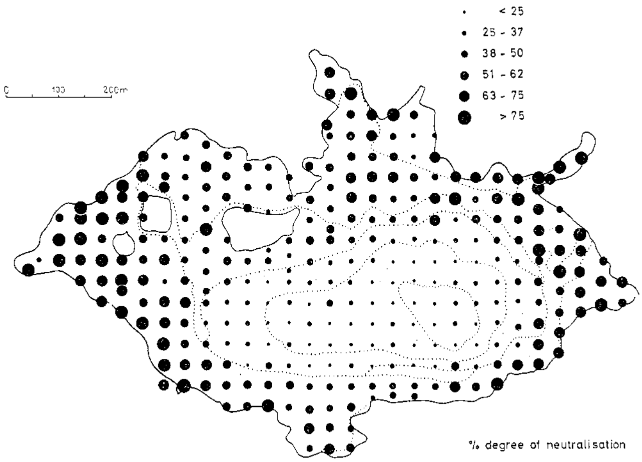

Fig. 55. Distribution of the degree of neutralization of the peat on Jägarmossen.—Dotted lines: boundaries between the plant communities.

peat lands visited has shown that values as low as 20 % or less for drained peat land are uncommon. It also seems that very high percentages (≧ 75 %) for such sites are uncommon. The acidification following on draining evidently leads to a decrease in degree of neutralization too.

Determinations of total nitrogen, phosphorus, potassium and calcium have been made on peat from the sample areas only, so that a smaller number of analyses have been obtained.

The nitrogen content of the peat from the same vegetation type

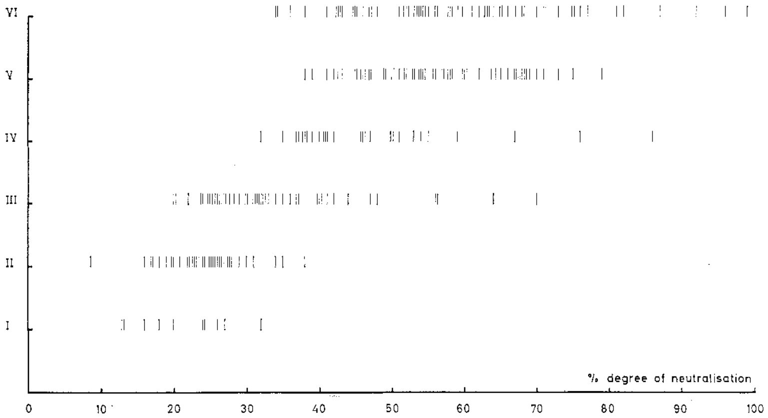

Fig. 56. Distribution of the degree of neutralization of the peat in the different plant communities on Jägarmossen.—For symbols, see Fig. 46.

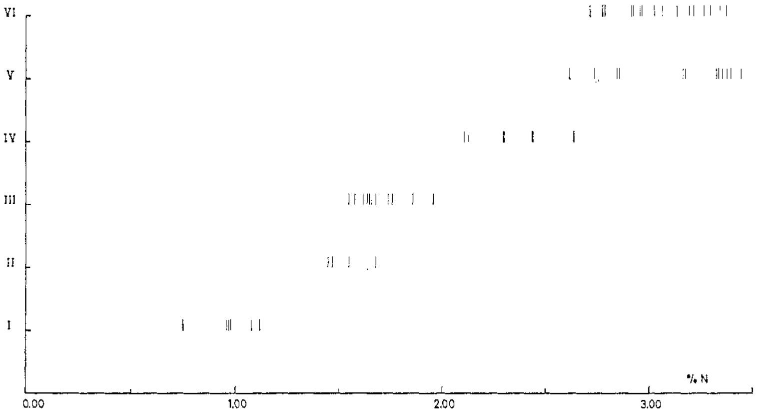

Fig. 57. Distribution of the nitrogen (N) content of the peat in the different plant communities on Jägarmossen—Each line indicates a sample from a sample area. I—VI, see Fig. 3.

can vary considerably (see Malmström 1952), but usually bog peat is low in N in contradistinction to various kinds of fen peat, where values as high as 3—5 % on an ash-free basis, have been recorded for extremely rich fens (Sjörs 1961 a, p. 25, 50).

For Jägarmossen there is a strong tendency towards increasing peat N content in the direction from the poor *Ledum*-pine wood towards the richer meadow-forest communities of the periphery (Fig. 57). Average N content varies from 1 to 3.5 %. The lowest recorded N content was 0.75 % (the *Ledum*-pine wood) and the highest was 3.5 % (the *Oxalis*-spruce wood). The clay gyttja reaches as high a value of N as 4.7 % of the loss on ignition, which is as high as Sjörs (1961 a,

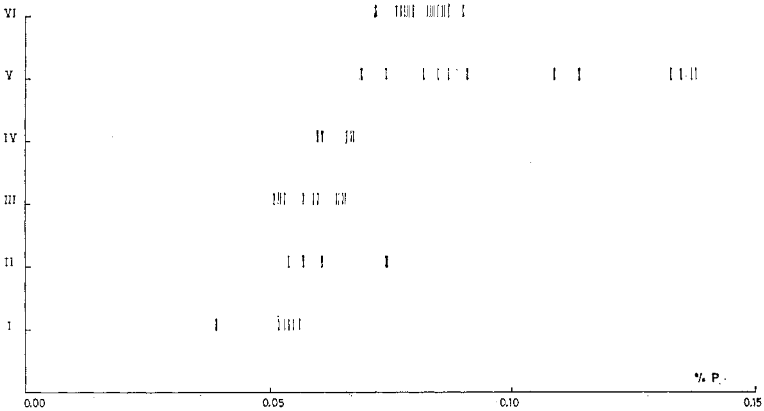

Fig. 58. Distribution of the phosphorus (P) content of the peat in the different plant communities on Jägarmossen.—For symbols, see Fig. 57.

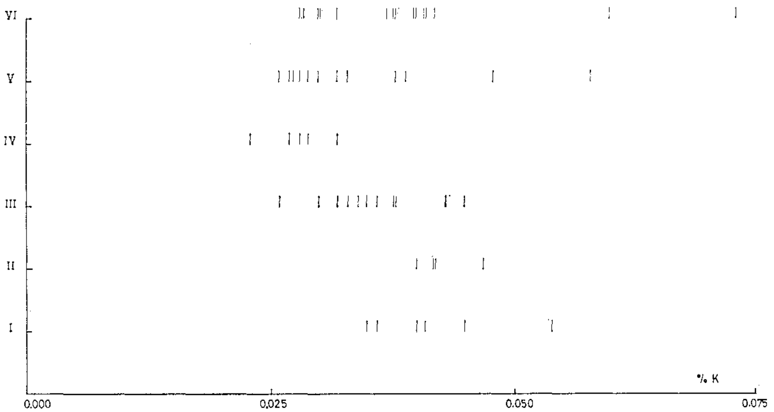

Fig. 59. Distribution of the potassium (K) content of the peat in the different plant communities on Jägarmossen.—For symbols, see Fig. 57.

p. 46) measured for forest mull. On pure peat the highest value measured in the present study was 4.7 % N from Gisselås mire in Jämtland and the lowest was 0.47 % N from Måsmossen in eastern Uppland. Similar tendencies have been reported by other authors: Osvald (1937, Table 9) quotes 2.4 % N for a number of fen peat soils and 1.3 % for bog peat soils (cultivated?); Persson (1962, pp. 66—69, 75), 4—5 % N for various extremely rich fens; Malmer (1962 a, pp. 304—306; 1962 b, pp. 58—60), 0.6—2.9 % N for bog and fen sites.

The results of the phosphorus analyses are in agreement with the known fact that the phosphorus content of peat is generally low in comparison with that of a mineral soil (a notable exception is peat

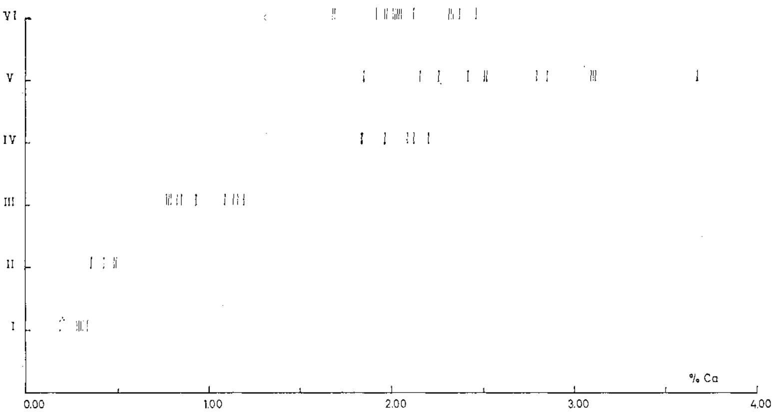

Fig. 60. Distribution of the calcium (Ca) content of the peat in the different plant communities on Jägarmossen.—For symbols, see Fig. 57.

containing some vivianite). The percentage contents have the same numerical values as the surrounding mineral soil (Ch. 3), but because the apparent density of the mineral soil is 5—15 times that of the peat, the store of phosphorus is at least 5—15 times less than in the mineral soil.

In the surface samples from Jägarmossen the P contents vary from 0.04 to 0.14 %. There is an even, but not particularly large increase in percentages and weights per unit area from the centre of the peat land to its marginal areas, from a mean value of about 0.05 % P in the *Ledum*-pine wood to 0.11 % P in the *Oxalis*-spruce wood (Fig. 58 and Table 28). This is not a general rule as bog peat and "better" fen peat often have similar P contents (Osvald 1937, p. 220). Bog peat may even have a higher P content than fen peat, so that the P reserve may sometimes be the same in different peat types (Malmer 1962 a, p. 202). Similar results, from limited material were shown by Lukkala (1929 b) for three different forest plant communities on different peat substrata. In Sjörs' (1961 a, p. 50) material the rich fens usually have considerably higher P contents than the poor fens or ombrotrophic bogs.

When the drier soil and younger plant communities of Jägarmossen were formed it is assumed, that the communities nearest to the mineral soil obtained more P from the mineral soil-water than communities farther out. Nevertheless there are examples that show that even in the central areas the surface peat has about the same percentage content of P as in the peripheral areas, thus supporting some published data. In the main, however, there is a consistent variation between the plant communities studied, which is in agreement with Mattson and Karlsson's (1944, p. 194) analyses of various peat-forming plants. It has also been shown that the P content of the green parts of more demanding plants is higher than that of less demanding (op. cit.).

The comparatively even distribution of the percentage P contents between the plant communities may be explained by a higher uptake by the vegetation in the originally P richer (and on the whole more eutrophic) parts, and a lower uptake in the P poorer (more oligotrophic) parts.

P contents > 0.1 % have been obtained only within the sample areas next to the non-peaty land, where the thickness of the peat is small (0.3—1.0 m). The surrounding mineral soil and the mineral soil below the peat certainly has an effect. At present there is not likely to be any supply from surrounding mineral soil because there are ca. 60 cm deep marginal ditches. However, the slight solubility of the phosphorus means that the greater part of phosphorus fixed in peat (plant remains) before ditching still remains there, although a certain amount has been taken up by the present vegetation.

The highest phosphorus contents (0.20—0.25 % P, see Fig. 43) have been recorded from some very wet birch communities rich in grass and herbs on the large Kerstinbo mire in W Uppland.

The potassium content is, Fig. 59, exceedingly low in comparison with a mineral soil and the concentration to the superficial parts of the soil is extremely pronounced.

At a depth of 0—20 cm in the sample areas, the K contents vary between 0.023 and 0.073 % (mean of 41 analyses 0.038 % K). At 0—10 and 10—20 cm depths, 13 samples of each, the first group has a mean of 0.047 % (0.028—0.067 %) and the second 0.020 % (0.014—0.027 %), so that 10—20 cm below the soil surface the K content is already less than half that of the layer above. In all samples from the surface layer (0—20 cm) only once does the K content reach the same value as the P content. The quotient P/K is, on average, 2: 1 (1.0—4.6: 1) in the layer 0—20 cm. The layers 0—10 and 10—20 cm have the average values 1.9: 1 (1.2—5.0: 1) and 3.3: 1 (1.6—5.5: 1). From this follows that the relation between P and K increases by an average of almost 75 % when sampling depth is increased 10 cm. This implies that K content diminishes appreciably more rapidly with depth than P content; the differences at depths > 20 cm are still greater (see below, c.). By comparison, in the surrounding mineral soil the P/K ratio is 0.07—0.3: 1.

The comparatively high contents of P and K in the superficial, well aerated, parts of the peat presumably mainly depend on the concentration that is occurring and has occurred in living and recently dead organisms (roots, fungi, bacteria, animals, etc.). Yet a preliminary investigation showed that only about 10 % of the total amount of potassium in a soil sample was in the roots.

Potassium is the only plant nutrient studied that does not show any regular variations in total percentages between the plant communities (see e.g., Heikurainen 1953, p. 136) except that there is slightly less K in the more productive areas (Fig. 59). This is also likely with regard to the primarily low K content of peat and its main occurrence as easily soluble ions (Ch. 14). As for P (and also for other nutrients) the consumption is highest in the productive stands, but the availability of K is more limiting (see Ch. 14). The comparatively high calcium contents may also to a certain degree be unfavourable for the K economy. At higher Ca concentrations, the Ca ions will tend to replace the exchangeable K, which then may be leached out from the site by drainage water.

As will be shown later, the K analyses are fairly typical of a drained, forested peat land on a moderately lime-rich substratum. Thus K contents in the surface peat (0—20 cm) higher than 0.08 % and lower than about 0.02 % are fairly rare in other peat lands studied.

Calcium has about the same distribution pattern as nitrogen in the area, with increasing values from the centre towards the boundaries (Fig. 60). In contrast to phosphorus and potassium, there is increasing calcium concentration with increasing depth in the peat (see below, b.).

On the whole, none of the other nutrients shows so great differences between the various plant communities as calcium. Thus the range between the *Ledum*-pine wood and the *Oxalis*-spruce wood is 0.3—3.0 % Ca, and the differences between the heath-forest communities (I—III) and the meadow-forest communities (IV—VI) are very distinct (Fig. 60).

Recent agricultural chemical investigations have led to other methods of determining easily soluble nutrients and nutrient reserves (Ch. 10. C.). An account of the results of these methods applied to P and K for the peat samples from Jägarmossen is given below. The agricultural classification is included to make interpretation of the analyses easier. Both for AL- and HCl-soluble P and K there are five classes based on increasing yield with increasing content of the various nutrients in the soil (see Fredriksson 1961 b).

Table 16. Standards for the evaluation of ammonium lactate extractable (AL) and hydrochloric acid extractable (HCl) soil phosphorus and soil potassium analyses for agricultural purposes. Mg per 100 g air-dry arable soil (see Fredriksson 1961b)

	Classes				
	I	II	III	IV	V
K-AL.	> 4	4.0— 8.0	8.1— 16	17 — 32	> 32
P-AL.	> 2	2.0— 4.0	4.1— 8.0	8.1— 16	> 16
K-HCI.	>50	50 —100	101 —200	201 —400	>400
P-HCI.	>20	20 — 40	41 — 60	61 — 80	> 80

It must be emphasized that at present these "site classes" probably cannot be applied neither to mineral nor to organic forest soils. There is as yet (as far as is known to the author) not a single experiment in forestry where these methods are studied or applied to forest ecological problems. As an example of the difficulties which may arise, the present investigation shows that there is a negative relation between annual increment of growth of the tree stands and the contents of P-AL in the soil. For total P the relation is positive. Under such circumstances it seems hazardous to apply the unmodified AL or HCl methods to forest sites. It must, however, be remembered that these analyses are intended for practical farming and more particularly for preparation of fertilization programmes. Therefore it is not to be expected that they would immediately be applicable to forestry purposes.

In the diagrams and maps the original units are used, mg/100 g of soil, but in contrast to agricultural routine the values are computed per unit of oven-dry and not air-dry matter. Such values are not very greately different since, on average oven-dry matter analyses are about 10 % lower than air-dry. Moreover, the classes on the maps are more detailed than in agricultural practice because there are no or very few samples falling in the higher classes.

For P-AL and P-HCl (ammonium lactate-soluble and hydrochloric acid-soluble phosphorus) there are certain characteristics which differ from those of total P. There seems to be no correlation between P-HCl and the various plant communities (Figs. 61, 62). The mean values fall in the range 18 to 22 mg/100 g of soil and the order between them is quite irregular, e.g., the *Ledum*-pine has the same P-HCl value as the *Maianthemum*-spruce wood and the bilberry-pine wood the same as the grass-rich birch-spruce wood. However, if the P-HCl is computed on a kg/ha basis the picture becomes somewhat different, because of the denser peat of the meadow-forest communities. Hence there is the regular order of increasing values (mean) from the central to the peripheral part of the area, but as seen in Fig. 62, there is also considerable variation within a single vegetation type, so that most of the analyses are over-lapping.

The AL method (as well as the HCl method) has been in use only a relatively short time, but as the P analyses give values in close correlation (Karlsson and Jonsson 1959) to Egnér's well-known lactate method which has been used for a long time, it may be permissible to equate the two kinds of analyses on making comparisons with data in the literature. Unfortunately there is only a very scanty material for comparisons in forest ecological literature and particularly in literature about forested peat land. For virgin peat soils there are, however, some comprehensive collections of data from Finland (Kaila 1956 a, b), but none of her methods are the same as that used in the present investigation.

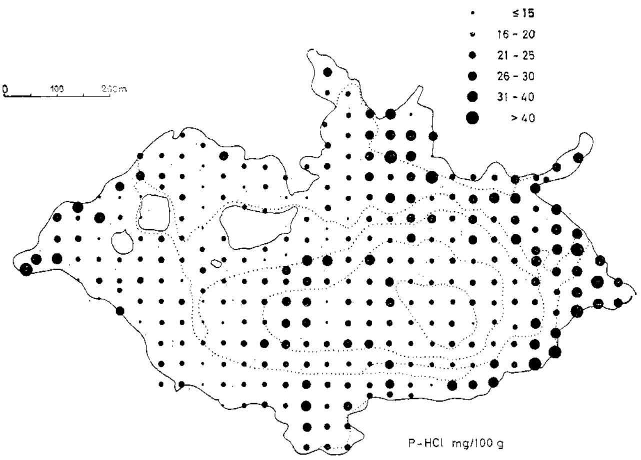

Fig. 61. Distribution of the P-HCl content of the peat on Jägarmossen.—Dotted lines: boundaries between the plant communities.

As a rule, only a small fraction of the total phosphorus is extractable with the AL solution (or lactate solution according to Egnér). As low values as 1 % have been reported by Sjörs (1961 a, p. 24). For 13 samples from Jägarmossen, an average of 9 % (2—17) was obtained with the AL method (35—40 % of total phosphorus with the HCl extraction).

Sjörs (op. cit. p. 50) has listed lactate P values of 3—8 mg/100 g for ombrotrophic and poor fen sites and 1—18 mg for various rich fens sites. In the main it seems that the P-AL values from Jägarmossen are in agreement with those of the poor sites but lower than

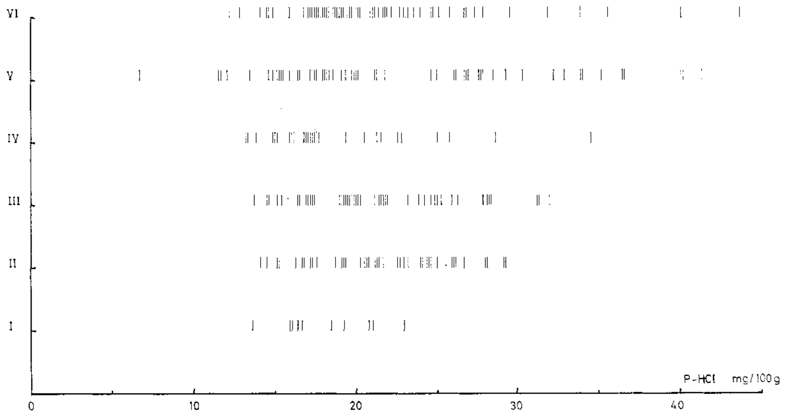

Fig. 62. Distribution of the P-HCl content of the peat in the different plant communities on Jägarmossen.—For symbols, see Fig. 46.

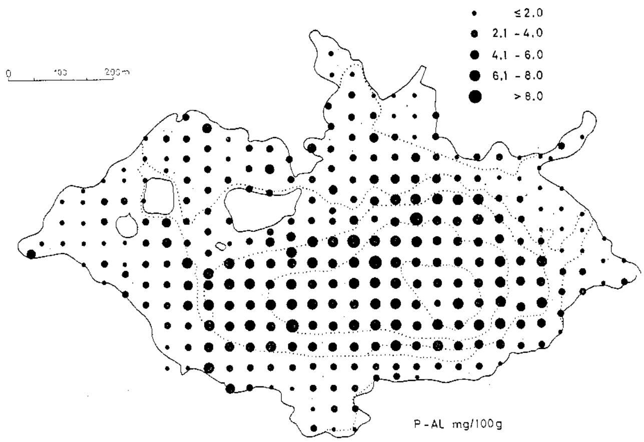

Fig. 63. Distribution of the P-AL content of the peat on Jägarmossen.—Dotted lines: boundaries between the plant communities.

those of the rich sites. Only once was P-AL as high as 10 mg/100 g of soil. Even Sjörs' values for "forest mull" (op. cit. p. 46), which is poor in soluble P, are generally higher than those for Jägarmossen.

On Jägarmossen there is a very characteristic distribution pattern for the values from P-AL analyses (Figs. 63, 64). The highest are for the poor communities of the heath-forest type and the lowest for the communities of the meadow-forest type, i.e., just the opposite of most of the other properties studied. However, the lowest mean value from the heath-forest is from the *Ledum*-pine wood, but this is not as low as any of those for the meadow-forest. The bilberry-pine wood has

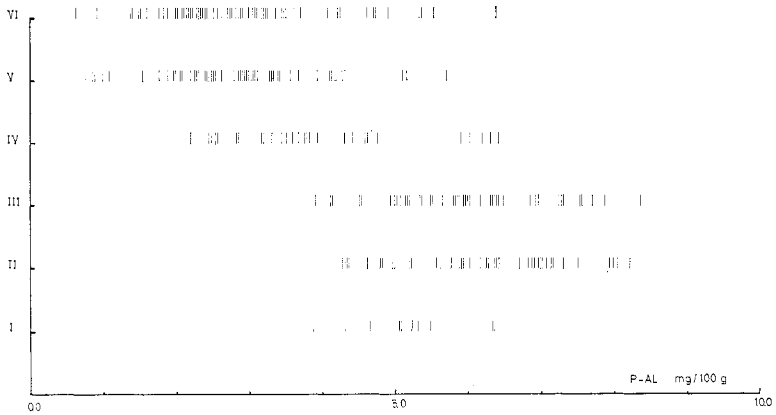

Fig. 64. Distribution of the P-AL content of the peat in the different plant communities on Jägarmossen.—For symbols, see Fig. 46.

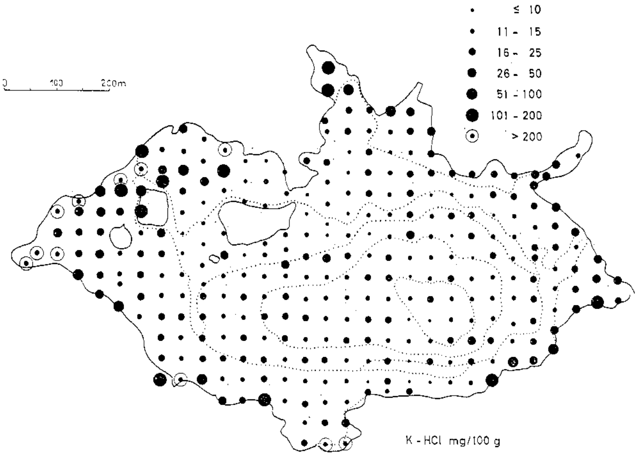

Fig. 65. Distribution of the K-HCl content of the peat on Jägarmossen.—Dotted lines: boundaries between the plant communities.

the highest mean P-AL value of all communities and then there is a gradual decrease in P-AL towards the non-peaty land. The differences on a percentage basis are so great that it makes little difference if P-AL is computed on a kg/ha basis and except for slight deviations the order between the communities remains the same.

For K-AL and K-HCl (Figs. 65—68), there are tendencies similar to those for P-AL and P-HCl. Thus as seen in Fig. 66, there are very small differences in K-HCl between the plant communities. The mean values are about the same for the communities I and IV (12—13 mg/100 g) and for II, III, V and VI (15—17 mg/100 g), but the varia-

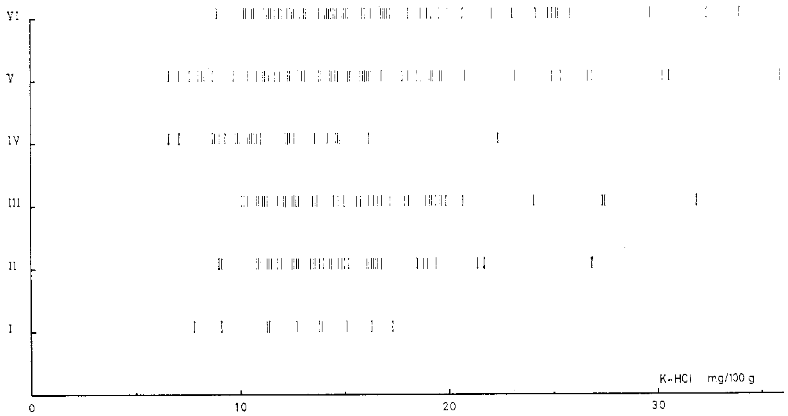

Fig. 66. Distribution of the K-HCl content of the peat in the different plant communities on Jägarmossen.—For symbols, see Fig. 46.

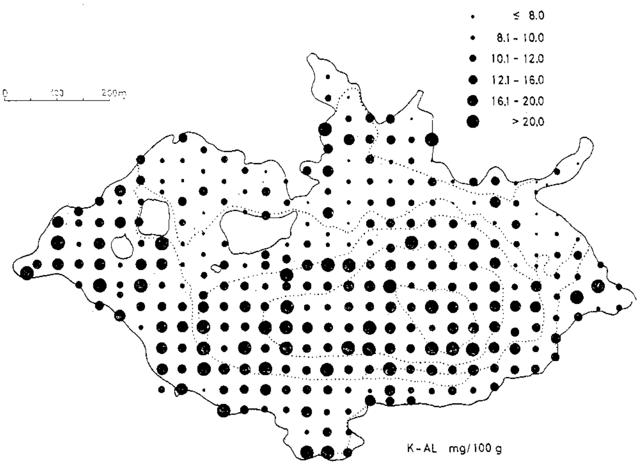

Fig. 67. Distribution of the K-AL content of the peat on Jägarmossen.—Dotted lines: boundaries between the plant communities.

tion within a single community is very large. When K-HCl is computed in kg/ha, there is a slight increase from the central area to the peripheral part, but the *Maianthemum*-spruce wood still has as low a mean value as the poor pine wood area. The map, Fig. 65, shows that the influence from the mineral soil is very strong at the boundary with the non-peaty land. It is especially the underlying clay gyttja that has a fairly high percentage of K. Moreover, the gyttja soil has a much higher apparent density than the peat, and therefore the differences become still more marked when computing K-HCl in kg/ha.

The distribution of K-AL is (Figs. 67, 68), on average, similar to

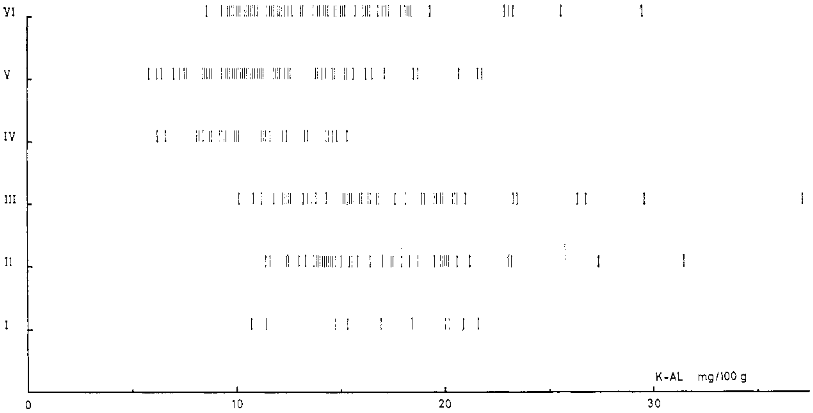

Fig. 68. Distribution of the K-AL content of the peat in the different plant communities on Jägarmossen.—For symbols, see Fig. 46.

that of P-AL, i.e., fairly high values in the heath-forest and low in the meadow-forest. But the K-AL values are more irregular in that quite high values are obtained for peat from the central area as well as for mineral soil-mixed peat at the boundary.

b. Vertical distribution

Some properties of the peat, similar to those treated in the preceding section, will now be discussed in relation to depth.

In the centre of each sample area a vertical profile was dug to varying depths. The profiles were at the most 2 m deep, but sampling never occurred at depths greater than 1 m. In three profiles (Jm 3, 5 and 8) the subsoil (clay gyttja) was reached before 1 m (50, 50 and 70 cm respectively) and sampling was not continued to greater depths; in two profiles (Jm 7 and 12) the subsoil was reached at the 90—100 cm level. The other profiles consisted of peat to a depth of at least 100 cm. Only half the number of profiles is shown in the Figures 69—75; these profiles have been selected as representative of each plant community (I—VI), but the others are also discussed in the text.

The results of the analyses may be roughly divided into three groups: (1) those that increase with depth, viz., ash content, pH and calcium content; (2) those that decrease with depth, viz., potassium and phosphorus content, and (3) those that change only slightly or irregularly with depth, viz., apparent density, nitrogen content.

At other sites studied it was found that the degree of neutralization, specific conductivity and extractable calcium (AL and HCl) also increase with depth. Total magnesium seems first to decrease (0—30 cm) and then to increase. Extractable potassium and phosphorus (AL and HCl), like total P and K, also decrease with depth. Exchange capacity seems to be fairly constant throughout a profile, provided no strata with extreme properties occur.

The regular increase in ash content with increasing depth is shown in Fig. 69. The profile from the *Ledum*-pine wood (I, Jm 1) differs from the others in having the maximum value (3.2 %) already in the 0—10 cm level. After that the values decrease down to the 40—50 cm level (0.96 %, absolute minimum for all profiles), which is followed by a secondary maximum (1.8 %) in the 70—80 cm level. The comparatively high value at the surface is a phenomenon of quite general occurrence concerning peat of a more or less ombrotrophic origin in Europe (von Post 1926; Mattson et al. 1954; Assarsson 1961; see also Tamm 1958). For the other profiles this effect is masked by the increase in ash content that follows humification of the peat.

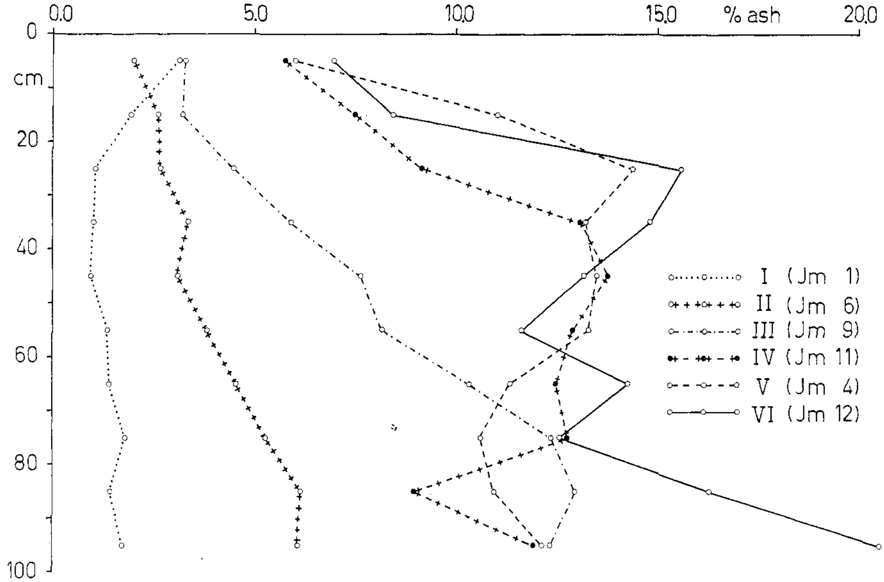

Fig. 69. Vertical distribution (cm below soil surface) of the ash content of the peat in different sample areas (plant communities).—For sample areas Jm 1, 4, 6, 9, 11 and 12 and plant communities I—VI, see Figs. 2 and 3.

Mattson et al. (1954) suggest that the higher ash concentration in the surface layers is closely correlated with intensified farming in more recent periods. This has contributed to the increased amounts of air-borne, and later deposited, material. It is thought to be mainly SiO_2 and $Fe_2O_3 + Al_2O_3$ which raise the ash content in this way. Assarsson (1961), however, considers that he cannot "support the anemophorous supply". Binns (1962) also has doubts about the effects of air-borne matter. Fraser (1933, p. 58) ascribes the high ash contents of the surface peat "to the unavoidable inclusion of living plants in the sample". However, the air-borne matter must be important because *most of the ash is composed of silica and aluminum compounds*, which probably cannot reach an ombrotrophic site in considerable quantities in any other way than through the atmosphere, even if there is a vertical capillary movement (Assarsson 1961, p. 21).

In the profiles not affected by the mineral-rich subsoil, the ash contents usually vary between 3 and 6 % at the surface and 12—14 %, and sometimes somewhat higher contents, at the bottom. Differing from this pattern is profile Jm 8 (V, not shown in Fig. 69) in which the ash content is nowhere lower than 11 % (11.2—13.2 %). In *Carex* and *Carex*-"brown mosses" peat in general, the surface layers

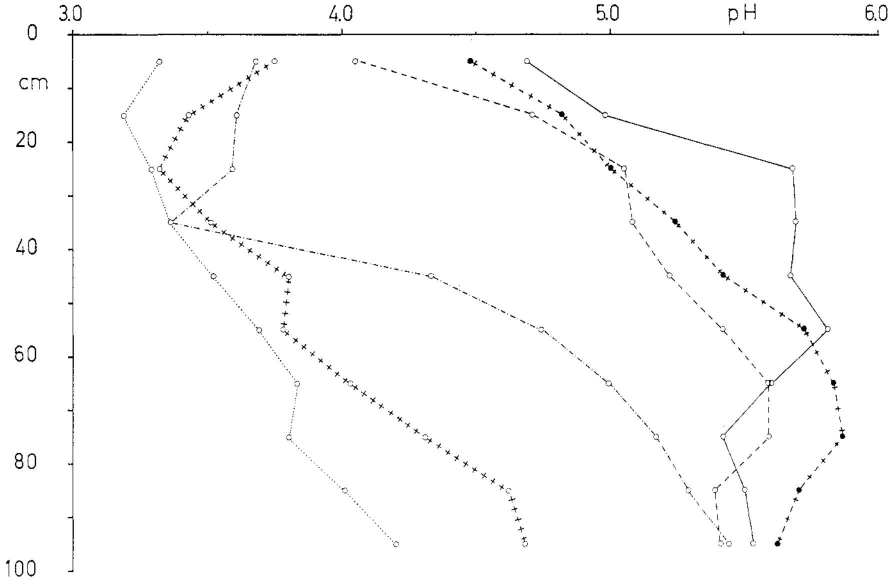

Fig. 70. Vertical distribution of the acidity (pH) of the peat in different sample areas (plant communities).—Cf. legend in Fig. 69.

usually have a lower ash content (< 10 %), and reach values as high as those of Jm 8 only at greater depths. See also Heikurainen's (1953) very high ash values for eutrophic pine mires in N Finland.

For some profiles there are no great changes between the different levels (e.g., II and III) while others show considerable changes (e.g., V and VI with a doubling for a 10 cm increase in depth.

The variations in pH (Fig. 70) are still more pronounced than those in ash. In all profiles there is an increase in pH with increasing depth, but some irregularities should be pointed out. In the heath-forest profiles, but in none of those from the meadow-forest, there is in the surface layers a decrease in pH. This effect is probably due to drying of the surface peat. The very high water-table within the *Ledum*-pine wood (I) has hindered such a development, but where the water-table is low (II, III, Jm 6 and 9 and also Jm 2 on the boundary between heath-forest and meadow-forest) it is evident. In the true meadow-forest profiles there has certainly also been such a pH decrease but the very high Ca content (Fig. 71) of that area probably has a strongly buffering effect.

The greatest difference (2.3 units) between surface peat and bottom peat is shown for profile Jm 10 (III) with pH 3.6 at the top and 5.9 at the bottom, and the least (0.8 units) in profile Jm 12 (VI) with

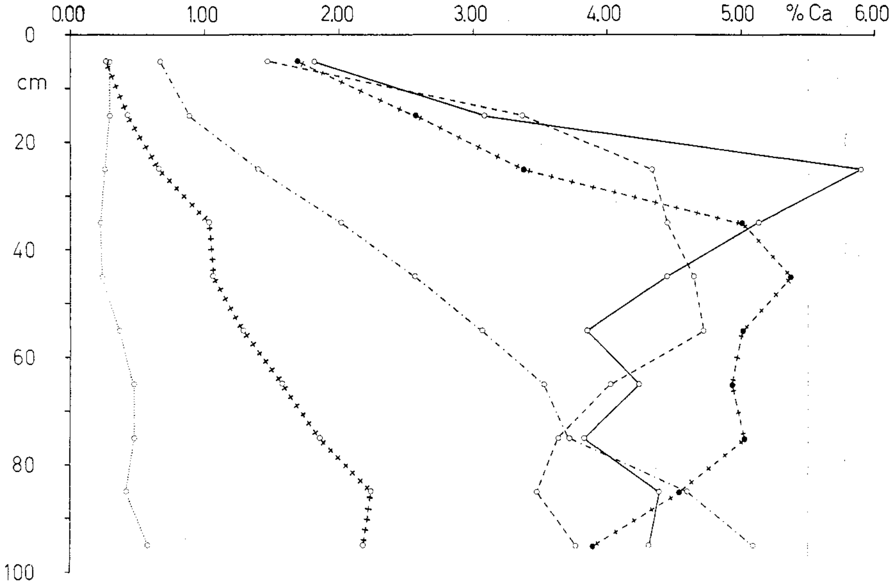

Fig. 71. Vertical distribution of the calcium (Ca) content of the peat in different sample areas (plant communities).—Cf. legend in Fig. 69.

pH 4.7 and 5.5 at the top and bottom, respectively. The average variation between top and bottom is about 1.5 units.

Calcium (Fig. 71) also shows a marked increase with depth. Its property of being fairly easily leached is shown by the moderate contents in the 0—10 cm level and the pronounced increases in the next one or two decimeters. In the *Ledum*-pine wood the situation is different, however. There a high permanent water table impedes a downward leaching water movement. On the other sites such movement is likely to occur. However, the situation becomes rather complicated because other peat types with other qualitative properties and other original contents of calcium are met with at greater depths. The permeability of the material may also be decisive (Troedsson 1957). Thus, because of the various habitats in which the peat has been formed, the profiles become different from one another. Profile Jm 1 (I), *Ledum*-pine wood, has developed in an oligotrophic site (poor fen) and has on the whole, about the same Ca contents throughout (see also above). Most of the other profiles show an increase in Ca content from the top to the 30—50 cm level and then more or less constant values. The profiles Jm 2, 6 and 9 (III + IV, II and III) have a steady increase in Ca down to 100 cm and not even a tendency towards a decrease at the bottom in spite of the very high Ca percentages.

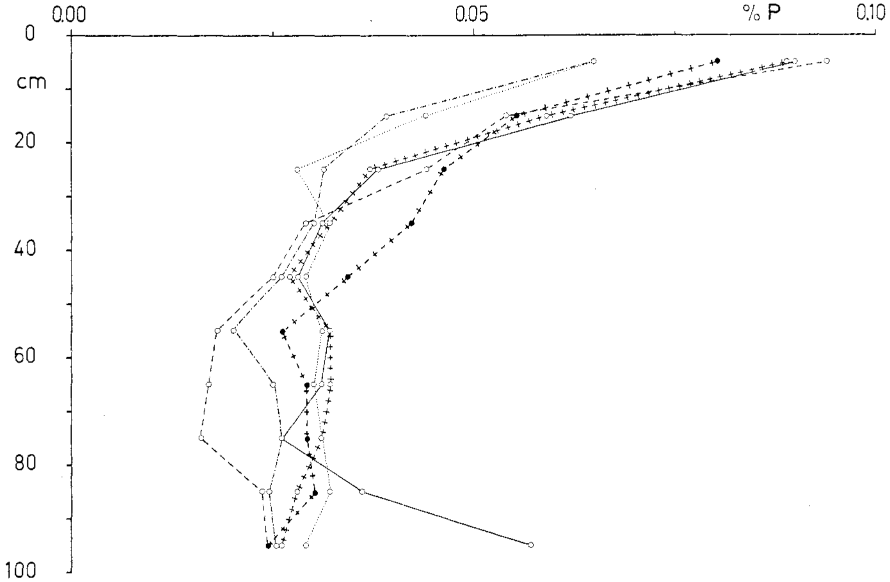

Fig. 72. Vertical distribution of the phosphorus (P) content of the peat in different sample areas (plant communities).—Cf. legend in Fig. 69.

These differences between the profiles are most easily explained by the suggestion that the peat composed of the most lime-rich communities has not yet been reached at the bottom of the latter series of profiles. In consequence of the greater filling-in of lime-poor peat in the centre of the area, contemporary deposits are met with at greater depths in the central than in the peripheral parts. That the lime content was once also high there is shown by the very rich lime precipitation (calcareous mud) during the last epoch of the former lake (see Fig. 33).

Total phosphorus decreases with increasing depth (Fig. 72) to a depth of not more than about 30—40 cm below the soil surface, after which it is fairly constant. The content in the surface layer (0—10 cm) of 0.04—0.14 % has already changed to 0.03—0.06 % in the 10—20 cm level, below which the contents on average are 0.03 % (> 0.02 —> 0.04 %) down to the bottom. The effect of the vegetation on the vertical distribution of P, suggested earlier, is fairly evident.

The decreasing P content with depth contrasts in part with the investigation by Kaila (1956 a). She found that there was no regular relation between P content (total) and depth except for "some tendency to an increase in the P content with increasing depth in the peat lands of lower quality, in peat lands of higher quality the opposite

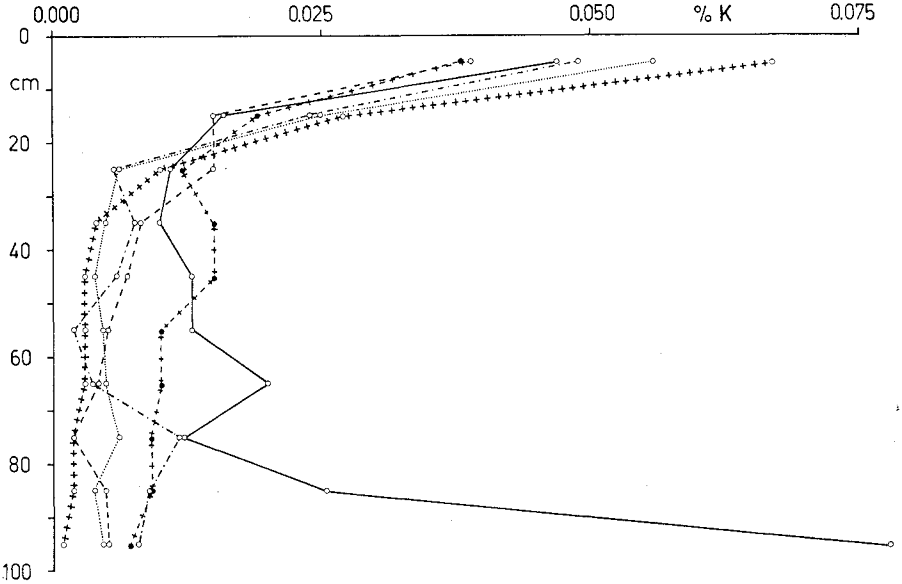

Fig. 73. Vertical distribution of the potassium (K) content of the peat in different sample areas (plant communities).—Cf. legend in Fig. 69.

often holds true" (op. cit. p. 92). However, all profiles from Jägarmossen, as well as those from other sites in Uppland show decreasing P content with depth even on poor sites.

A peculiar feature of the stratification of P is its very even concentration below the main part of the rooting region. It was suggested above that the vegetation gradually reduces the level of P to a uniform concentration irrespective of the other properties of the peat. It is conceivable, although speculative, that the difference between the P content of the surface layers and the "constant" content of about 0.025 % P in the layers below, is that part of the total phosphorus which enters into the circulation between substratum and living organisms, making allowance for that part leached out of the site. For the measured P contents and an assumed average apparent density of about 150 g/dm^3, the P in circulation would then be 45—375 kg per ha to a depth of 20 cm, for the sample areas. To some extent this opinion is supported by an investigation by Kaila (1956 a), according to which the solubility of organic as well as inorganic P diminishes noticeably at greater depths in the peat. Kaila also found that the easily extractable P is taken up by the organisms; some of it can even be removed by leaching water.

The distribution of potassium (Fig. 73) is very like that of P. The ease with which K is released from a peat soil is shown in the profiles where it can be seen that much of the K is concentrated in the surface soil. In peat from a greater depth than 20 cm, the K content is exceedingly low. A large number of the analysis values are as low as one or a few thousandths of a per cent. It is difficult to put these values in perspective because accounts for sample series in deep, vertical profiles are fairly rare in the literature, and methods of analysis are different. According to Kaila and Kivekäs (1956), K accumulation in the surface layer seems to be fairly typical for a peat land.

On Gisselås mire, a calcareous mire in the province of Jämtland, Booberg (1930, p. 206) obtained a minimum of 0.02 % K_2O in samples from 65—75 cm below the surface (0.05—0.08 % in the surface 0—20 cm), but the present author has, for three potassium-deficient sites on the same mire, obtained only 0.004—0.009 % K in the level 10—20 cm below surface. Von Post (1926, p. 37) mentioned 0.01 % K_2O as the lowest content in the 50—100 cm layer in a 9 m deep profile. Numerically comparable K contents were reported by Løddesøl (1934, p. 108) for a sampling depth of 40—60 cm on various peat lands. Malmström (1935 and 1952) reported K_2O contents of less than 0.01 % even in superficial layers on the nutrient-poor Häll mires in the province of Västerbotten. Binns (1962) found ca. 0.01 % K at a depth of 20—25 cm.

The clay gyttja is K-rich; some samples reach about 1 %, which is even more than that of the subsoil of the surrounding mineral soil. The K contents of mineral soils are, however, often very variable. For instance, O. Tamm (1940, p. 58 and 121) mentioned K_2O contents of 0.43—3.14 % in glacial till. Because of the high K content of the clay gyttja, the variation within the profiles reaching this is very distinctive (Fig. 73, VI). Thus, in profile Jm 8 (V) the ratio between the lowest and highest contents is about 1:150, which is a ratio not approached in any of the other profiles. But also within purely peaty profiles the variations are large; in Jm 6 (II) the ratio between the lowest and highest contents is 1:70. Between the profiles this ratio can reach as high as 1:1 000. In this respect the peat soils differ markedly from mineral soils (at least those uncultivated). It should be remembered that the differences in concentration found in the peat do not, to more than a small degree, depend on the various qualities of the peat as such, but on other factors such as the uptake of the organisms, leaching etc. The range of K contents in all the peat types studied is very moderate.

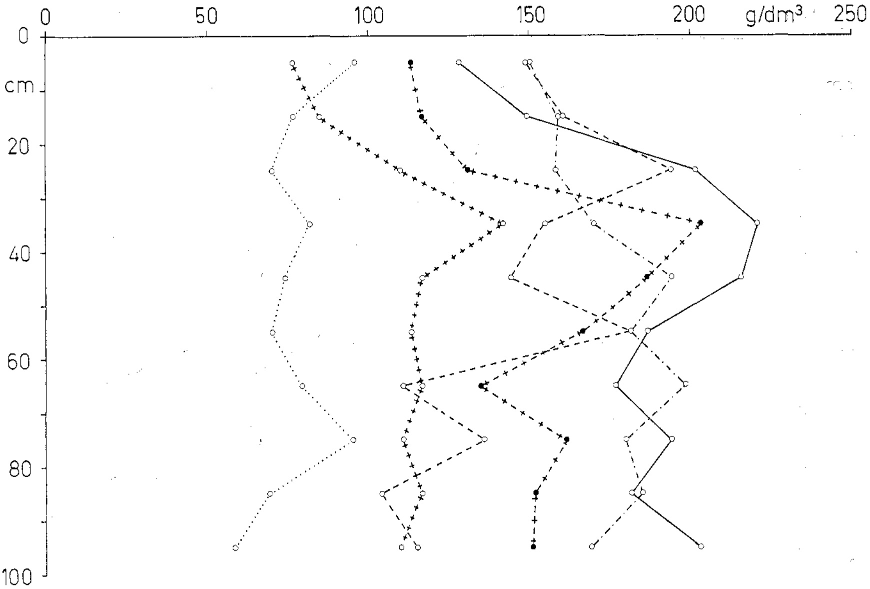

Fig. 74. Vertical distribution of the apparent density (g/dm³) of the peat in different sample areas (plant communities).—Cf. legend in Fig. 69.

Within the third group—no or irregular changes with depth—apparent density and nitrogen show, in the main, the same features, but there are minor deviations here too.

Apparent density (Fig. 74) seems to be a sensitive characteristic of the nature of the material sampled. In some profiles with an apparently homogeneous stratigraphy large variations were found even with only small changes in depth. On investigating the peat more thoroughly it was found that the variations were due to fallen, almost completely humified, trees which were difficult to discern in the samples when the peat was wet. The tree remains had a lower apparent density than the peat proper. This relation is exemplified in the bottom of profile Jm 4 (V).

In the *Ledum*-pine wood (Jm 1) the highest apparent density is at the surface, the lowest at the bottom of the profile. In all other profiles, the highest apparent density is at a level below 20 cm, except for those profiles reaching the clay gyttja, in which the maximum occurs. While the peat proper has apparent densities of < 300 g/dm³, the clay gyttja reaches 300—800 g/dm³. The very ash-rich clay gyttja at Jm 5 even has as high a value as many clay soils in general, about 1 300 g/dm³. In the profiles reaching the clay gyttja, it was found that the transition zone between the gyttja and the peat is very re-

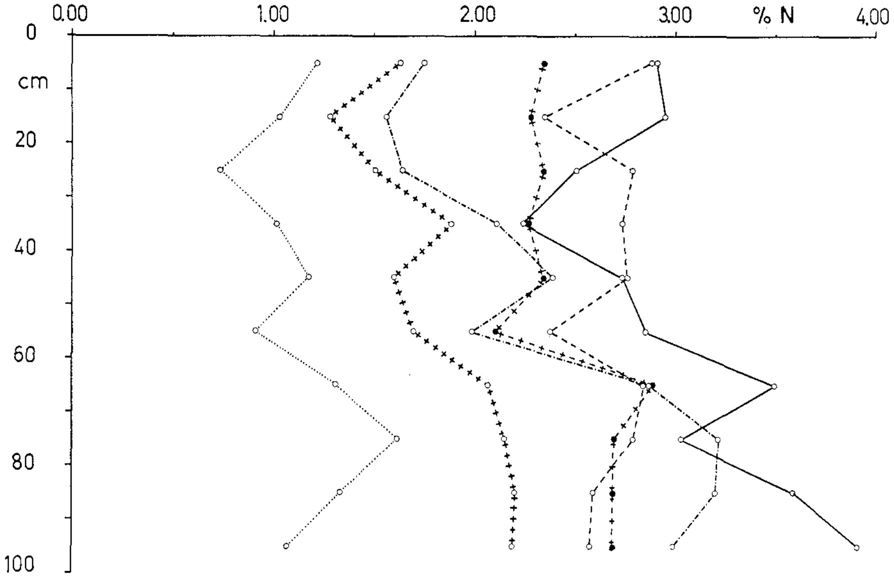

Fig. 75. Vertical distribution of the nitrogen (N) content of the peat in different sample areas (plant communities).—Cf. legend in Fig. 69.

stricted. No noticeable increase in apparent density indicating the proximity of the gyttja, occurs until the sample auger cuts into it; see for instance Jm 12 (VI) and compare with the ash distribution (Fig. 69).

As seen in Fig. 75, there are no marked features in the nitrogen variation within the profiles; most of the changes are apparently irregular. In three of the purely peaty profiles (Jm 2, 6 and 9) there is an obvious increase with depth (compare calcium), but in two others the values at the top are higher than those of the bottom sample (Jm 1 and 4; the *Ledum*-pine wood and the *Oxalis*-spruce wood). The greatest variations in nitrogen content (calculated on a dry matter basis) of the profiles occur when the profiles reach the ash-rich clay gyttja. In this nitrogen resembles the other analyses, except pH which is not to any noticeable extent affected by the clay gyttja. In a profile with only peat the ratio between highest and lowest N content is never more than 2:1, but in a profile with clay gyttja this ratio becomes 7:1 because of the fairly low percentage of nitrogen in the clay gyttja. When N percentage is calculated on the basis of organic matter (which, on principle, it should be) the picture becomes considerably changed. Then N contents reach the same numerical values in the clay gyttja as in the peat, and sometimes the highest values of peat are exceeded

(Jm 8). The variations between various peat types are partly illustrated by the ratio between highest and lowest N contents of about 5:1 ("peat mull", with degree of humification H_{9-10}: low-humified *Sphagnum* peat with rhizomes of *Scheuchzeria,* H_{2-3}).

c. Store of nutrients

The total store of nutrients in the soil might be assumed to be a factor of prominent importance for estimates of the potential productivity of a site.

The relations between productivity and the store of nutrients, however, are far from solved, and some of the ideas expressed in the literature seem at first, to be quite contradictory. For instance, Osvald (1937, p. 221) wrote referring to nitrogen, that the property most important from a practical point of view, is the quantity per hectare to a certain depth (usually 20 cm). Romell (1955), also referring to nitrogen, but with a general bearing as well, wrote of "the great importance of the *store* of nutrients as a site factor, the store of nitrogen in the first place — — —." Jansson (1959), on the other hand, is of the opinion that a determination of the static store of nitrogen is fairly meaningless; it would be better to try to make an estimation of the "net mineralization". He further wrote (op. cit.; transl.), "that it is of little use, to calculate analysis data in kg per ha and then try to relate these figures to the demand of the crops. Instead, the analysis data should be treated as relative numbers, of which a high value denotes favourable equilibrium conditions, i.e., a rapid restoration of the plant-available fraction gradually drawn off by the uptake of the crops."

Surely it is a common view that the store of nutrients should be regarded as relative magnitudes; this is largely the case where forest nutrition problems are concerned. The relationship between productivity and store of nutrients is probably more complicated for forest crops than for field crops since it is affected to a larger extent by other factors (water balance, tree species distribution, stand age, rotation, etc.) than the individual properties of the trees. For field crops, with their short rotation period and the more controlled conditions of cultivation, it is therefore usually easier to determine the nutrient requirements of the plants to maintain a certain production during average circumstances.

In forestry the quantity of nutrients removed by the crop is, at least in Scandinavian forestry, still of fairly small importance to the nutrient economy, since the most important parts of the trees (needles, twigs,

Table 17. Standards for the evaluation of peat soil analyses, according to Hjertstedt (1936)

	Ash %	Apparent density g/dm³	Lime	Nitrogen	Jägarmossen Number of sample areas			
			10³ kg to 20 cm depth					
	1	2	3	4	1	2	3	4
Slight			<1	<2	—	—	1	1
Very low	< 5	<100	1—2	2—4	4	1	2	2
Low	5—10	100—150	2—3	4—6	5	5	1	3
Tolerably low		150—200	3—4	6—8	—	4	1	1
Moderate	10—15	200—250	4—6	8—10	3	2	2	3
Tolerably high		250—300	6—8	10—12	—	—	2	2
High	15—20	300—350	8—10	12—14	—	—	2	—
Very high	>20	>350	10—12	14—16	—	—	1	—
Unusually high			>12	>16	—	—	—	—

bark in many cases, stumps and roots) are left in the forest. Of greater importance is the quantity of nutrients contained by the trees, withdrawn from the circulation. This is especially obvious on sites with a suboptimal supply of nutrients (see Ch. 11 and 14).

Two tables concerning the store of nutrients in peat soils are presented below. Table 17 is a summary of classification of peat analyses according to Hjertstedt (1936) and Osvald (1937). For comparison, the analyses from the 12 sample areas on Jägarmossen are included and distributed with respect to the various classes. This summary was intended for agricultural purposes and cannot be directly applied to forestry, but it gives a rough estimate of the nutrient status of the various sites.

With regard to ash content and apparent density, the number of sample areas suitable for cultivation is two and three, respectively, and with regard to nitrogen and lime only five and seven. It can thus be seen that it is very difficult to apply practical experience from farming to practical forestry. All the sample areas, except one, have, as will be shown later, a forest production which far exceeds the average for that part of the country and is equal in magnitude to that on the best sites. However, it must be remembered that the present tree stands are the first generation only.

It was found that the distribution of tree roots at various levels in the soil was only exceptionally restricted to the 0—20 cm level. The summary in Table 18 shows that, in general, there is fairly even root distribution to a depth of 25—30 cm, sometimes still deeper. This means that a nutrient store greater than the stated standard (Table 17) is at the disposal of the trees. Below the levels mentioned the root

Table 18. Total quantity of nutrients down to the level of greatest root frequency and greatest root depth within the individual sample areas (see text)

Sample area no.	Plant community[1]	Greatest root frequency cm	N	P	K	Ca	Greatest root depth cm	N	P	K	Ca
			10^3 kg per hectare					10^3 kg per hectare			
Jm 1	I	10	1.0	0.06	0.05	0.3	20	1.5	0.08	0.06	0.5
2	III+IV	25	5.8	0.18	0.08	4.5	60	14.4	0.35	0.10	16.2
3	V	25	14.5	0.63	0.16	11.7	50	25.2	0.94	0.54	19.8
4	V	30	12.5	0.45	0.11	18.0	50	19.8	0.54	0.14	32.5
5	VI	30	12.5	0.38	0.26	10.8	45	20.7	0.81	0.99	24.3
6	II	25	4.5	0.15	0.11	1.4	60	11.7	0.29	0.13	5.8
7	VI	30	13.5	0.35	0.11	14.4	65	32.4	0.58	0.22	51.3
8	V	25	13.5	0.38	0.18	15.3	50	24.3	0.50	0.22	32.4
9	III	35	8.6	0.22	0.14	5.8	70	22.5	0.39	0.16	25.2
10	III	30	8.1	0.23	0.11	5.0	65	21.6	0.43	0.14	25.2
11	IV	35	9.9	0.25	0.10	14.4	40	11.7	0.31	0.12	19.8
12	VI	50	19.8	0.40	0.17	38.7	75	32.4	0.52	0.24	56.7

[1] See Fig. 3 and Ch. 4. B.

frequency falls off very rapidly; as is shown by the maximum depths. Within the *Ledum*-pine wood (Jm 1) the root frequency is already low at a depth of 12—14 cm.

It seems wise, when studying forest trees, not to use a standard depth for evaluating the store of nutrients within reach of the tree roots, but to make an estimation based on the root depths of the trees within the individual stands. When, as in Table 18, this method is applied, the differences in store of N and Ca become still more pronounced, and the "anomalies" in the distribution of K and P stores less evident.

Part III

Forest production and nutrient status

Chapter 11. Production

A. Methods

The study of production comprised 12 sample areas distributed within the various plant communities (Fig. 2). Within each sample area standing crop and annual increment were measured twice, 1959 (spring) and 1963 (autumn). Annual increment was determined as the difference between the measurements in 1959 and 1963 and estimated on the basis of measurements on felled sample trees and increment cores for the two five-year-periods before.

Naturally total yield since the formation of the stands had been of great interest (Lundberg 1952, see also below, B), but uncontrolled fellings and thinnings at different times makes it indeterminable.

All trees $\geqq 4.5$ cm at breast height were numbered by tags and calipered twice to the nearest mm. The two measurements were made in two directions at right angles to each other. Number, species and diameter were recorded. Trees with technical defects, injuries and diseases were specially noted as K-trees. After calipering, standing sample trees were selected for further observation. The number of these was based upon the total number of each tree species, excluding the K-trees, and the estimated distribution of the tree species (according to basal area). All standing sample trees were labelled R-trees in the record, and G-trees for those of largest diameters (the number of G-trees was determined similarly to the R-trees), and RG when these two categories coincided. Height, "crown boundary", i.e., the lowest green parts of the crowns, and bark thickness were measured on the standing sample trees. Finally, 25 R-trees were taken for borings at breast height. The increment cores were taken alternately in a N-E-S-W direction.

For further observations ten trees among the R-, RG- and G-trees were felled. Only one of these was allowed to fall in the diameter class 4.5—9.9 cm. If the felled trees had not been bored before at breast height a core was taken there. Moreover increment cores were taken at stump height to determine the age of the tree. Age determination was also made in the field

Table 19. Survey of stand data

Sample area no.	Plant community 1)	Tree species	Age year	Stand before thinning					Remaining stand				
				Mean diameter cm	Mean height m	No. of trees per hectare	Basal area o.bark m² per hectare	Volume o.bark m³ per hectare	Mean diameter cm	Mean height m	No. of trees per hectare	Basal area o.bark m² per hectare	Volume o.bark m³ per hectare
Jm 1	I	pine											
Spring 1949												7.52	25.8
" 1954												8.86	36.0
" 1959			39	10.4	8.8	1364	11.52	52.9	10.1	8.7	1282	10.36	47.3
Autumn 1963			44	11.5	9.8	1282	13.24	65.5	11.5	9.8	1282	13.24	65.5
Jm 2	III+IV	spruce											
Spring 1949												24.44	199.5
" 1954												29.07	257.2
" 1959			82	21.6	19.8	908	33.15	305.0	21.2	19.7	848	29.80	273.8
Autumn 1963			87	23.1		848	35.63	338.6	23.7	20.8	800	35.15	334.8
Jm 3	V												
Spring 1949		spruce										21.45	142.0
"		birch										3.56	23.7
												25.01	165.7
Spring 1954		spruce										28.40	215.0
"		birch										4.72	35.9
												33.12	250.9
Spring 1959		spruce	69	18.2	17.5	1259	32.68	274.4	17.9	17.4	1117	28.21	236.6
"		birch		22.1	18.9	142	5.43	45.8	22.1	18.9	142	5.43	45.8
						1401	38.11	320.2			1259	33.64	282.4
Autumn 1963		spruce	74	19.4		1117	32.95	301.1	20.2	19.3	1000	32.14	296.3
"		birch		23.4		142	6.11	53.5	23.4	20.1	142	6.11	53.5
						1259	39.06	354.6			1142	38.25	349.8
Jm 4	V												
Spring 1949		spruce										16.05	111.9
"		birch										4.70	32.5
												20.75	144.4
Spring 1954		spruce										20.94	161.1
"		birch										5.68	43.4
												26.62	204.5
Spring 1959		spruce	64	19.3	17.6	843	24.61	204.6	18.6	17.2	724	19.67	161.9
"		birch		23.1	18.5	154	6.48	53.5	23.1	18.5	154	6.48	53.5
						997	31.09	258.1			878	26.15	215.4
Autumn 1963		spruce	69	20.1		724	23.00	197.7	20.9	18.3	653	22.31	193.0
"		birch		24.2		154	7.09	60.6	24.6	19.3	119	5.67	48.3
						878	30.09	258.3			772	27.98	241.3
Jm 5	VI												
Spring 1949		spruce										3.92	16.6
"		birch										6.45	33.4
												10.37	50.0
Spring 1954		spruce										7.50	37.6
"		birch										9.37	57.4
												16.87	95.0
Spring 1959		spruce	51	12.4	12.2	891	10.83	63.7	11.6	11.5	808	8.51	48.1
"		birch		16.9	15.5	533	11.92	85.7	16.9	15.5	533	11.92	85.7
						1424	22.75	149.4			1341	20.43	133.8
Autumn 1963		spruce	56	13.8		809	12.09	77.7	14.1	13.5	767	11.95	77.1
"		birch		18.3		532	13.99	108.8	18.9	17.1	483	13.55	105.8
						1341	26.08	186.5			1250	25.50	182.9
Jm 6	II												
Spring 1949		pine										9.42	47.4
"		spruce										2.27	8.6
												11.69	56.0
Spring 1954		pine										12.65	73.1
"		spruce										3.48	15.1
												16.13	88.2
Spring 1959		pine	41	15.2	12.9	858	15.60	99.1	15.2	12.9	779	14.14	89.7
"		spruce		8.1	9.0	936	4.78	22.8	8.1	9.0	936	4.78	22.8
						1794	20.38	121.9			1715	18.92	112.5
Autumn 1963		pine	46	16.8		779	17.18	117.9	16.8	14.3	772	17.12	117.5
"		spruce		9.9		936	7.15	38.3	10.0	10.6	907	7.07	38.0
						1715	24.33	156.2			1679	24.19	155.5
Jm 7	VI												
Spring 1949		spruce										2.66	9.0
"		birch										7.55	37.0
												10.21	46.0
Spring 1954		spruce										5.41	22.5
"		birch										9.41	56.5
												14.82	79.0
Spring 1959		spruce	39	12.5	10.1	683	8.40	41.7	12.1	9.8	600	6.85	33.4
"		birch		19.0	15.8	392	11.10	79.6	19.0	15.8	392	11.10	79.6
						1075	19.50	121.3			992	17.95	113.0
Autumn 1963		spruce	44	14.4		600	9.75	55.3	14.4	11.8	600	9.75	55.3
"		birch		21.0		392	13.56	104.0	21.1	17.2	383	13.39	102.7
						992	23.31	159.3			983	23.14	158.0

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1) See Fig.3.

of the sample areas on Jägarmossen

Sample area no.	Plant community 1)	Tree species	Age year	Stand before thinning					Remaining stand				
				Mean diameter cm	Mean height m	No. of trees per hectare	Basal area o.bark m² per hectare	Volume o.bark m³ per hectare	Mean diameter cm	Mean height m	No. of trees per hectare	Basal area o.bark m² per hectare	Volume o.bark m³ per hectare
Jm 8	V												
Spring 1949		spruce										12.03	80.1
"		birch										4.14	27.6
"		alder										4.38	28.0
												20.55	135.7
Spring 1954		spruce										15.60	114.2
"		birch										4.90	35.9
"		alder										5.18	36.4
												25.68	186.5
Spring 1959		spruce	74	17.5	17.4	766	18.40	146.3	16.3	16.9	683	14.22	110.8
"		birch		19.1	17.4	200	5.76	45.8	19.1	17.4	200	5.76	45.8
"		alder		22.7	18.0	150	6.09	46.5	22.7	18.0	150	6.09	46.5
						1116	30.25	238.6			1033	26.07	203.1
Autumn 1963		spruce	79	18.2		683	17.85	151.7	19.0	18.9	617	17.56	150.7
"		birch		20.0		200	6.27	52.8	20.0	18.6	200	6.27	52.8
"		alder		24.7		150	7.17	58.6	24.7	19.5	150	7.17	58.6
						1033	31.29	263.1			967	31.00	262.1
Jm 9	III												
Spring 1949		spruce										22.10	154.7
"		pine										0.43	2.7
"		birch										0.34	2.3
												22.87	159.7
Spring 1954		spruce										26.85	214.1
"		pine										0.48	3.5
"		birch										0.41	3.2
												27.74	220.8
Spring 1959		spruce	66	19.0	18.2	1054	29.87	256.1	18.8	18.0	967	26.92	229.7
"		pine		16.0	16.4	27	0.54	4.2	16.0	16.4	27	0.54	4.2
"		birch		21.5	18.5	13	0.47	3.9	21.5	18.5	13	0.47	3.9
						1094	30.88	264.2			1007	27.93	237.8
Autumn 1963		spruce	71	20.6		967	32.25	302.7	20.8	19.9	947	32.16	302.3
"		pine		17.1		27	0.62	5.1	17.1	17.9	27	0.62	5.1
"		birch		22.8		13	0.53	4.7	22.8	19.8	13	0.53	4.7
						1007	33.40	312.5			987	33.31	312.1
Jm 10	III												
Spring 1949		spruce										15.20	84.1
"		birch										3.42	21.1
"		pine										2.08	11.7
												20.70	116.9
Spring 1954		spruce										17.38	105.9
"		birch										4.15	28.1
"		pine										2.55	15.8
												24.08	149.8
Spring 1959		spruce	50	12.8	13.2	1516	19.55	128.4	12.4	13.0	1433	17.44	113.3
"		birch		14.8	15.6	283	4.88	35.6	14.8	15.6	283	4.88	35.6
"		pine		13.9	13.7	200	3.03	20.2	13.9	13.7	200	3.03	20.2
						1999	27.46	184.2			1916	25.35	169.1
Autumn 1963		spruce	55	13.3		1433	19.92	141.1	13.7	14.4	1325	19.45	139.0
"		birch		16.1		283	5.75	44.3	16.1	16.7	283	5.75	44.3
"		pine		14.8		200	3.45	24.5	16.1	15.1	158	3.22	23.2
						1916	29.12	209.9			1766	28.42	206.5
Jm 11	IV												
Spring 1949		spruce										17.86	116.8
"		birch										2.34	15.1
												20.20	131.9
Spring 1954		spruce										21.99	160.2
"		birch										3.61	25.9
												25.60	186.1
Spring 1959		spruce	68	16.8	16.5	1142	25.41	200.4	16.4	16.3	1054	22.25	174.3
"		birch		17.3	16.7	184	4.35	33.8	17.0	16.6	177	4.02	31.1
						1326	29.76	234.2			1231	26.27	205.4
Autumn 1963		spruce	73	17.4		1054	25.09	209.9	18.4	17.6	925	24.59	207.7
"		birch		18.1		177	4.55	36.7	18.4	17.7	170	4.54	36.6
						1231	29.64	246.6			1095	29.13	244.3
Jm 12	VI												
Spring 1949		birch										9.50	64.3
"		spruce										0.38	1.3
												9.88	65.6
Spring 1954		birch										12.84	93.2
"		spruce										0.82	3.1
												13.66	96.3
Spring 1959		birch	39						17.0	16.1	653	14.82	111.9
"		spruce							9.2	7.2	214	1.42	5.5
											867	16.24	117.4
Autumn 1963		birch	44	18.7		653	17.88	141.3	18.8	17.3	629	17.55	139.1
"		spruce		11.5		214	2.22	9.7	11.5	8.5	214	2.22	9.7
						867	20.10	151.0			843	19.77	148.8

1) See Fig.3.

by counting the annual rings to the pith on the cut surface of stump. Allowance was made for stump height. A control measurement of tree height and crown boundary was made on the felled trees too. Ultimately the lengths of the leaders of the last ten years was determined by measuring the distance from branch-whorl to branch-whorl. A control of this measurement was made by cutting the stem at intervals and counting the annual rings.

To facilitate observations on later occasions, the number of every tree measured was painted on the tree as well as a cross (breast height cross) in one of the directions where breast height diameter was measured, but always facing the same direction.

B. Stand data

Table 19 is a summary of the calculations made at the Department of Forest Yield Research at the Royal College of Forestry. It is based on the measurements described above. The table is the main result of the production study. Some of the field data collected have been useful for other purposes as well. Thus, tree height, tree diameter and crown boundary have been used in the description of the vegetation (Ch. 4. C.). The annual ring measurements have been used to demonstrate the diameter development of the trees before and after draining (Ch. 6).

The diameter in the table is the diameter of mean basal area tree and height is the mean height weighted by basal area. The basal area of a single tree is the actual cross sectional area of the stem at breast height and it may also be used to designate the sum of the cross sectional areas at breast height of all the trees growing on a specified unit, and stated in terms of e.g., m^2 per hectare.

The table shows that spruce is the dominant tree species on most of the sample areas. Making allowance for trees < 4.5 cm diameter at breast height, no sample area lack spruce. Exceptionally spruce is the only tree species in a sample area, but usually it grows associated with birch as in six sample areas. On two sample areas (Jm 9, 10) there is a mixture of spruce, pine and birch. On sample area Jm 8 more alder is present than birch and therefore it has been treated separately. Pine is most abundant in the centre of the area (Jm 1, 6) and birch in the formerly open lagg (Mjölnar fen, Jm 5, 7 and 12).

Tree distribution according to basal area, shows that pine occupies a range of 2—100 % (four sample areas) of the total stand, spruce 11—100 % (11 sample areas), birch 2—89 % (nine sample areas) and alder 23 % (one sample area). There are alders on other sample areas too, but their share of the stand is so small that they have not been treated separately, and are included in the figures for birch. On some occasions, scattered birches also have been included in the figures for the conifers (on Jm 2, e.g., there are 36 birches per ha compared with 764 spruces).

Stand age could not be determined with very great accuracy since the age of only ten trees per sample area was determined. The average ages are probably too high in many cases, as the trees sampled for age were the larger ones (see above, A.). The age stated can only be regarded as fully representative of the stand when the stands are rather even-aged (mainly sample areas Jm 1, 2, 6 and 12). Usually the individual tree ages vary greatly, since the stands originated as older slow-growing "tussock-trees" with new colonizers between them. The maximum age difference between the oldest and the youngest trees measured may reach 70—80 years (Ch. 6.).

In the main there are no especially large or tall trees on this peat land. Maximum data are given in Ch. 4. C. It is notable that birch is often taller and of a larger diameter than spruce where these two species grow together.

The number of stems per unit surface area shows considerable variation with extreme values of 772 and 1766 stems per ha. Most of the sample areas have 900 to 1500 stems per ha. The average value is 1300. These figures imply that the average tree has ca. 8 m^2 of soil surface at its disposal.

The volume of the stands also vary a great deal. The *Ledum*-pine wood has the lowest volume and some parts of the *Oxalis*-spruce wood the highest, but even sample area Jm 9 (bilberry-spruce wood) has an appreciable volume of timber although the vegetation of this area gives a fairly poor impression. These variations can be a consequence of historical development. Thus, the nutrient-poor bilberry-pine wood (Jm 6) has about the same volume figure as that of sample areas Jm 7 and 12 (grass-rich birch-spruce wood).

Volume and basal area increment for the three periods measured (1948—1953, 1953—1958, 1958—1963), Table 20, show that on average the lowest annual growth was for the middle period and the highest for the last (mean annual volume increments for all sample areas for the three periods are 9.2, 8.6 and 9.8 m^3 per ha, respectively).

It is not clear whether these differences are real, but if so, there are several possible causes of the changes in growth rate, some of a temporary character and some of more precise nature. At first the high water table affected tree development adversely, but when the water regime improved during the course of time, nutrient conditions may have gained in importance. On areas where growth has decreased

Table 20. Annual increment in basal area and volume during three five-year-periods 1948-1963. Last period measured as difference in standing crop between 1958 and 1963, earlier periods estimated from measurements on increment cores and felled sample trees

Sample area no.	Plant community[1]	Annual basal area increment m^2 per ha				Annual volume increment m^3 per ha			
		1948—1953	1953—1958	1958—1963	1948—1963	1948—1953	1953—1958	1958—1963	1948—1963
Jm 1	I	0.27	0.53	0.58	0.46	2.0	3.4	3.6	3.0
2	III+IV	0.93	0.82	1.17	0.97	11.5	9.6	13.0	11.4
3	V	1.62	1.00	1.09	1.24	17.0	13.9	14.4	15.1
4	V	1.18	0.89	0.79	0.95	12.0	10.7	8.6	10.5
5	IV	1.30	1.18	1.13	1.20	9.0	10.9	10.5	10.1
6	II	0.89	0.85	1.08	0.94	6.4	6.7	8.7	7.3
7	VI	0.92	0.94	1.07	0.98	6.6	8.4	9.3	8.1
8	V	1.02	0.91	1.05	1.00	10.2	10.4	12.0	10.8
9	III	0.97	0.62	1.10	0.90	12.3	8.6	15.0	12.0
10	III	0.68	0.68	0.75	0.71	6.6	6.9	8.2	7.1
11	IV	1.08	0.83	0.68	0.87	10.9	9.6	8.2	9.6
12	VI	0.76	0.52	0.77	0.68	6.2	4.2	6.7	5.7

[1] See Fig. 3 and Ch. 4. B.

the increased nutrient consumption may be one of the causes. Thus, growth decrease is most pronounced for areas with the lowest recorded soil potassium content (Jm 4 and 11). Certainly increased stand density may be of essential importance too, not only as a factor in competition for nutrients, but because of decreased light supply as well.

For some of the sample areas in which growth has increased (Jm 1, 5 and 7), the high water table was probably unfavourable for a long time, but when the surface layers of the peat were sufficiently drained, the trees of these areas were also able to increase in growth (see also next paragraph and Ch. 12).

Some old stand data have made it possible to make a rough reconstruction of the forest stands on Jägarmossen around the time of draining (1918—22). It is noticeable that at the time of draining there was no stand with an estimated volume of > 20 m^3 per ha (Table 21) and even in 1931 the highest volume measured was 60 m^3 per ha. This means that the mean annual growth has been well above 10 m^3 per ha during the last 30 years for some areas.

C. Whole tree harvest data: dry matter and chemical elements

1. Methods

In a 10—15 m wide strip around the sample areas Jm 1 (*Ledum*-pine wood, Fig. 4) and Jm 9 (bilberry-spruce wood, Fig. 7), ten sample trees were selected for felling (August 1963) in four of the diameter classes

Table 21. Data on the early stand development on Jägarmossen based on surveys in 1927 and 1931. Data from the recent (1963) sample areas in the same stands included for comparison

Stand no. Sample area no.	Year	Mean diameter cm	Mean height m	No. of stems	Basal area m^2	Volume over bark m^3	Annual increment m^3
				Per hectare			
1	1912	4.5		655	1.06	2.9	
	1917	5.2		884	1.88	5.9	0.6
	1922	5.6		1 284	3.18	11.0	1.3
	1927	6.4		2 003	6.47	25.1	4.6
	1931	6.3	5.5	4 544	14.13	44.4	7.1
Jm 8	1963	20.1	18.8	967	31.00	262.1	12.0
7	1912	6.4		750	2.40	6.3	
	1917	6.9		837	3.16	9.2	0.6
	1922	7.9		884	4.38	14.3	1.4
	1927	9.9		1 130	8.67	33.8	6.6
	1931	9.4	7.7	1 851	12.78	60.1	7.2
Jm 2	1963	23.7	20.8	800	35.15	334.8	13.0
12	1912	4.9		464	0.86	2.4	
	1917	5.3		719	1.57	4.9	0.5
	1922	5.5		1 236	2.98	10.4	1.4
	1927	6.5		2 056	6.78	26.8	5.4
	1931	7.0		3 288	12.62	47.4	6.4
Jm 9	1963	20.7	19.8	987	33.31	312.1	15.0
15	1912			1 060	1.41	3.9	
	1917			1 460	2.71	8.4	0.9
	1922			2 070	5.00	17.4	2.2
	1927			2 860	10.57	42.1	8.1
	1931			3 300	13.63	55.7	9.7
Jm 3	1963	20.6	19.4	1 142	38.25	349.8	14.4
16	1912	3.3		507	0.43	0.9	
	1917	3.9		1 001	1.17	3.4	0.5
	1922	4.4		1 934	2.98	9.6	1.6
	1927	5.4		3 854	8.78	31.9	7.6
	1931	5.6	5.5	3 764	9.22	32.9	5.1
Jm 10	1963	14.3	14.8	1 766	28.42	206.5	8.2

obtained from measurements of trees within the sample areas. Three trees were cut from each of the two larger classes and two from each of the two smaller classes. Trees with defects (K-trees) were not accepted as sample trees. Fellings within the sample areas was avoided since it would affect later production studies.

After felling, the branches were cut off and a typical branch was taken (subjectively) from each tenth of the crown length. These branches were

Table 22. Oven-dry weight and nutrient content of a pine stand, 44 years old, on three meters deep low-humified *Sphagnum* peat (sample area Jm 1). Volume of the stand 65.5 m^3 per ha, number of stems 1282 per ha, annual increment 3.6 m^3 per ha. For other data see Tables 19 and 20. For nutrient percentages of oven-dry weight see Table 24. Store of nutrients in the peat to the level of greatest root frequency included for comparison. Estimated annual growth, tentative figures only

Part of tree	Oven-dry weight 10^3 kg per ha	Proportion of parts %	N	P	K	Ca	Mg
			Kg per ha in stand above ground				
Wood	24.2	61.4	18.4	1.9	8.2	12.1	4.6
Bark	3.0	7.6	10.2	1.3	4.7	18.6	2.0
Living branches	7.1	18.0	31.8	4.0	13.4	21.2	4.5
Needles	3.5	8.8	47.2	4.8	17.0	11.8	4.5
Dead branches	1.6	4.2	4.9	0.3	0.7	5.4	0.4
Total	39.4	100.0	112.5	12.3	44.0	69.1	16.0
Estimated annual growth:							
Wood	1.3		1.0	0.10	0.45	0.65	0.25
Bark	0.2		0.5	0.05	0.25	1.05	0.10
Living branches[1]	0.3		1.3	0.15	0.55	0.85	0.20
Needles[2]	1.2		15.7	1.6	5.7	4.0	1.5
Total	3.0		18.7	1.9	7.0	6.6	2.0
Immobilized in trunk (wood and bark)	1.5		1.5	0.2	0.7	1.7	0.4
Store of nutrients in the peat to the level of greatest root frequency. Kg per ha			1 000	60	60	300	

[1] Total amounts in living branches divided by 25, the approximative age of the oldest living branches.

[2] Total amounts in needles divided by 3, the average age of the needles.

used to determine the oven-dry weight of the crown and the ratio between branches and needles. A composite sample of dead branches was taken from each site, ten per cent of the dead branches from every sample tree. Total fresh weight of trunk, living branches and dead branches was determined in the field. The trunk volume was later determined from measurements collected at the same time.

Spruce needles were left to dry on the branches. Pine needles were stripped off the branches before air-drying. Sample discs from the trunk were taken at stump height (1 %), 12.5, 25, 37.5, 50, 62.5, 75 and 87.5 % of the height above ground level. The discs were used to determine trunk oven-dry weight and ratio between wood and bark. Bark was peeled off before air-drying. Air-dry weight was determined on all parts separately. Oven-dry weight was determined on ground samples after drying in a vacuum oven (70° C).

To check whether the felled trees were representative, discs also were taken at breast height to compare the diameter growth during the last five-year-period for the sample trees with that of trees of the same diameter class within the sample area. The growth values agreed well on the whole.

Chemical analyses were performed with the methods outlined in Ch. 10.

Table 23. Oven-dry weight and nutrient content of a spruce stand, about 60—70 years old, on 1.6 m deep highly humified *Sphagnum*-cyperaceous peat (sample area Jm 9). Volume of the stand 312.1 m^3 per ha, number of stems 987 per ha and annual increment 15.0 m^3 per ha. For other data see Tables 19 and 20. For nutrient percentages of oven-dry weight see Table 25. Store of nutrients in the peat to the level of greatest root frequency included for comparison. Estimated annual growth, tentative figures only

Part of tree	Oven-dry weight 10^3 kg per ha	Proportion of parts %	N	P	K	Ca	Mg
			Kg per ha in stand above ground				
Wood	117.7	66.3	77.7	9.4	29.4	78.8	11.8
Bark	10.0	5.6	53.9	7.0	20.7	128.2	8.3
Living branches	29.3	16.5	170.2	19.1	49.9	161.4	18.2
Needles	15.9	9.0	210.1	33.6	65.3	128.9	22.3
Dead branches	4.7	2.6	22.0	1.3	2.3	23.9	0.6
Total	177.6	100.0	533.9	70.4	167.6	521.2	61.2
Estimated annual growth:							
Wood	5.7		4.0	0.45	1.4	4.0	0.6
Bark	0.5		2.6	0.35	1.0	6.1	0.4
Living branches[1]	0.7		4.3	0.50	1.2	4.0	0.5
Needles[2]	2.0		26.3	4.2	8.2	17.1	2.8
Total	8.9		37.2	5.5	11.8	31.2	4.3
Immobilized in trunk (wood and bark)	6.2		6.6	0.8	2.4	10.1	1.0
Store of nutrients in the peat to the level of greatest root frequency. Kg per ha			8 600	220	140	5 800	

[1] Total amounts in living branches divided by 40, the approximate age of the oldest living branches.

[2] Total amounts in needles divided by 8, the average age of the needles.

2. *Results*

The results are given in Tables 22 and 23. Some comparison with investigated stands on other sites may be illustrative, although data for closely comparable stands are not obtainable. Two pine stands for comparison are from two poor sites (experiments no. 873 and 876) about 400 km SW of Jägarmossen but with a climate not very different from that in Uppland. Another stand (experiment no. 728) is from a poor site 800—900 km N of Jägarmossen and with a much shorter vegetation period than in Uppland (about 118 days against about 163 days with $\geqq +6^\circ$ C mean temperature).

It is noticeable (Table 24) that the nitrogen percentages generally are higher for all parts of the trees on Jägarmossen than on the other sites. Phosphorus and potassium percentages are somewhat irregular, but in the main the Jägarmossen samples do not differ much from those of the other sites. For calcium there is a remarkably high value

Table 24. Comparison between nutrient content in different parts of pine on different localities and on Jägarmossen

Part of tree	Locality	N	P	K	Ca	Mg
		Per cent				
Wood	M	0.06	0.007	0.051	0.039	
	H	0.06	0.005	0.041	0.040	
	S	0.05	0.004	0.034	0.053	
	Jm	0.08	0.008	0.034	0.050	0.02
Bark	M	0.28	0.037	0.12	0.16	
	H	0.20	0.022	0.08	0.18	
	S	0.26	0.045	0.17	0.39	
	Jm	0.34	0.043	0.16	0.62	0.07
Living branches	M	0.37	0.050	0.24	0.14	0.056
	H	0.28	0.037	0.18	0.20	0.057
	S	0.32	0.037	0.18	0.28	
	Jm	0.45	0.056	0.19	0.30	0.06
Needles	M	1.38	0.15	0.60	0.19	0.092
	H	1.24	0.13	0.69	0.20	0.098
	S	0.92	0.09	0.30	0.44	
	Jm	1.36	0.14	0.49	0.34	0.13
Dead branches	M	0.28	0.015	0.038	0.12	0.027
	H	0.23	0.012	0.034	0.14	0.016
	S	0.19	0.011	0.030	0.24	
	Jm	0.30	0.018	0.040	0.33	0.02

Explanations: M. Experiment 873, province Småland; stand volume 109 m^3 per ha, annual increment 4.1 m^3 per ha. Soil: sediment (sand). H. Experiment 876, province Småland; stand volume 90 m^3 per ha, annual increment 3.4 m^3 per ha. Soil: sediment (sand). S. Experiment 728, province Lappland; stand volume 90 m^3 per ha, annual increment 2.1 m^3 per ha. Soil: sandy moraine. Age 69 years. Jm, Jägarmossen, sample area Jm 1.

Data for M and H from unpublished data (see Tamm 1963). S from Popović and Burgtorf (1964, in press).

for pine bark from Jägarmossen, up to four times higher than that of the other bark samples.

The fairly high nutrient contents of pine on Jägarmossen suggest the possibility of a yield greater than that obtained. Therefore it seems possible that nutrient content is not the only, and perhaps not the most important, growth-limiting factor at present. The water-regime, with sometimes very high water tables may have a growth depressing effect. The high acidity and the special microbiological conditions may also contribute to a low growth rate, but it should be noted that the total nutrient content of the stand or percentage of nutrients in the crown of the trees, etc., are less good indicators of the nutrient status than well-exposed leaves, which will be treated in the next chapter.

Table 25. Comparison between nutrient content in different parts of spruce on Frodeparken and Jägarmossen

Part of tree	Locality	N	P	K	Ca	Mg
		Per cent				
Wood	F	0.07	0.006	0.039	0.048	0.011
	Jm	0.06	0.008	0.025	0.067	0.010
Bark	F	0.45	0.059	0.24	0.57	0.074
	Jm	0.54	0.070	0.21	1.28	0.083
Living branches	F	0.44	0.054	0.17	0.28	0.052
	Jm	0.58	0.065	0.17	0.55	0.062
Needles	F	1.13	0.19	0.39	0.44	0.085
	Jm	1.32	0.21	0.41	0.81	0.14
Dead branches	F	0.25	0.019	0.04	0.16	0.021
	Jm	0.47	0.028	0.05	0.51	0.013

Explanations: F. Experiment 883 (Frodeparken), province Halland. Stand volume 287 m^3 per ha, annual increment 13.5 m^3 per ha. Age 52 years. Soil: sandy moraine, formerly used as arable land (see Tamm 1963). Jm. Jägarmossen sample area Jm 9.

Table 25 gives some comparative data for spruce, obtained for a high quality site about 450 km SW of Jägarmossen. The table shows that only wood of spruce from Frodeparken has higher nitrogen content than that of the Jägarmossen trees. All P values are higher for the trees on Jägarmossen, but K is lower in wood and bark. Calcium is obviously higher for the Jägarmossen trees; in the main the percentages are double those for the trees at Frodeparken. For magnesium, the needles only of the spruce from Jägarmossen have a considerably higher content. For Ca the values at Jägarmossen seem to fairly well reflect the habitat conditions. The Ca percentages of the peat are very high in the rooting zone (Fig. 71).

Chapter 12. Foliar analysis and nutrient status

Sampling of needles and leaves was according to the general principles developed at the Department of Forest Ecology at the Royal College of Forestry (see Tamm 1951, 1955, 1956 a, 1964, in press). The seasonal variation in nutrient content of the leaves of the common forest trees in Sweden shows that the most suitable time for collecting birch leaves is shortly before the fall of the leaves, and for conifer needles during winter, since the nutrient contents of the leaves are most constant at these times (Tamm 1955).

The analyses are based on birch leaves collected in late August and spruce and pine needles collected in November. Only current needles were used.

Suitable shoots of up to 6—7 m tall trees were cut with pruning scissors on a pole; and shoots of taller trees, which were more generally required were obtained by using a shot-gun. Within the sample areas an equal portion of shoots was taken from each of the ten sample trees (objectively selected) and these ten samples were mixed and treated as a composite sample of that area. Needles and leaves were taken from well-exposed twigs in the top of the crown.

Birch leaves and spruce needles were prepared as soon as possible (the same day) for air-drying and pine needles for drying in a vacuum oven (70° C). Before drying, pine needles and birch leaves were removed from the twigs, spruce needles were left to dry on the twigs.

Spruce needles and birch leaves were collected from all sample areas, pine needles from three sample areas only, the areas where pine is more abundant. On sample area Jm 1 spruce and birch occur only as an understorey under pine. Hence the light climate is somewhat different from that for the same species on the other sample areas, where all sample trees are of about the same height.

Before presenting the analysis data, some concepts have to be defined. "The 'nutrient status' of a forest stand is a measure of the degree in which the nutrient requirements for maximum growth are satisfied. A stand with optimum nutrient supply has thus a very good (or optimum) nutrient status, while the opposite is true of stands on many poor sites. It is thus clear that the nutrient status can be optimum or in excess with respect to some plant nutrients at the same time as it is very low in others" (Tamm 1964, in press).

Deficiency is defined according to Tamm (1956 a), i.e., a nutrient state where growth is much increased on supply of the deficient element(s) in an available form. "Deficiency level" implies a concentration of nutrients in the leaves, where growth is strongly inhibited and visible symptoms of deficiency are usually seen on the foliage. For seedlings in nutrient solutions, Ingestad (1962) has precisely defined different nutrient levels.

From Table 26 and from work cited the following statements can be made:

Nitrogen: Nutrient status clearly suboptimal for all tree species on every sample area. On some sample areas the nitrogen concentration is, however, somewhat closer to the optimum range than on others (e.g.,

Table 26. Nutrient concentrations in leaves of pine, spruce and birch from the different sample areas in the years 1959 and 1963. Per cent of oven-dry weight. Suggested deficiency levels are included

Sample area number	Year	PINE					SPRUCE					BIRCH				
		N	P	K	Ca	Mg	N	P	K	Ca	Mg	N	P	K	Ca	Mg
Jm 1	1959	1.34	0.15	0.49	0.20		1.09	0.14	0.58	0.31		1.62	0.19	0.49	0.79	
	1963	1.62	0.18	0.53	0.34	0.15	1.10	0.14	0.52	0.32	0.12	1.78	0.19	0.46	0.80	0.40
2	1959						1.36	0.18	0.57	0.49		2.05	0.15	0.58	0.84	
	1963						1.38	0.16	0.42	0.66	0.12	2.50	0.16	0.54	1.10	0.34
3	1959						1.39	0.14	0.63	0.58		2.54	0.13	0.77	0.95	
	1963						1.44	0.14	0.53	0.72	0.10	2.68	0.14	0.79	1.30	0.23
4	1959						1.41	0.16	0.28	0.49		2.36	0.19	0.57	1.01	
	1963						1.62	0.19	0.23	0.60	0.11	2.66	0.18	0.51	1.24	0.28
5	1959						1.43	0.17	0.91	0.48		2.07	0.11	0.68	0.95	
	1963						1.30	0.17	0.77	0.63	0.12	2.60	0.14	0.80	1.15	0.28
6	1959	1.46	0.17	0.41	0.15		1.46	0.20	0.50	0.42		1.97	0.19	0.67	0.76	
	1963	1.60	0.17	0.46	0.29	0.14	1.51	0.22	0.50	0.57	0.15	2.65	0.24	0.83	0.86	0.40
7	1959						1.50	0.16	0.70	0.44		2.04	0.10	0.47	0.97	
	1963						1.45	0.15	0.68	0.60	0.12	2.45	0.12	0.66	1.08	0.24
8	1959						1.52	0.17	0.71	0.53		2.06	0.15	0.79	1.02	
	1963						1.65	0.16	0.52	0.78	0.15	2.56	0.20	0.91	1.16	0.19
9	1959						1.48	0.18	0.71	0.53		2.06	0.17	0.59	0.83	
	1963						1.60	0.20	0.50	0.64	0.16	2.88	0.20	0.72	1.14	0.34
10	1959	1.39	0.16	0.38	0.15		1.36	0.16	0.45	0.49		2.11	0.15	0.46	1.03	
	1963	1.41	0.15	0.40	0.26	0.12	1.30	0.15	0.40	0.50	0.12	2.36	0.16	0.54	1.14	0.33
11	1959						1.38	0.14	0.35	0.52		2.22	0.12	0.59	1.07	
	1963						1.26	0.14	0.28	0.62	0.12	2.50	0.13	0.48	1.21	0.28
12	1959						1.51	0.21	0.79	0.38		1.95	0.11	0.42	1.07	
	1963						1.52	0.24	0.74	0.54	0.13	2.67	0.13	0.54	1.07	0.26
Suggested deficiency levels according to Tamm (1956 a) and		1.1-1.6	0.09-0.10				0.8-1.3	0.07-0.08	0.15-0.30			1.8-2.4	0.08-0.10	0.29-0.34		
Ingestad (1962) "Range of moderate deficiency"		1.1-2.4	0.08-0.15	0.44-0.9	0.03-0.04	0.06-0.20	0.9-1.8	0.07-0.10	0.3-0.7	0.02-0.09	0.09-0.13	2.4-3.4	0.1-0.2	0.5-1.5	0.06-0.16	0.22 0.29

spruce on Jm 4, 8 and 9). For birch the deficiency is severe on Jm 1.

Phosphorus: Satisfactory nutrient status for pine and spruce. For birch there is a moderate deficiency on Jm 2, 3, 5 and 10 and a strong deficiency on Jm 7 and 12 (Mjölnar fen).

Potassium: Suboptimal nutrient status for pine on every sampled area. For spruce the supply of potassium appears to be satisfactory on Jm 5, 7 and 12 (the sample areas of Mjölnar fen). A moderate deficiency is suggested on Jm 2, 6 and 10 and a severe deficiency on

Jm 4 and 11. For birch, plots Jm 1, 2, 4 and 10—12 appear to be potassium-deficient.

Calcium and magnesium: All stands have a nutrient status apparently falling within the optimum range with regard to these elements.

Thus, on the basis of the present analyses and data obtained in field experiments (Tamm 1956 a) and in nutrient solutions (Ingestad 1962) it is probable that nitrogen and potassium, especially nitrogen, are the elements most limiting for the growth of the tree species studied. For spruce, however, potassium seems to be the specific deficient element on some sample areas (Jm 4 and 11, see also birch on these areas) and development is so far advanced that there are visible symptoms of deficiency. Se further Table 20, from which it is apparent that yield on these areas has decreased continually during the whole measuring period. The K content of the birch leaves on the same areas is, however, not particularly low, but lies in the middle of all analyses for this species. Phosphorus appears to be the element limiting growth of birch, in the first place, and this species difference is to be noticed.

From Table 26 it is further seen that from 1959 to 1963 the nitrogen status has improved for pine in the centre of the peat land (Jm 1 and 6), the other nutrients have not changed very much. Nitrogen concentration in spruce leaves has increased on half the number of the sample areas and decreased on four of them. Phosphorus has not changed much. The potassium situation has, however, become more unfavourable, since in most of the areas there is a decreased K concentration in the leaves, and for the areas (Jm 4 and 11) in which there was already a critical K state in 1959 it has now become still worse.

For birch, on the other hand, the situation is quite different. All sample areas show an improved N state and also the Ca concentration has increased, but probably this latter is without significance for the growth. In most of the sample areas there is an increased P concentration in the leaves, but it is still very low. For K the concentration in the leaves is higher in eight of the sample areas and lower in the other four, which include Jm 4 and 11, in which K is also low in spruce leaves. Even if allowance is made for the "normal" fluctuations in the nutrient content of the leaves, it appears that the general trend in nutrient status for the period studied (1959—63) has been a deterioration for the conifers but an improvement for the birch.

From the different foliar analyses it is now evident that on the peat land there are some areas with a comparatively favourable nutrient status, while others are far from this. Within the central area the nitrogen content of the peat is so exceedingly low (0.75—0.80 %, but the total store is considerable), that the supply to the trees is expected to be strongly limiting, but most of the area has such high nitrogen percentages and such large stores of N that the supply should be sufficient. Nevertheless nitrogen is limiting growth for the whole area. For a drained peat land site not far from Jägarmossen, Tamm (1956 b) found similar conditions, i.e., high N content in the peat but low in the foliage. A peat with a total N content of 2—$2^1/_2$ % is usually designated "remarkably nitrogen-rich" (Malmström 1952), see also Tamm (1956 b), and a peat with > 1.3 % N is considered capable of maintaining a tree stand, provided other nutrients are adequate (Malmström, verbal communication). This may be compared with the present N contents ranging between 2 and 3.5 % for the largest part of the area and the still low leaf contents. Presumably it is not the N percentage content as such which determines the nutrient status of the vegetation, but its availability.

The potassium conditions appear to be somewhat clearer. 0.085 % of K (0.1 % K_2O) has been suggested as a minimum level for peat able to support a prolonged forest yield (Malmström et al. 1956). Nowhere on Jägarmossen is such a high value obtained, but at most the K content reaches about one half to three quarters of it (see Ch. 10.2.). Under such circumstances it is not unexpected that growth there is inhibited because of scarcity for potassium. Paradoxically enough it also seems that K contents > 0.08 % are extremely rare on high quality drained peat land sites.

At a phosphorus content of less than 0.045—0.090 % (0.1—0.2 % P_2O_5), the resources are regarded as "poor and possibly insufficient" (Malmström et al. 1956). More than half the number of the surface peat analyses of Jägarmossen have < 0.07 % P, one-third has 0.07—0.09 % and only one-sixth > 0.09 %, i.e., a sufficient content in comparison with the above stated preliminary minimum level. Nevertheless, the yield of the stands is far above the average for the part of the country. However, judging from the foliar analyses there is a phosphorus deficiency in birch at least.

The relations between nutrient contents in the leaves and current increment are far from being clear, and possibly such relationships are not to be expected in the present case because of the very low nutrient contents which often obtain. Under such circumstances it is meaningless to try to elucidate relations between yield and leaf nutrient

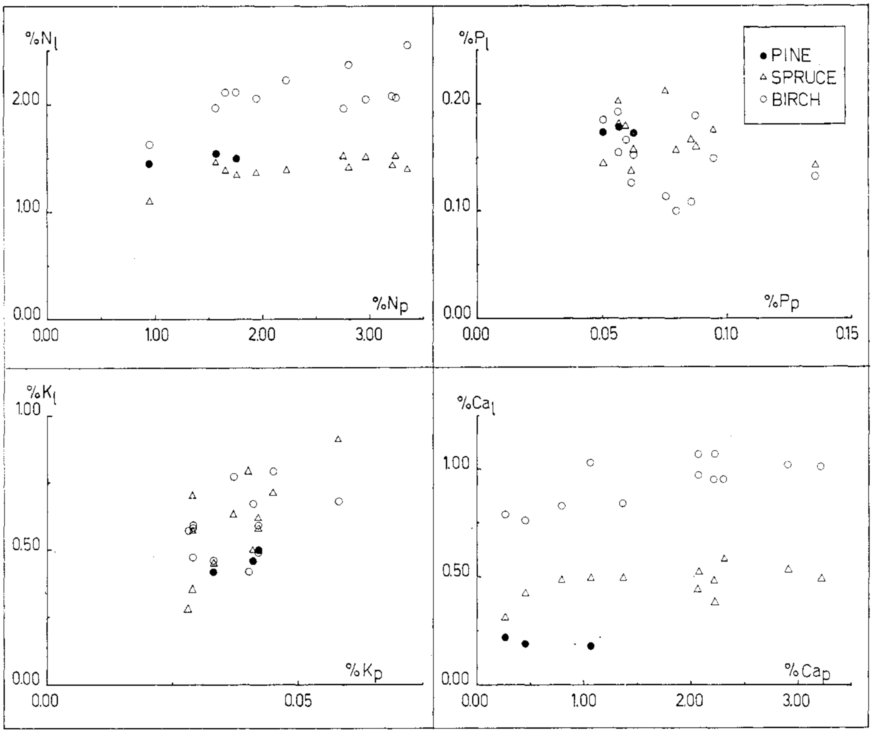

Fig. 76. Relationships between the contents of nitrogen (N), phosphorus (P), potassium (K) and calcium (Ca) in the leaves of the trees (index "l") and in the peat (index "p") in the same sites.—For symbols, see figure.

contents (Tamm 1956 a). Thus for Jägarmossen no relations are found between yield and leaf contents of N, P and K. For Ca there seems to be a certain relation, and increased Ca content in leaves is followed by increased yield.

For stands on mineral soils, however, fairly good correlations were obtained for site classes and nitrogen and phosphorus concentration in the leaves, but not for the calcium concentration (Nebe 1963; Wehrman 1963).

It is known that the plants discriminately take up dissolved substances from soil water, but the uptake is not in the same proportions as the elements are there (see, e.g., Stålfelt 1960, p. 55). To demonstrate the selective uptake the quotients in Table 27 have been computed (content in exposed leaves divided by content in peat in the same site), see also Figs. 76 and 77. The tree species behave somewhat differently, but generally the variations between them are not particularly large. For all species the nitrogen quotient has the range 0.4—

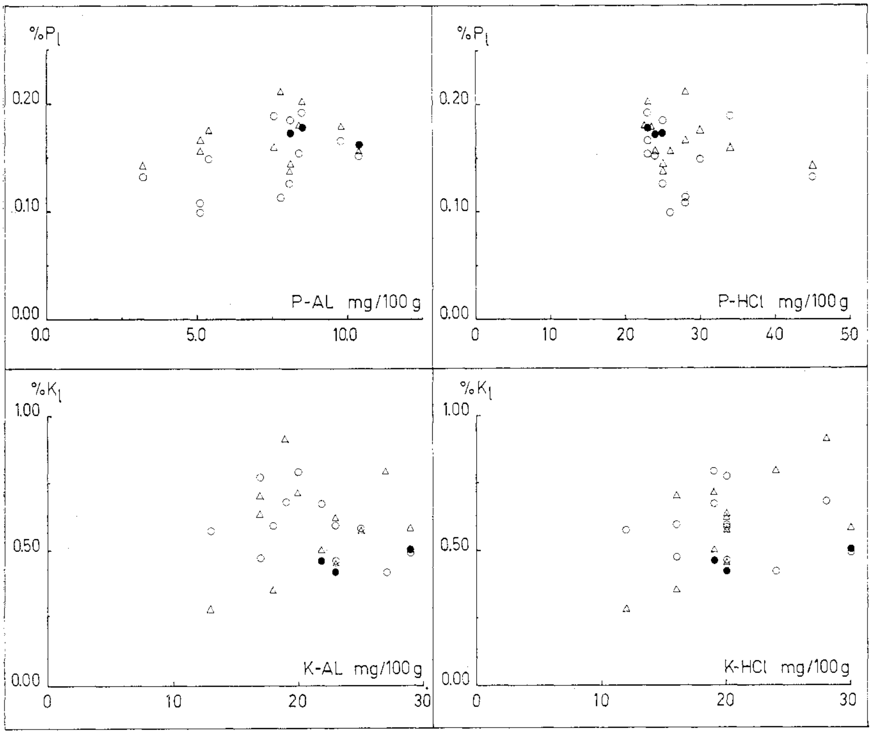

Fig. 77. Relationships between the contents of total phosphorus (P) and total potassium (K) in the leaves of the trees (index "l") and the contents of P-AL, P-HCl, K-AL and K-HCl in the peat.—For symbols, see Fig. 76.

1.7, with low values for the meadow-forest area and high for the heath-forest area. It is interesting that quotients of the same size were found by Malmer and Sjörs (1955) for shoots of *Rhynchospora alba* on a bog site. The figures obtained indicate no concentration of N in the plants. For phosphorus there seems to be a concentration in the plants since the quotient has the average value 2—3. The figures again agree surprisingly well with those for *Rhynchospora alba* (1.4—3.9). But calculations based on acetic acid extractable P in peat (Malmer and Sjörs 1955) gave the quotients 36—83, and for P-AL in Jägarmossen peat 20—45, which suggests a strong uptake of easily soluble P. The quotient for potassium is very much higher than that of the other elements studied. Evidently there is a very strong concentration of K in the leaves. It is remarkable that both the highest and the lowest quotient for spruce occurs in sample areas Jm 4 and 7, with about the same K content in the peat (0.027 and 0.028 % K). Moreover, the lower quotient is for an area (Jm 4) with greater stand-

Table 27. Relation between nutrient concentration in the leaves (index »l») and in the peat (index »p») for the different sample areas and tree species

Sample area number	PINE				SPRUCE				BIRCH			
	$\frac{N_l}{N_p}$	$\frac{P_l}{P_p}$	$\frac{K_l}{K_p}$	$\frac{Ca_l}{Ca_p}$	$\frac{N_l}{N_p}$	$\frac{P_l}{P_p}$	$\frac{K_l}{K_p}$	$\frac{Ca_l}{Ca_p}$	$\frac{N_l}{N_p}$	$\frac{P_l}{P_p}$	$\frac{K_l}{K_p}$	$\frac{Ca_l}{Ca_p}$
Jm 1	1.5	3.0	12	0.9	1.1	2.5	13	1.1	1.7	3.5	11	2.8
2					0.7	3.0	18	0.4	1.2	3.0	20	0.8
3					0.4	1.0	17	0.3	0.8	1.0	23	0.5
4					0.6	2.0	9	0.2	1.0	2.0	20	0.3
5					0.4	2.0	16	0.2	0.7	1.5	14	0.4
6	1.0	2.5	10	0.5	1.0	3.5	12	1.2	1.5	3.5	17	1.8
7					0.5	2.0	23	0.2	0.8	1.5	19	0.5
8					0.5	2.0	15	0.2	0.7	2.0	20	0.4
9					1.0	3.0	15	0.8	1.4	3.0	16	1.2
10	0.8	2.5	12	0.2	0.8	2.5	12	0.5	1.2	2.0	15	1.0
11					0.6	2.0	11	0.2	1.0	2.0	18	0.6
12					0.5	3.0	20	0.2	0.8	1.5	13	0.5

ing crop and annual increment than that of the higher one. Possibly this is caused by a simple "dilution effect", i.e., a higher standing crop has a greater bulk of living tissue to support from the same concentration in the substratum than a stand of less volume and less living tissue. For K-AL the quotient are about two to three times higher than those for K total.

The quotient for Ca shows that in the main there is no concentration of Ca in the trees except in birch on Jm 1. It seems that birch in general has higher quotients than the conifers; see also Table 26. Possibly there is a specific species difference in that property. Birch is generally regarded as a greater "Ca consumer" than pine and spruce, and this is also evidenced by the deficiency level for Ca, which is higher for birch than for the conifers.

Malmer and Sjörs (1955) reported a considerable concentration of K by the shoots of *Rhynchospora*. The quotients varied between 15 and 50 (acetic acid soluble K in peat). From figures of Aaltonen (1956) for mineral soils and varying forest types, the following quotients can be calculated for birch: P 31 (21—42); K 105 (60—140); Ca 33 (8—70)!

The quotients mentioned should not be taken as exact values, but only as a rough estimate of the selective nutrient uptake. Such figures cannot be calculated exactly because of varying concentrations in leaves and also in soil, from time to time. The present figures are mean values based on foliar content in 1959 and 1963. Although the figures are slightly different for leaves from the individual years they are nevertheless of about the same size. They are of ecological interest because they indicate that on such sites there usually is no concentration in the leaves of nitrogen and calcium, as compared with the substratum, but slight concentration of phosphorus and strong or very strong concentration of potassium. Compare also the quotients calculated from Aaltonen's figures.

As a conclusion to this chapter it may be stated that the present data do not support the idea of using foliar analysis as a method in evaluating site fertility. From results for several Finnish forest stands Aaltonen (1950, 1956) came to the same conclusion and so did Viro (1961) for different forest sites in Europe. Nebe (1963) and Wehrmann (1963) have been considerably more optimistic in this respect. However, leaf analysis is very useful in giving an estimate of the actual nutrient status of the tree stand.

Chapter 13. Some relationships between vegetation and habitat properties

A. Introduction

This chapter is devoted to a general discussion of the three groups of observations described above (vegetation, habitat conditions and yield data for the forest trees) and it will be presented in the form of a study of the relations between these observations.

Relationships between plant communities and soil properties have been studied for a long time and the literature is extensive (see, e.g., Braun-Blanquet 1951, and literature cited by him). Valmari (1921) made a summary of various forest types in Finland and related them to site classes. But in general accounts of the relations between forest yield and soil properties are rather few (Ilvessalo 1923; Hickock et al. 1931). In itself this is to be expected as it is difficult to examine these relations in detail in natural forest stands, because of the variations within the stands (differences in age, proportion between tree species, genetical origin, historical development, forest fires, fellings, thinnings, drainings, etc.). Thus, at the very beginning of such an investigation doubts exist about the possibilities of obtaining a material of homogeneous origin.

In several recent investigations, however, attempts have been made to correlate site index or forest growth data (leader growth, basal area and volume increment) with soil properties (Zöttl 1960; Mader and Owen 1961; Pawluk and Arneman 1961; Rennie 1962 and literature cited by him; Fiedler and Nebe 1963; Heinsdorf 1963), or with nutrient status of the trees (Aaltonen 1950, 1956; Viro 1961; Nebe 1963; Wehrmann 1963). Sometimes rather good correlations have been obtained.

In the present restricted case, yield seems to be fairly well correlated with various plant communities ("forest types") and these in their turn with the soil content of various nutrients etc.

It is found that the properties most clearly different between the different vegetation types are the contents of nitrogen and calcium in the peat. Phosphorus shows a similar trend, but not quite so distinctly.

B. Plant communities

The classification of the vegetation in heath-forest communties and meadow-forest communities fits well with differences in soil properties (Table 28, see also Diagrams, Fig. 46 et. seq. and the differences in several of the analytical values between the types I—III and IV—VI). The more detailed units of classification (the associations based on the qualitative properties of the vegetation) are also characterized by certain ranges of soil data, as are also certain of the characteristic species of the communities. But it must be remembered that often it is not the nutrient conditions as such which are solely determinative for the distribution of a species. Nutrient contents may possibly not even be the properties of greatest importance. On the other hand, at a certain nutrient level a certain species or a combination of species is better adapted to a site than another, provided no differences occur in other environmental properties.

Ledum palustre, Eriophorum vaginatum and *Rubus chamaemorus* in the field layer and pine in the tree layer, in the main have the same area of distribution (Figs. 5 and 14). These species are qualitatively and quantitatively the most important of the pine-wood area. Within this area the N content of the peat varies from 0.75 to 1.70 %, P from 0.04 to 0.06 %, K from 0.03 to 0.04 % and Ca from 0.18 to 0.80 %, pH is 3.0—3.6. The species mentioned are most abundant at the lower ends of these ranges. At the higher ends they occur more scattered (not so distinctly for *R. chamaemorus*). At the same time as the nutrient percentages rise, the distance to the water level does the same. At the higher nutrient levels, it seems no longer possible for some of these species to compete with the less demanding ones characterizing the neighbouring communities. Otherwise it is well-known, for instance, that *Eriophorum vaginatum* endures considerable quantities of nutrients without the habitat becoming unfavourable (Tamm 1954); its fertility even increases with increases in the nutrient concentrations. *Ledum* has similar properties; its small sensitivity to a high N content (> 2.5 % in the peat), for instance, is exemplified by an occurrence in northern Uppland. It may be more sensitive to a high lime content or a high pH. Water conditions seem to be of less importance for this species (when not extreme) since it grows on very wet sites in Central and S Sweden as well as on fairly dry sandy-silty sediments in N Sweden. In this respect it resembles *Vaccinium uliginousum,* one of its most common associates.

The cause of the gradual change in vegetation is possibly not the nutrient increase as such in the present case, but more likely the more intense interference from the less demanding species which are able to play an increasingly important role in the community. Addition of a dense tree layer of spruce certainly produces unfavourable conditions for *Ledum* and *Eriophorum* (see Table 8 regarding the change in degree of cover of these species during the period after draining).

In the surrounding community (the bilberry-spruce wood), the degree of cover and the frequency of bilberry increase and some herbs are added. But the position of the bilberry becomes more hazardous when habitat conditions alter towards the periphery of the community. In the zone where bilberry occurs free from *Eriophorum, Ledum* and *Rubus,* the N content rises to 1.5 to 2.0 %, P and K are unchanged, Ca reaches 1 % and pH about 4.0.

If the importance of the nutrient properties is masked to some extent by other habitat properties in the case of the heath-forest communities, it is somewhat clearer in the meadow-forest communities. These comprise a relatively uniform area, with respect to both historical development and the present state (stand age, species composition of the stand, density, water conditions, dispersal possibilities, etc.). A large part of the differences in the field and bottom layer vegetation may therefore be ascribed to differences in the substratum.

The soil data for the *Maianthemum*-spruce wood (IV) and the *Oxalis*-spruce wood (V) differ in many respects from one another (Table 28). Because of the gradual change in many properties (de-

Table 28. Average values (with standard errors) for chemical properties of peat in the different plant communities. Concentration figures on an oven-dry basis. Samples from the layer D-20 cm below soil surface

Plant community[1]	I	II	III	IV	V	VI	0[2]	M[3]
Number of samples[4]	10	40	46	28	58	62	—	—
Apparent density g/dm^3	96.3 ± 6.9	113.0 ± 2.4	120.0 ± 2.3	136.5 ± 4.6	164.4 ± 3.6	143.9 ± 3.2	178	499
Ash per cent	2.3 ± 0.1	3.0 ± 0.1	4.2 ± 0.2	6.8 ± 0.4	9.6 ± 0.4	9.2 ± 0.4	17.8	72.0
pH	3.20 ± 0.05	3.38 ± 0.03	3.73 ± 0.04	4.30 ± 0.05	4.51 ± 0.04	4.57 ± 0.04	4.7	5.6
N (total) per cent	0.98	1.54	1.73	2.32	3.14	3.01		
P (total) per cent	0.051	0.062	0.058	0.064	0.105	0.081		
K (total) per cent	0.042	0.043	0.035	0.028	0.035	0.040		
Ca (total) per cent	0.28	0.44	0.94	2.04	2.70	2.14		
P-AL mg/100 g	5.2 ± 0.2	6.2 ± 0.2	6.0 ± 0.2	4.0 ± 0.2	2.8 ± 0.1	2.9 ± 0.1	2.3	1.3
P-HCl mg/100 g	18.1 ± 0.9	21.6 ± 0.7	21.4 ± 0.7	18.8 ± 1.0	22.1 ± 1.1	21.6 ± 0.8	31	25
K-AL mg/100 g	17.0 ± 1.2	17.0 ± 0.5	17.3 ± 0.8	10.8 ± 0.5	11.9 ± 0.4	14.2 ± 0.6	15	12
K-HCl mg/100 g	12.9 ± 1.0	14.8 ± 0.6	16.1 ± 0.7	11.7 ± 0.6	16.3 ± 0.9	16.8 ± 0.7	24	140
P-AL kg per ha	10.9 ± 1.0	15.6 ± 0.5	16.1 ± 0.5	11.9 ± 0.6	10.0 ± 0.5	9.3 ± 0.5	8	12
P-HCl kg per ha	38.6 ± 3.2	53.8 ± 1.8	56.3 ± 2.2	58.9 ± 4.3	88.2 ± 5.7	71.3 ± 3.9	114	240
K-AL kg per ha	35.8 ± 3.3	42.2 ± 1.9	46.0 ± 1.9	32.9 ± 1.5	44.8 ± 2.5	46.1 ± 1.6	46	112
K-HCl kg per ha	27.0 ± 2.5	37.0 ± 1.4	42.6 ± 1.8	35.4 ± 1.5	64.4 ± 4.7	54.2 ± 2.9	60	1 330
Specific conductivity $ohm^{-1}\ cm^{-1} \cdot 10^{-6}$	37.3 ± 12.2	107.4 ± 8.6	158.4 ± 8.0	212.5 ± 16.4	296.8 ± 11.0	282.7 ± 10.1	262	283
Cation exchange capacity meq. per 100 g	126.8 ± 7.1	147.6 ± 3.2	151.4 ± 3.5	173.7 ± 4.3	169.5 ± 3.8	147.0 ± 4.0	146	65
Degree of neutralization per cent	21.3 ± 2.0	24.4 ± 0.9	34.3 ± 1.6	47.9 ± 2.4	56.5 ± 1.4	59.3 ± 1.9	54	71

1) See Fig. 3 and Ch. 4.B. 2) See Fig. 3 and Ch. 5.B. "Others". 3) Mineral soil-mixed peat from the boundary with the non-peaty land. 4) Values without standard errors (plant communities I—VI) concern a low number of samples (4—12) than that given in column head.

creasing towards the heath-forest and increasing towards the *Oxalis*-spruce wood) it seems permissible to suppose that the optimum conditions for the *Maianthemum*-spruce wood are realized on Jägarmossen. On average, values for many analysis data for the *Maianthemum*-spruce-wood (IV) are about 30—50 % lower than for the *Oxalis*-spruce wood (V). It should be noted that the characteristic species of the former, *Maianthemum bifolium,* also occurs in type III, but more scattered. It has thus a considerably wider amplitude than the community itself. In that respect it is similar to *Oxalis acetosella,* the characteristic species of the *Oxalis*-spruce wood; both species have quite a wide amplitude on the peat land, but they never occur in the most oligotrophic communities (I and II). Within the eutrophic communities (the meadow-forest) they occur regularly, but with very variable frequency (see Tables 5—7). It has not been possible to determine if the optimum conditions for the *Oxalis*-spruce wood are realized on Jägarmossen or on any other peat land visited, because no community of still higher quality has been seen. (In this case optimum has a subjective significance mainly relating to the productivity of the community.) Communities related to Cajander's (1921) "Sanicula-Typ (ST)" probably represent one of the most luxuriant of all the forest communities in this part of the country.

The grass-rich birch-spruce wood which, with respect to vegetational development, is at an intermediary stage developing to types IV and V, also shows analysis data intermediate between these communities.

C. Tree stands

The area of distribution of the woody species and their general relationships to habitat have been discussed in Ch. 4. C. In the present section the relation of annual increment of the four most common tree species (pine, spruce, birch and alder) to some soil properties will be discussed. The account will be largely in the form of simple diagrams, in which the sum of the yields of these species is the dependent variable.

It has not been possible to establish statistically significant relationships between yield and soil because of the small number of sample areas with known yield. The only case where an indication of a statistical significance was obtained for the soil properties studied, was for the relation yield/per cent P (total) in peat. From the diagrams it is evident that one of the three sample areas in which more

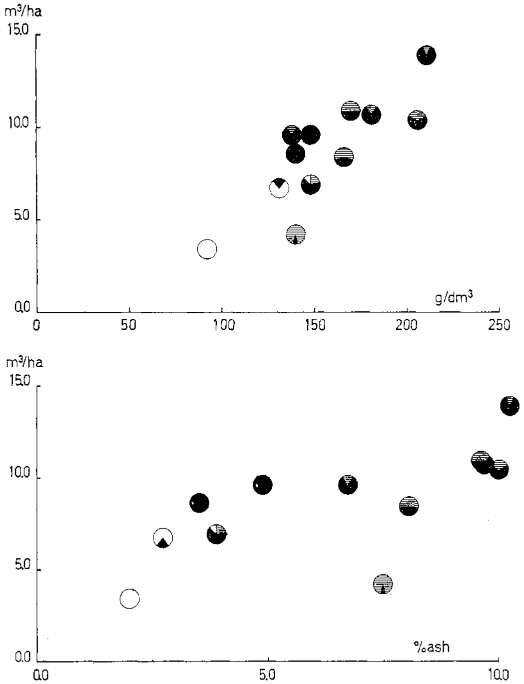

Fig. 78. Relationships between growth (of the trees) and apparent density (g/dm³) and ash content of the peat.—Each circle represents one of the sample areas investigated. White sector: pine. Black sector: spruce. Pied sector: broad-leaved trees (mainly birch, but also alder).

than half the production is from broad-leaved trees often differs from the others. On the whole the birch-rich stands are characteristic of the areas where tree stands are not yet stabilized after draining. Hence they do not represent more than a part of their potential productivity. This is particularly true of sample area Jm 12, with ca. 90 % birch by volume (see Fig. 12 and Table 19). But in broad outlines there seem to be increasing yields associated with increasing contents of some plant nutrients in the peat, and also with some other soil properties, but the variations are wide. (For information on the nutrient status of the trees in relation to the substratum and yield of the stands in relation to nutrient status, see Ch. 12.)

Apparent density. Fig. 78 shows that there is increasing yield with increasing apparent density. In reality this implies that yield is correlated with the store of all kinds of nutrients, since the stores increase with increased apparent density, even if the percentage contents are unaltered or somewhat smaller. For peat soils this relation

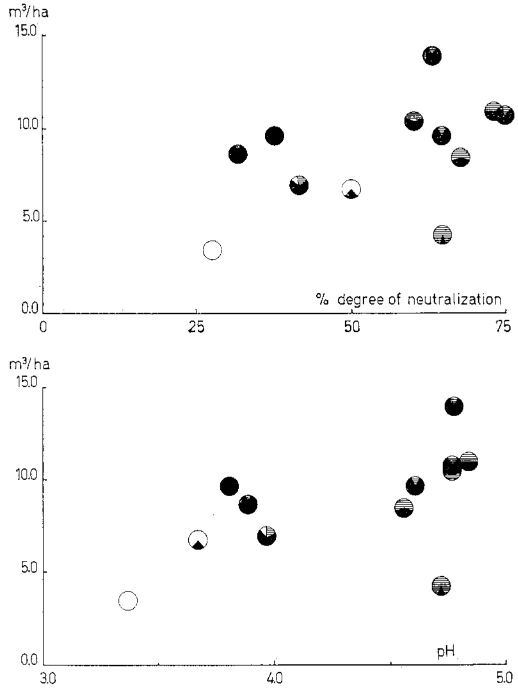

Fig. 79. Relationships between growth (of the trees) and degree of neutralization and acidity (pH) of the peat.—For symbols, see Fig. 78.

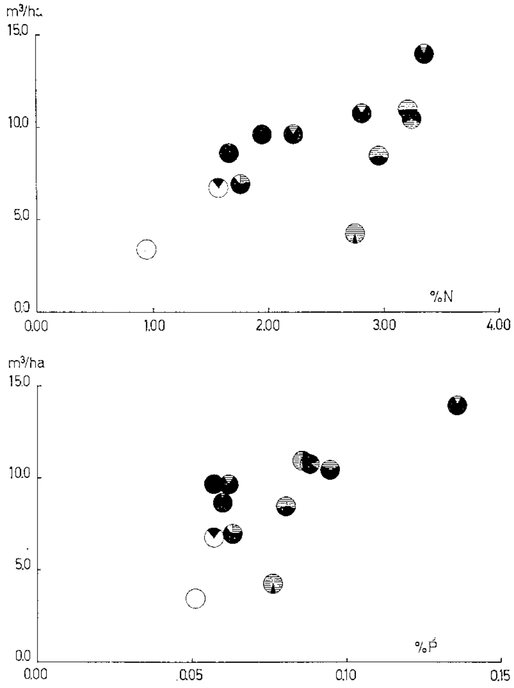

Fig. 80. Relationships between growth (of the trees) and contents of nitrogen (N) and phosphorus (P) of the peat.—For symbols, see Fig. 78.

appears not to have been studied previously; for mineral soils a not very successful attempt was made by Pawluk and Arneman (1961) to correlate site index with apparent density of the B_2 horizon.

Ash content (Fig. 78) gives a total expression of the contents of inorganic matters in the soil, including such elements which are of little or no direct importance as plant nutrients (silica, aluminum, etc.).

In Fig. 79 is shown the relation yield/pH and yield/per cent degree of neutralization. These two soil properties are closely related to one another (they are different expressions of the acid and base status) and alone they do not give an unequivocal expression of site quality. But their greatest advantage is that they sum several important site properties in one expression. Regarding pH relations, see also Ch. 10. D.

Nitrogen (Fig. 80). There is a slight tendency to a positive relation between yield and percentage of N, but the variations are wide. An example of the variation around the general trend is offered by sample areas Jm 8 and 9, both with a yield of 10—12 m^3 per ha and year but with N percentages varying between 1.7 and 3.3, and a store of nitrogen to a depth of 20 cm varying from 4000 kg to 11000 kg per ha. Ilvessalo (1923) wrote, that on some investigated mineral soil sites there is an obvious relation between increment and store of nitrogen, and he also stated that an increase in the nitrogen store in the soil of 1000 kg entails an increased yield of about 1.1—1.8 m^3 per ha and year. A rough estimate from the present data gives a corresponding annual increase of 1.2—1.3 m^3 per ha. Zinke (1961) reported a linear regression between site index and soil nitrogen contents for *Pinus ponderosa* stands on different mineral soils, and Zöttl (1960) a curvilinear relationship between yield and nitrogen released on incubation.

Phosphorus (Fig. 80). Since, of all properties studied, yield appeared to be best correlated with apparent density, it was an obvious step to make a study of yield/store of P to certain depths. Three variants were studied: Store between (a) 0 to 20 cm, (b) 0 to 40 cm and (c) to the level of greatest root frequency (see Ch. 10. c.). The best correlation, but not significant, was obtained for (c), which incidentally emphasizes the significance of root depth determinations. But in this, and other examples too, interpretations should be made with care because of the few data available.

Yield shows a negative relation to AL-extractable P (see Ch. 10. C.; Fig. 82) and to HCl-extractable P a very weak positive relation. The greater part of the AL-extractable P might possibly be rapidly taken up by the vegetation on high quality sites, so that this "fraction" of P decreases more in such sites than in those of poorer quality. There is the same tendency for mull soils (Ch. 10. D.). Valmari (1921) also obtained such an inverse relation, which as he wrote, was unexpected ("... Diese unerwarteten Ergebnisse ...").

Potassium (Fig. 81). There is no correlation between yield and total K. See also the distribution of K within the various plant communities (Ch. 10. D. 2.). Between yield and K-HCl a suggestion of a very weak (negative) relation is seen and between yield and K-AL a somewhat stronger relation. The negative tendency may probably be explained in the same way as for P-AL. Potassium is probably the least differentiating of the macro nutrients, both for type of vegetation and for its productivity, unless deficiency prevails.

Calcium (Fig. 81). There is a slight tendency to a positive relation between yield and Ca content of the peat. But it is certainly not Ca

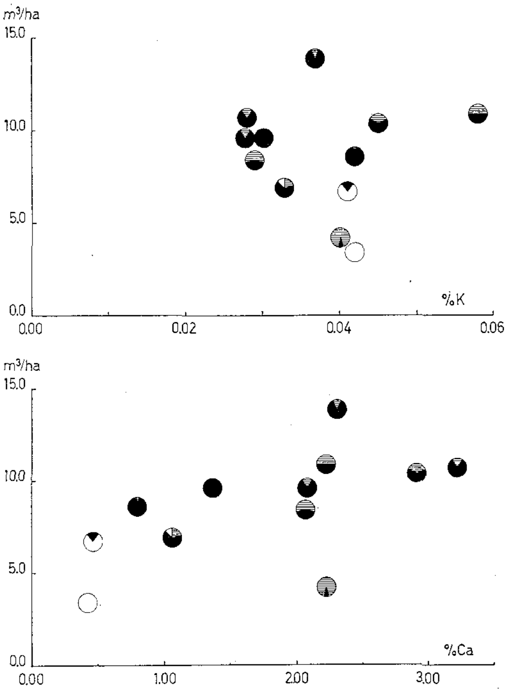

Fig. 81. Relationships between growth (of the trees) and contents of potassium (K) and calcium (Ca) of the peat.—For symbols, see Fig. 78.

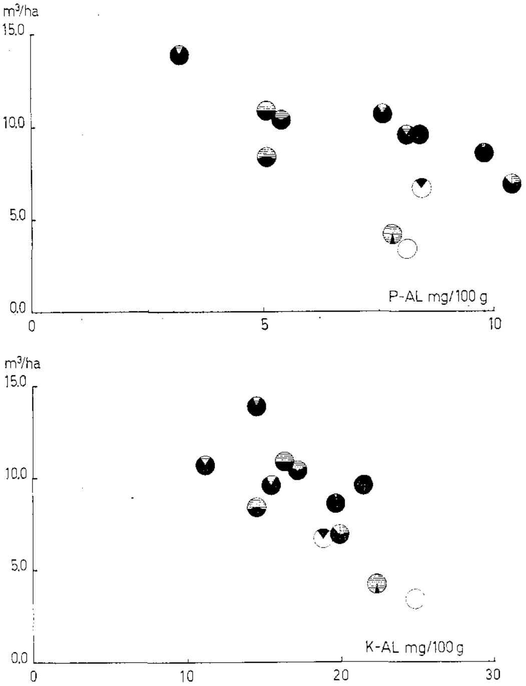

Fig. 82. Relationships between growth (of the trees) and contents of P-AL and K-AL of the peat. —For symbols, see Fig. 78.

as a nutrient element only which is important, but secondary effects of Ca: pH regulation, effect on the structure of the peat (particularly marked for the highly humified woody fen peat, "peat mull", of the peripheral parts of the area), stimulating the activity of earth-worms, etc. For mineral soils, Valmari (1921) obtained a good correlation between forest types and store of Ca to 20 cm depth in the soil; see also Viro (1951). Fiedler and Nebe (1963), on the other hand, only obtained a moderate relation between height increment and per cent Ca in the A horizon.

Generalized conclusions about the individual relations may not be drawn from the above account. It must be remembered that at the same time as soil chemical properties change, certain physical ones change as well, e.g., structure of the peat (parent matter), water conditions, light conditions, etc., and the chemical and physical properties are more or less mutually interdependent, as well as the various chemical ones. Another objection to a simple interpretation of the diagrams is the uneven tree species distribution within the various stands; and age differences are also a disadvantage. But nevertheless some more general trends seem to be fairly well illustrated by the diagrams.

Chapter 14. Nutrient economy

When the former mire was drained, the habitat was subject to far-reaching ecological consequences. Water supply from the surroundings was then concentrated to narrow, more or less deep drainage-courses between which areas were cut off from mineral soil-water supply. Thus the store of most nutrients in the peat at the disposal of the vegetation can be said to have been determined by its size at the time of draining. Hence it follows that the present vegetation draws upon a capital which is not renewed. However, there are still some "items of income": (1) Supply by air and precipitation; (2) nitrogen fixation, symbiotic fixation by *Alnus* is the most obvious; (3) mobilization of the nutrients in the peat by the gradual process of humification. In the last case it is not a question of a direct income, only a transformation of the nutrients in the peat ("weathering") into an accessible form (in reality a consumption of capital). For mineral soils, however, soil weathering is regarded as an increase in capital (Ovington 1962, p. 151). The atmospheric supply of some nutrients is sufficiently large to be considered when making a balance sheet for an area with low reserves of many of the nutrients.

The supply of nutrients by air and precipitation can be estimated fairly well, since the sampling station Erken is situated only 14 km ENE of Jägarmossen (see Egnér and Eriksson 1955). There are also precipitation and air analysis data for Ultuna about 45 km westwards, but these are probably not fully representative because of a different precipitation and the situation of the station in a large farming district. See Table 29 which contains data according to Egnér and Eriksson 1955.

Compared with the total stores of N and Ca in peat, the supply in precipitation is infinitely small, usually $< 1/1000$, but with regard to available N this supply is possibly not without importance. The two stands investigated show that above ground there is an annual im-

Table 29. Precipitation and supply of chemical elements in the precipitation at the stations Erken (Er) and Ultuna (Ul) in Uppland (see Egnér and Eriksson 1955)

Year	Precipitation mm		NO_3-N		NH_3-N		K		Mg		Ca	
			kg ha^{-1} $year^{-1}$									
	Er	Ul	Er	Ul	Er	Ul	Er	Ul	Er	Ul	Er	Ul
1955	411	366	0.60	0.81	0.77	1.35	1.18	0.65	0.51	0.54	2.61	2.99
1956	412	438	0.34	0.66	0.99	1.17	2.00	0.72	0.86	0.64	2.64	3.06
1957	583	646	0.56	1.05	0.65	1.30	1.11	0.85	0.65	0.87	2.90	3.08
1958	508	639	0.81	1.09	1.00	1.64	1.82	0.79	0.85	0.66	4.37	3.02
Average 1955—58	478	522	0.58	0.90	0.85	1.36	1.53	0.75	0.72	0.63	3.13	3.04

mobilization of nitrogen amounting to 1.5—6.6 kg per ha. The supply in precipitation is about 1.5—2.0 kg per ha and year. For the best growing stands the losses by fixation in the trunks (wood + bark) probably cannot be compensated for, but for the stands of medium and low growth these two items can be balanced. There is also another item of income, viz., gaseous NH_3, the supply of which may possibly reach 10—20 kg per ha and year (Egnér 1953). However, in relation to the annual uptake all these sources would not be sufficient if the greater part of the N taken up was not released in the litter fall. Ovington (1962, p. 175), for instance, has calculated the total uptake of N for a 55 year-old extremely well-growing pine stand to be 4817 kg per ha, i.e., an average of 88 kg per year. Ebermayer (1876) stated that a well-growing spruce stand with a rotation of 120 years took up about 70 kg ha and year.

There is little information on the amounts of P supplied in precipitation in Sweden. Tamm (1953) stated a value of 0.01—0.1 ppm for rain water (filtered samples which seem to give much too low values) and Tamm (1958) 0.1 kg water soluble P per ha and year (filtered samples). With an annual precipitation of 500 mm the former values corresponds to a quantity of 0.05 to 0.5 kg per ha and year. The stands in question have 1.9 and 9.4 kg P in wood, i.e., on average 0.04 to 0.14 kg P has been fixed in wood per year. The present uptake for wood and bark is 0.2 to 0.8 kg per ha and year.

The annual supply of K in precipitation (about 1.5 kg per ha) barely compensates the losses by K fixation in wood, which are estimated to be 0.5—1.4 kg per ha and year for wood only, and 0.7—2.4 kg for wood and bark. For a 55 year-old pine stand Ovington (1962) calculated the total uptake of K to be 1933 kg per ha (35 kg per ha and year) but only 150 kg (8 % of the total) was present in the living trees. For the spruce stand mentioned above, Ebermayer (1876) calculated the total annual K uptake to be only 7—8 kg per ha.

Calcium in precipitation probably is not quite sufficient to balance the uptake by the trees in all the stands.

Magnesium supply, about 0.7 kg per ha and year, is of the same magnitude as the fixation in the trunk (wood + bark).

The supply of nitrogen through fixation by microorganisms possibly is considerable. The only tree species with root nodules likely to be of importance in this connexion, *Alnus glutinosa,* occurs especially in the marginal area as shown in Fig. 15.

On the gradual humification of the peat, nutrients are mobilized by the disintegration of the more or less complicated compounds present in the former living plants. In principle, this release corresponds to the weathering in a mineral soil, but in peat the reserves of some nutrients are fairly limited. The quantities released by decomposition have not been estimated.

Besides the nutrient "losses" mentioned (incorporation of nutrients into the wood and bark), there is a considerable uptake into the other parts of the tree (needles, leaves, branches), see e.g., Ebermayer (1876), Rennie (1955) and Ovington (1962) regarding total uptake. Some of these nutrients are returned to the soil in litter fall. Examples of yearly turn over of nutrients in litter of various species are given by Lindquist (1938), Romell (1939 b), Mork (1942), Julin (1948), Sjörs (1954), etc. See also Miller (1963 a, b).

A real loss from the site does not occur before the harvested trunks are removed. Otherwise there is a dynamic equilibrium between litter fall and nutrient uptake, but there are leaks from the system.

Water run-off is responible for the loss of considerable quantities of nutrients. The annual run-off from Jägarmossen can be estimated as 175 mm per year (Ch. 9). On the basis of this value and a number of drainage water analyses an estimate of the yearly loss of nutrients has been calculated (Table 30). The nutrient content of drainage water is characterized by the habitat condition, so that there are fairly high values for calcium in water sampled at different times. Compare for instance the analyses by Viro (1953) of 0.26 kg P, 4.1 kg K, 11.2 kg Ca and 4.1 kg Mg per ha and year for the estimated run-off losses in five Finnish rivers. In the present case it must be remembered that the drainage water originates not only in the peat land, but the greater part of it is from the surrounding non-peaty land. The relation peat land/total catchment area is 1: 5. The supply of nutrients to the peat land in water from the non-peaty land may reduce the fig-

Table 30. Order of magnitude of the nutrient store of the peat land and some of the items in the nutrient balance (atmospheric supply, losses by leaching, immobilization in harvested trees). All figures in kg per ha

	N	P	K	Ca	Mg
Nutrient store to level of (a) greatest root frequency	1000-20000	60—630	50—260	300—39000	—
(b) level of greatest root depth	1700-36000	90—1050	70—600	500—63000	—
Nutrient supply by atmosphere (references, see text)	NH_3: 10—20(gaseous) NO_3:0.3—0.8 NH_3:0.7—1.1	0.05—0.5	1.1—2.0	2.6—4.4	0.5—0.9
Annual immobilization in wood and bark	1.5—6.6	0.2—0.8	0.7—2.4	1.7—10.1	0.4—1.0
Annual loss by drainage water (leaching)	< 1	0.05—0.3	1—4	50—70	3—5
Nutrient balance in relation to tree growth	Changes small and probably not important	A decrease in phosphorus store, probably not critical	A decrease in potassium store, often critical	Changes not important	Changes probably not important

ures for losses by leaching somewhat for some nutrients. Otherwise the store of potassium, for instance, which amounts only to 75—200 kg per ha to a depth of 20 cm, would be expected to be leached out of the site within a few hundreds years. In the "balance sheet" (Table 30), however, no account has been taken of this supply of nutrients to the site. Even if allowance is made for a considerable portion of the potassium in run-off water coming from the mineral soil, the K situation of the peat land must be regarded as critical for the vegetation. More intensive forestry for a long time can hardly be contemplated without application of potassium fertilizers.

In recent years "the whole tree-method" has come into use in Swedish forestry (as experiments as yet). This means that the whole cut tree is removed from the growing site to a central place for conversion. If such a felling technique were to be applied to sites such as Jägarmossen, the present parlous nutrient balance would probably be completely destroyed. From Tables 22 and 23 it can be seen that the P content in the trees is 20—30 % of that in the peat horizons with the greatest root mass. The K content in the trees is 90—120 % of that in the peat!

Even if the trunks (wood and bark) only are removed, the P and

K stores would be considerably depleted (Tables 22, 23 and 30). Symptoms of K deficiency already occur in some places. They are most evident around sample area Jm 4, the most potassium poor part of Jägarmossen (< 0.03 % K in the 0—20 cm layer), but other parts of the peat land also have so low K contents in the peat, that visible K deficiency symptoms may appear at any time. On Prästgårdsängen in NE Uppland, K deficiency was fully evident and retarded growth occurred at a K content < 0.025 % in the peat. The P content was at the same time 0.065 % (Tamm 1956 b). An application of a K fertilizer in that case removed the deficiency symptoms and stimulated growth; application of a P fertilizer, on the other hand, strengthend the K deficiency symptoms. On other peat land areas in Uppland similar observations have been made. At an average K content in the peat of slightly less than 0.03 % on Jägarmossen, a high yield still occurs.

However, the interpretation of K analyses of a peat substratum are rather complicated presumably because of the mobility of the K ion. Even if the deficiency symptoms are removed, growth may be appreciably retarted (Ch. 12). Judging from the analyses of exposed leaves a growth response for K application would still be expected on some of the plots with the highest K contents of the peat found on Jägarmossen (0.05—0.06 %).

An attempt was made to determine the K concentration in peat at which deficiency symptoms first appear. For the well grow stands on Jägarmossen, 0.026—0.028 % K seemed to be such a concentration limit, and based on some other sites it was thought that at 0.023—0.027 % K the deficiency symptoms would appear. Recent data obtained have, however, shown the difficulty of determining such a limit (Table 31). It is probable that we must regard the problem as dynamic and not static. If so, the low K percentages as such may be of little importance as long as some K is released gradually by humification of the peat, i.e., as soon as K is released from the litter, etc., it is taken up by the vegetation.

It is also a common experience that the K content in peat is often precariously small and in the soil water quite insufficient, but yet fairly normal growth and also K content of the plants are found (Malmer and Sjörs 1955; Malmer 1958). However, when attempts are made to raise the plant production of the site by planting a cultivated crop or a more demanding tree stand, the risk of deficiency occurring is obvious. See also Fig. 73, which shows that the original mire vegetation had the ability to extract K down to a content of a few thou-

Table 31. *Potassium contents of peat on sites deficient and non-deficient in potassium, based on visual symptoms on spruce*

Locality	Deficient	Non-deficient
	% K in peat samples from 0—20 cm depth	
Gisselås, province Jämtland	0.016	
» » »	0.017	
Robertsfors, province Västerbotten	0.025	0.044
» » »	0.022	0.048
Kerstinbo mire, province Uppland	0.024	0.028
» » » »	0.021	0.020
Nolmyra, province Uppland[1]		0.017
Postboda, province Uppland	0.019	
» » »	0.013	
Botarbomossen, province Uppland[1]		0.026
Prästgårdsängen, province Uppland	0.016	
» » »[2]	0.014	
Stormossen, province Uppland	0.019	
Måsmossen, province Uppland	0.016	0.023
» » »	0.016	0.026
Jägarmossen, sample area Jm 2		0.028
» » » Jm 4	0.027	
» » » Jm 11	0.028	

1) Earlier with deficiency symptoms. Positive growth response to K application.
2) Fertilized with H_3PO_4.

sandths of a per cent while the surface layers have about ten times as much.

With regard to P there also is some risk of leaching losses, but these are far from being as serious as for K. The absolute figures of P losses are only about one tenth of those for K, and the store of P is considerably greater. Furthermore the requirement for P of most common forest trees present is only about 15—20 % of that for K.

Another source of income not earlier taken into account is the more remote mineral-rich soil under the peat. Even now the more deep-rooted vegetation in the peripheral areas (Jm 3, 5, and possibly also Jm 8) is affected. The clay gyttja, which is the nearest stratum rich in mineral matter, moreover has a considerable K content which is of greatest interest in this discussion.

Chapter 15. Summary of Parts I—III

1. Jägarmossen consists of 45 hectares (110 acres) of afforested peat land drained in 1918—22. It is situated in the province Uppland, E Central Sweden about 60 km (37 miles) NNE of Stockholm. Height above sea level is ca. 35 m (115 ft.). The retreating inland ice left the area about 7700 B.C. In this part of the country the main part of the peat land (as well as Jägarmossen) has arisen through filling-in of shallow lakes by sediments and vegetation. The catchment area of Jägarmossen is about 220 hectares (544 acres), so that the approximate ratio between peat land and catchment area is 1: 5. Mean annual temperature is + 5 to + 6° C, the annual precipitation is somewhat more than 500 mm. The vegetation period ($\geqq + 3°$ C) is about 200 days.

2. The present vegetation on Jägarmossen has been classified in six communities (associations) which have been described. They are: I. *Pinus – Ledum – Pleurozium* ass (*Ledum*-pine wood). II. *Pinus – Vaccinium myrtillus – Pleurozium* ass (Bilberry-pine wood). III. *Picea – Maianthemum – Vaccinium myrtillus – Pleurozium* ass (Bilberry-spruce wood). IV. *Picea – Oxalis – Maianthemum – Brachythecium rutabulum* ass (*Maianthemum*-spruce wood). V. *Picea – Oxalis – Brachythecium rutabulum* ass (*Oxalis*-spruce wood). VI. *Picea – Betula pubescens – Calamagrostis canescens – Melica nutans – Brachythecium rutabulum* ass (Grass-rich birch-spruce wood). It is characteristic that the communities are concentrically arranged around the *Ledum*-pine wood in the middle of the area (Fig. 3).

3. Most of the woody species have been treated in some detail and distribution maps of the majority are included (Fig. 5, 14—28). Some species are restricted to the central, dwarf shrub-rich and on the whole nutrient-poor communities (e.g., *Ledum palustre, Pinus silvestris,* Fig. 5, 14). Other species are restricted to the peripheral, herb-rich and on the whole nutrient-rich communities (e.g., *Alnus glutinosa, Fraxinus excelsior,* Fig. 15, 27), and some species seem to have no decided preference with regard to environmental features (e.g., *Rhamnus frangula, Sorbus aucuparia,* Fig. 23, 25). They occur all over the peat land.

4. In general it seems that drainage of this type of peat land favours an increase in frequency of species which have a larger nutrient demand than the species which were part of the original vegetation of the mire. For example, in the bottom layer the heath-forest mosses,

Hylocomium splendens, Pleurozium schreberi and *Dicranum* spp. give way to *Brachythecium* spp., *Rhytidiadelphus triquetrus, Mnium* spp. etc., and in the field layer the dwarf shrubs are displaced by herbs, e.g., *Oxalis acetosella* and *Maianthemum bifolium*. In the most nutrient-deficient parts, *Sphagnum* spp. disappear and are replaced by *Hylocomium splendens, Pleurozium schreberi,* etc. *Eriophorum vaginatum, Vaccinium uliginosum* and *V. oxycoccus,* etc., in the field layer are replaced by *V. myrtillus* and *V. vitis-idaea* (Tables 8—12).

5. The annual ring diagrams (Fig. 29—32) show clearly that the effect of drainage of Jägarmossen is to increase the growth of the trees (pine, spruce and birch). Already in five years after drainage there is a noticeable increase in annual ring width of spruce in most areas. But in the formerly very wet margin areas of the peat land, now covered by a mixed stand of birch and spruce, an obvious increase in annual ring width of spruce is not seen until after 15—20 years.

6. Jägarmossen occupies a spoon-shaped depression once a lake, which was cut off from the sea probably 4500—5000 years ago. The most common peat types are *Sphagnum* peat, *Sphagnum*-cyperaceous peat and woody fen peat. Under the peat clay gyttja, algal gyttja and calcareous gyttja horizons occur. The total thickness of the gyttja layers is > 2 m. The peat land slopes weakly ($< 0.^\circ 1$) from N to S and from W to E with the outflow towards the east. The greatest measured thickness of the peat layer is 3.1 m and half the area has peat layers > 1 m thick (Table 13 and Fig. 34). The subsidence of the peat has resulted in a 'gain' of ground of ca. 3 % of the total area of Jägarmossen. Almost 11 km (6.7 miles) of ditches were dug, i.e., a fairly thorough draining, but the water table is still very high in some places (Fig. 35).

7. Peat analysis has revealed that there are positive relationships between: (1) Apparent density (g/dm^3) and ash content. (2) Calcium (Ca) content and ash content. (3) Acidity (pH) and ash content. (4) pH and Ca content. (5) Nitrogen (N) and pH. (6) N and ash content. (7) N and phosphorus (P) content for samples from 0—20 cm depth only, but not for samples from greater depths.

An increase in acidity on drying of peat of up to one pH unit was obtained for the pH range 3—7 with greater deviations from the fresh peat at the higher pH values.

The total quantities of nutrients down to the level of *greatest root frequency* were: N 1.0—20.0, P 0.06—0.63, K 0.05—0.26 and Ca 0.3—38.7 $\cdot 10^3$ kg per ha. Similar quantities of nutrients to the level of *greatest root depth* were: N 1.5—32.4, P 0.08—0.94, K 0.06—0.99 and Ca 0.5—56.7 · 10^3 kg per ha.

The distribution of the analyses in the different communities shows three main features radiating out from the centre (*Ledum*-pine wood) towards the periphery, i.e., from the oligotrophic to the eutrophic part of the peat land. (a) Increasing values: pH, apparent density, specific conductivity, cation exchange capacity (not so distinct), degree of neutralization, percentages (total) of nitrogen (N), phosphorus (P) and calcium (Ca). (b) Analysis values irregular: percentage (total) of potassium (K) and percentages of hydrochloric acid extractable P and K (P-HCl and K-HCl). (c) Decreasing values: ammonium lactate extractable K and P (K-AL and P-AL).

The vertical distribution of the analyses also may be roughly divided into three groups: (a) Those that increase with depth, viz., ash content, pH and Ca content; (b) those that decrease with depth, viz., K and P contents, and (c) those that change slightly or irregularly with depth, viz., apparent density, N content.

On other sites studied it was found that the degree of neutralization, specific conductivity and extractable Ca (Ca-AL and Ca-HCl) also increase with depth. Total magnesium seems first to decrease (0—30 cm, rooting zone) and then to increase. K-AL, P-AL, K-HCl and P-HCl, like total K and P, also decrease with depth. Cation exchange capacity seems to be fairly constant throughout the profile.

8. The number of stems of the various stands varies between about 800 and 1800 per ha. The volume of the stands varies between 66 and 350 m^3 per ha and the annual increment (period 1958—63) between 3.6 and 15.0 m^3 per ha. It is estimated that the annual increment was > 10 m^3 per ha for a large area of the peat land during the last 30 years.

9. The dry matter and chemical elements of the tree stands have been calculated by felling and analysing sample trees from a low-quality and a high-quality site (Jm 1 and Jm 9, see Fig. 4 and 7 and Tables 22, 23). The pine stand (Jm 1), 65.5 m^3 per ha, contained 39.4 · 10^3 kg oven-dry matter per ha and the weight proportions of each part of the trees were: 61.4 % wood, 7.6 % bark, 18.0 % living branches, 8.8 % needles and 4.2 % dead branches. Total nutrient contents in the stand above ground were: N 112.5, P 12.3, K 44.0, Ca 69.1 and Mg 16.0 kg per ha. The spruce stand, 312.1 m^3 per ha, contained 177.6 · 10^3 kg oven-dry matter per ha and the weight proportions of each part of the trees were: 66.3 % wood, 5.6 % bark, 16.5 % living branches, 9.0 % needles and 2.6 % dead branches. Total nutrient con-

tents in the stand above ground were: N 533.9, P 70.4, K 167.6, Ca 521.2 and Mg 61.2 kg per ha. Compared with data for other stands investigated, the nutrient content of the trees shows no fundamental differences between different sites and climates. However, there are exceptions, probably dependent on varying habitat properties. Thus the bark of pine and all parts of the spruce on Jägarmossen have unusually high Ca contents. High Ca percentages occur in the rooting zone of the spruce site (Fig. 71, Jm 9). The pine site, however, is not particularly high in Ca.

10. Foliar analysis has revealed relatively low concentrations of N, P and K in exposed leaves over large parts of Jägarmossen.

The significance of foliar analysis as a method of determining nutrient status of stands is discussed with regard to sites where more than one nutrient is deficient. Although difficulties are met with in the interpretation of foliar concentrations under such conditions, it is concluded that the supply of N, P and K is often suboptimal on Jägarmossen. The relations between foliar concentrations and peat concentrations of some elements are also discussed.

11. The best relation between forest growth and environment appears to be between growth and plant community. The data obtained partly support the classical concept of forest types (Cajander 1909, 1921), viz., that a relationship exists between site quality (site index) and vegetation (see also Rennie 1962).

A detailed study of the yield on 12 sample plots in relation to a number of soil properties suggests a positive relationship between yield and apparent density, per cent ash, pH, degree of neutralization, percentages of N, P and Ca (total). In the case of P-AL and K-AL a negative trend was found, while total K showed no correlation at all with the yield.

12. Nutrient economy is discussed. An estimate revealed that the stores of nutrients are sufficient with regard to N, P, Ca and probably also Mg for a long time, despite annual losses of nutrients by immobilization in tree trunks and by leaching. However, both the store and supply of K is small and intensive forestry without application of K fertilizers would probably have fatal consequences. It was shown that the P content in the trees was 20—30 %, and the K content 90—120 % of that in the peat horizons with the greatest root mass.

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Abbreviations:

AFF: Acta forestalia fennica. Helsinki.
BN: Botaniska notiser. Lund.
CIFF: Communicationes instituti forestalis fenniae. Helsinki.
MSS: Meddelanden från statens skogsforskningsinstitut (Reports of the Forest Research Institute of Sweden). Stockholm.
SBT: Svensk botanisk tidskrift. Stockholm.
SGU: Sveriges geologiska undersökning. Stockholm.

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Sammanfattning

Skogsekologiska studier på dikad torvmark i Uppland. Del I—III.

1. Detta arbete är huvuddelen av en redogörelse över vegetations- och ståndortsförhållanden på »bättre», dikad och skogbevuxen torvmark i Uppland. Undersökningen har dels omfattat ett detaljundersökt område, Jägarmossen, dels översiktliga studier på andra skogsdikade torvmarker. Det nu föreliggande arbetet behandlar i allt väsentligt det detaljundersökta området, men jämförelser med andra områden har gjorts.

För utarbetande av avsnitten om vegetationsutveckling (Chapter 5) och trädbeståndens utveckling (Table 21) har värdefulla uppgifter erhållits ur ett manuskript av jägmästare Gunnar Ullén (se References). Arbetet bakom denna undersökning leddes år 1927, beträffande skogsproduktionsförhållandena, av docent Erik Lund med biträde av jägmästare Erik Lindh. Docent Carl Malmström och fil. mag. Nils Willén svarade för de vegetations- och torvgeologiska (Fig. 33) undersökningar som samtidigt gjordes. Ullén företog en ny taxering av trädbestånden år 1931, varefter han sedermera sammanställde resultaten härav, liksom av den tidigare undersökningen.

Jägarmossen utgöres av en 45 ha stor, skogbevuxen torvmark, som dikades 1918—22. Den ligger i Upplands Ö del ca 60 km NNO om Stockholm på Skogssällskapets ekebyholmkomplex i Rimbo s:n. Den omslutes här av nivåkurvan för 35 m ö. h. och länshuvudväg nr 280. Den tillbakagående inlandsisen stod över trakten omkr. 7 700 f. Kr. Inom denna del av landet har större delen av torvmarkerna bildats genom igenväxning av grunda sjöar (igenväxningstorvmarker). Jägarmossens nederbördsområde är ca 220 ha, och förhållandet mellan torvmark och nederbördsområde är 1: 5. Årsmedeltemperaturen är + 5 till + 6° C, årsnederbörden (genomsnittliga) något mer än 500 mm. Vegetationsperioden varar omkring 200 dygn ($\geqq + 3^\circ$ C).

2. Den nuvarande vegetationen på Jägarmossen har uppdelats på sex växtsamhällen (associationer) vilka har beskrivits. De är: I. *Pinus – Ledum – Pleurozium* ass (skvattramtallskog). II. *Pinus – Vaccinium*

myrtillus – Pleurozium ass (blåbärtallskog). III. *Picea – Maianthemum – Vaccinium myrtillus – Pleurozium* ass (blåbärgranskog). IV. *Picea – Oxalis – Maianthemum – Brachythecium rutabulum* ass (ekorrbärgranskog). V. *Picea – Oxalis – Brachythecium rutabulum* ass (harsyragranskog). VI. *Picea – Betula pubescens – Calamagrostis canescens – Melica nutans – Brachythecium rutabulum* ass (gräsrik björk-granskog). I—III har förts till övergruppen hedskog (hedbarrskog), IV—VI har förts till övergruppen ängsskog (ängsbarrskog).

3. Flera vedväxter har behandlats rätt ingående och för de flesta har utbredningskartor upprättats. Några arter har sin huvudutbredning inom de risrika och på det hela taget näringsfattiga samhällena i centrum (t. ex. *Ledum palustre, Pinus silvestris;* Fig. 5, 14). Andra är i huvudsak begränsade till de perifera, örtrika och på det hela taget näringsrika samhällena (t. ex. *Alnus glutinosa, Fraxinus excelsior;* Fig. 15, 27) och andra har synbarligen inga bestämda anspråk med hänsyn till miljön, de förekommer spridda över praktiskt taget hela området (t. ex. *Rhamnus frangula, Sorbus aucuparia,* Fig. 23, 25).

4. Det förefaller som om dikning och torrläggning av en torvmark av detta slag gynnar sådana arter, som har större anspråk på substratet än de som ingick i den ursprungliga myrvegetationen, när stadierna före och efter torrläggning är jämförbara. Så är de tidigare mycket blöta kärrpartierna med ofta ytligt vatten och med många specifika blötmarksväxter ej jämförbara med de nuvarande skogbevuxna ört- och gräsrika områdena. Däremot är de områden som redan tidigare var jämförelsevis torra, med ytligt vatten endast vissa mycket våta perioder, väl jämförbara med de nuvarande samhällena på motsvarande platser.

I bottenskiktet har t. ex. *Hylocomium splendens, Pleurozium schreberi* och *Dicranum*-arter ersatts av *Brachythecium*-arter, *Rhytidiadelphus triquetrus, Mnium*-arter, etc. och i fältskiktet har risen ersatts av örter, t. ex. *Oxalis acetosella, Maianthemum bifolium* m. fl. I de mest näringsfattiga delarna (och tidigare också våta) har olika *Sphagnum*-arter följts av *Hylocomium, Pleurozium,* etc. *Eriophorum vaginatum, Vaccinium uliginosum* och *V. oxycoccus,* m. fl. i fältskiktet har följts av *V. myrtillus, V. vitis-idaea* m. fl. [se Tables (tab.) 8—12].

5. Årsringsdiagrammen (Fig. 29—32) visar klart dräneringseffekten på trädens (tall, gran och björk) tillväxt på Jägarmossen. Redan inom fem år efter dikningen har årsringsbredden ökat märkbart för gran inom de flesta undersökta provytorna. Även tall och björk rea-

gerade snabbt. Inom de tidigare mycket blöta kantpartierna visar granen däremot en starkt markerad eftersläpning i fråga om tillväxtökning (Fig. 31). Inte förrän 15—20 år efter dikningen kommer en verkligt markerad tillväxtreaktion.

6. Jägarmossen utfyller de djupare delarna av en skålformig fördjupning som en gång var sjö. Den avskars från havet för omkring 4 500—5 000 år sedan. De vanligaste torvslagen är *Sphagnum*-torv, *Sphagnum*-cyperacé-torv och olika kärrtorvslag. Under den egentliga torven är olika gyttjor lagrade på varandra: lergyttja, alggyttja och kalkgyttja (Fig. 33). Gyttjorna har en maximal mäktighet av > 2 m. Det största uppmätta torvdjupet är 3,1 m och mer än hälften av områdets yta har > 1 m mäktiga torvbildningar (Table 13, Fig. 34). Torvmarken lutar svagt (< 0,°1) från N mot S och från V mot Ö och den avrinner mot Ö. I kantområdet kan man räkna med en »vinst» av fastmark av omkring 3 % av totalarealen som en följd av torvens hopsjunkning (se även Fig. 13). Hopsjunkningen synes ha varit störst omedelbart efter dikningen (jfr Dawson 1956, s. 386). Frågan om en del av torvmarken har varit ombrotrof (dvs. helt avskuren från direkt tillförsel av fastmarksvatten) diskuteras, men kan ej anses löst. Närmare 11 km diken har tagits upp, dvs. en mycket effektiv dränering, men vattenståndet är alltjämt högt inom vissa delar (Fig. 35).

7. Torvanalyserna har gett positiva samband mellan: (1) Volymvikt (g/dm^3) och askhalt (% ash i diagrammen). (2) Calcium (Ca) halt och askhalt. (3) Surhetsgrad (pH) och askhalt. (4) pH och Ca-halt. (5) Kväve (N) halt och pH. (6) N och askhalt. (7) N och fosfor (P) halt för prov från 0—20 cm djup, men ej för prov från större djup.

En ökning av torvens surhetsgrad (pH) med upp till en pH-enhet vid provens torkning erhölls för pH-området 3—7, med större avvikelser vid högre pH-värden.

Totalmängderna av näringsämnen ned till nivån för *största rotfrekvens* var: N 1,0—20,0, P 0,06—0,63, K 0,05—0,26 och Ca 0,3—38,7 · · 10^3 kg per ha. Motsvarande värden till nivån för *största rotdjup* var: N 1,5—32,4, P 0,08—0,94, K 0,06—0,99 och Ca 0,5—56,7 · 10^3 kg per ha.

Torvanalysvärdenas fördelning (0—20 cm djup) i de olika växtsamhällena visar tre huvuddrag i riktning från centrum (skvattramtallskogen) mot periferien, dvs. från torvmarkens oligotrofa mot dess eutrofa del. (a) Stigande värden: pH, volymvikt, specifik ledningsförmåga, utbyteskapacitet (ej så utpräglat), neutralisationsgrad, totalhalter av N, P och Ca. (b) Analysvärdena oregelbundna: totalhalt av kalium (K) och halter av saltsyralösligt P och K (P-HCl och K-HCl). (c) Avtagande värden: ammoniumlaktatlösligt K och P (K-AL och P-AL).

I stort kan också analysvärdenas vertikala (0—100 cm) fördelning indelas i tre grupper: (a) De som ökar med ökat djup, nämligen askhalt, pH och Ca-halt; (b) de som avtar med ökat djup, nämligen K- och P-halt och (c) de som ändras mycket litet eller oregelbundet med ökat djup, nämligen volymvikt och N-halt.

På andra undersökta lokaler har det visat sig att neutralisationsgraden, specifika ledningsförmågan och halterna av Ca-AL och Ca-HCl också ökar med ökat djup. Totalhalten av magnesium tycks först minska (0—30 cm, rotzonen) och sedan öka. K-AL, P-AL, K-HCl och P-HCl, liksom total K och P, avtar också med ökat djup. Utbyteskapaciteten förefaller vara tämligen konstant längs hela profilen.

8. Uppmätningarna av trädbestånden på Jägarmossen har visat att stora växlingar råder mellan olika delar ifråga om antal stammar per ytenhet, trädslagsfördelning, volyminnehåll, tillväxt, m. m. Stamantalet på de 12 provytorna varierar mellan ca 800 och 1 800 per ha (Table 19); trädslagsfördelningen med avseende på grundytan är för tall 2—100 % (fyra provytor), för gran 11—100 % (elva provytor), för björk 2—89 % (nio provytor) och för klibbal 23 % (en provyta). Beståndens volyminnehåll växlar mellan 66 och 350 m^3 per ha och den årliga tillväxten (perioden 1958—63) mellan 3,6 och 15,0 m^3 per ha (Table 20). För en stor del av Jägarmossen har den löpande årliga tillväxten beräknats till $>$ 10 m^3 per ha (Table 21) under den senaste 30-årsperioden.

9. Några trädbestånds torrsubstansinnehåll och innehåll av olika kemiska element har beräknats genom att fälla och analysera provträd från en lågproduktiv och en högproduktiv lokal (Jm 1 och Jm 9; se Fig. 4 och 7 och Tables 22 och 23). Tallbeståndet (Jm 1), 65,5 m^3 per ha, innehöll 39,4 · 10^3 kg torrsubstans per ha och viktsproportionerna för varje del av träden var: 61,4 % ved, 7,6 % bark, 18,0 % levande grenar, 8,8 % barr och 4,2 % döda grenar. Beståndets totala näringsinnehåll ovan mark var: N 112,5, P 12,3, K 44,0, Ca 69,1 och Mg 16,0 kg per ha. Granbeståndet (Jm 9), 312,1 m^3 per ha, innehöll 177,6 · 10^3 kg torrsubstans per ha och viktsproportionerna för varje del av träden var: 66,3 % ved, 5,6 % bark, 16,5 % levande grenar, 9,0 % barr och 2,6 % döda grenar. Beståndets totala näringsinnehåll ovan mark var: N 533,9, P 70,4, K 167,6, Ca 521,2 och Mg 61,2 kg per

ha. Näringsinnehållet i dessa bestånd visar, jämfört med andra undersökta bestånd, inga grundläggande avvikelser med hänsyn till olika lokaler och klimat. Jämförelsebestånden ligger dels i Småland och Halland (400—450 km SV om Jägarmossen) och dels i Lappland (800—900 km N om Jägarmossen). Det finns dock vissa modifikationer sannolikt beroende på växlande miljöegenskaper. Sålunda har tallbarken och alla delar av granen på Jägarmossen mycket höga Ca-halter. Höga Ca-halter förekommer i rotzonen på granlokalen (Fig. 71, Jm 9). Tallokalen däremot har ej särskilt hög Ca-halt i substratet.

10. Analyser av väl belysta barr och blad har visat att halterna av N, P och K är låga för stora delar av Jägarmossen.

Bladanalysens betydelse som metod vid bestämning av trädbeståndens näringsstatus har diskuterats med hänsyn till lokaler med brist på flera ämnen än ett. Under sådana omständigheter är innebörden av olika halter svår att tolka, men trots detta antas att tillgången på N, P och K ofta är suboptimal på Jägarmossen. Sambanden mellan bladhalter och motsvarande halter i torven diskuteras för några element (Table 27, Fig. 76—77).

11. Det bästa sambandet mellan skoglig tillväxt och miljö, tycks finnas mellan tillväxt och växtsamhälle. De erhållna resultaten stöder den klassiska skogstypsteorien (Cajander 1909, 1921), nämligen att ett samband föreligger mellan en lokals produktionsförmåga och vegetationens karaktär.

En detaljundersökning av avkastningen på de 12 provytorna i relation till ett antal markegenskaper antyder ett positivt samband mellan tillväxt och torvens volymvikt, askhalt, pH, neutralisationsgrad, totalhalter av N, P och Ca. För P-AL och K-AL finns tecken till ett negativt samband och för totalkalium finns inget som helst samband med tillväxten (Fig. 78—82).

12. Näringshushållningen diskuteras. En beräkning visade att förråden av N, P och Ca och troligen också Mg är tillräckliga för en ur praktisk synpunkt obegränsad tid, trots de årliga förlusterna genom inlagring i trädstammarna (ved och bark) och utlakning. Förrådet av K är däremot litet och det är troligt, att ett intensivt skogsbruk utan tillförsel av K skulle få ödesdigra följder. Det har visats att P-innehållet i trädbestånden är 20—30 % och K-innehållet 90—120 % av förrådet i torven på motsvarande lokaler till nivån för största rotfrekvens. Konsekvenserna för näringshushållningen vid en tillämpning av den s. k. »hela träd metoden» i skogsbruket på dylika lokaler blir häri rätt klart illustrerade.

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Errata

p. 3, line 3, read: Introduction

p. 8, line 4 from the bottom, read: Ecology

p. 51, Table 6, read: Eurhynchium

p. 57, Table 7, read: Eurhynchium

p. 92, Table 8, read: Vaccinium myrtillus

p. 92, Table 8, read: Pohlia nutans

p. 102, Table 9, read: Athyrium filix-femina

p. 102, Table 9, read: Sphagnum girgensohnii

p. 107, Table 10, read: Fraxinus excelsior

p. 107, Table 10, read: Athyrium filix-femina

p. 107, Table 10, read: Polytrichum juniperinum

p. 111, Table 11, read: Juncus effusus

p. 141, line 4 from the bottom, read: of (instead of af)

p. 208, Table 28, line 2, read: 0-20 (instead of D-20)